SPATIAL VARIATION IN LIFE-HISTORY TRAITS OF THE MARBLED PARROTFISH, *LEPTOSCARUS VAIGIENSIS*, IN COASTAL KENYA

ALBERT GAMOE LOCHAM

DOCTOR OF PHILOSOPHY
(Zoology)

JOMO KENYATTA UNIVERSITY OF AGRICULTURE AND TECHNOLOGY

2016

Spatial variation in life-history traits of the marbled parrotfish, *Leptoscarus vaigiensis*, in coastal Kenya

Albert Gamoe Locham

Thesis submitted in fulfilment for the degree of Doctor of Philosophy in Zoology (conservation biology) in the Jomo Kenyatta University of Agriculture and Technology

2016

DECLARATION

This thesis is my original work and has not been presented for a degree in any other University.

Signature………………………………… Date………………………………….

Albert Gamoe Locham

This thesis has been submitted for examination with our approval as the University Supervisors:

Signature…………………………………Date…………………………………

Prof. Boaz Kaunda-Arara
UoE, Kenya

Signature…………………………………Date…………………………………

Dr. Joseph G. Wakibia
JKUAT, Kenya

Signature……………………………… Date…………………………………

Dr. Shadrack M. Muya
JKUAT, Kenya

DEDICATION

Dedicated to my mum, the late Asinyen Locham and dad Locham Lokonyi; and to each member of my larger family.

ACKNOWLEDGEMENTS

I would like to thank my supervisors; Prof. Boaz Kaunda-Arara, Dr. Joseph G. Wakibia and Dr Shadrack M. Muya for their guidance and support throughout this study. I thank the Director Kenya Wildlife Service (KWS) for permitting research in the Marine Protected Areas (MPAs). Thanks also to respective wardens especially Mr. Isaac Mugo and Dickson Korir for their logistical support in Malindi and Watamu Marine Parks and Reserves. The Kenya Marine and Fisheries Research Institute (KMFRI) provided laboratory facilities and I thank its Director for this. Additional thanks go to Pascal Thoya and Joseph Mukeka for assistance with Geographical Information System (GIS) work. I am grateful to Boaz Orembo, Summy Kazungu and Ben Ogola of KMFRI for help with laboratory work. Field sampling support was provided by Michael Kazungu and Omari Shaffi. I would also want to thank the State Department of Fisheries (SDF) for providing historical landings datasets. I make special mention of two persons: Mr. Abdallah Kazungu and Hussein Charo, whose constant cooperation in providing fish samples contributed immensely to the completion of this study. This work was funded by PADI Foundation and the Kenya National Council of Science and Technology.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

LIST OF ABBREVIATIONS/ACRONYMS

WIO	Western Indian Ocean
ITCZ	Inter-Tropical Convergence Zone
NEM	Northeast monsoon
SEM	Southeast monsoon
SST	Sea surface temperature
EACC	East African coastal current
SCC	Somali counter current
HCFRU	Hawaii Cooperative Fisheries Research Unit
UNEP	United Nations Environmental Program
FAO	Food and Agriculture Organization
NVH	Niche variation hypothesis
OFT	Optimal foraging theory
SBC	Santa Barbara channel
TL	Total length
SL	Standard length
ELEFAN	Electronic length frequency analysis
ANOVA	Analysis of variance
SNK	Student-Newman-Keuls

ANCOVA	Analysis of covariance
MDS	Multidimensional analysis
GSI	Gonadosomatic index
L_{50}	Length-at-first maturity
IRI	Index of relative importance
CA	Correspondence analysis
FI	Feeding intensity
Sk	Skewness index
LFA	Length-frequency analysis
ASP	‘‘Available sum of peaks’’
ESP	‘‘Explained sum of peaks’’
CI	Confidence interval
T^0C	Temperature in degrees centigrade

ABSTRACT

Phenotypic plasticity in life-history attributes of fishes is poorly studied in Western Indian Ocean (WIO) region but may be important in maintaining resilience of populations to disturbance events. This study examined the existence of phenotypic divergence in biological attributes of the commercially important marbled parrotfish (*Leptoscarus vaigiensis)* among reefs in coastal Kenya in an attempt to bridge the data gaps and understand ecosystem function. Phenotypic divergence in the reproductive, feeding, growth and mortality attributes of *L. vaigiensis* was studied during May 2011-April 2013 at six reef sites exposed to varying levels of fishing pressure in coastal Kenya. Baited fish traps were used to sample specimens of *L. vaigiensis,* an economically important species, within two no-take marine parks (Malindi and Watamu) and their adjacent Reserves in which regulated fishing is allowed. Monthly samples were also obtained from fishers operating at two unprotected sites (Kanamai and Vipingo). Biological attributes of the species were then compared between sites using a combination of univariate and multivariate statistical analysis. Results showed reproductive attributes of fish in the Parks and Reserves had higher fecundities than those on unprotected reefs indicating spatial differences in the reproductive potential of the species. However, fish at unprotected sites had higher fecundities at smaller sizes relative to larger fish at protected sites. Females at unprotected sites matured at lower lengths (13.4 cm, range, 11.8-14.8 cm, 95% CI) than those in marine parks (17.8 cm, range 17.5-18.1 cm, 95% CI) and reserves (17.4 cm, range, 16.2-18.4 cm, 95% CI) suggesting spatial difference in the trade-off between gonadal development and somatic growth likely influenced by differential fishing pressure. Feeding data showed higher niche breadths for fish from protected sites during the northeast monsoon (NEM) season and at fished sites during the southeast monsoon (SEM) season suggesting the influence of sites and seasonality on feeding activity. Results on growth showed higher asymptotic length ($L\infty$) estimate (~ 31 cm) for the species from a reserve site and lowest estimates (26-27 cm) from a marine park site. As expected, total mortality estimates ($Z\ yr^{-1}$) were lower for protected areas (1.69-1.96) and higher for reserve (2.87-9.15) and non-protected (4.39-5.30) sites. It is concluded that the potential for growth is influenced by fishing and other factors not covered in this study including temperature and food availability. Overall, the results indicated variable levels of phenotypic divergence in attributes of the species between sites. The real causes of this divergence cannot be partitioned between fishing mortality, genetic variability or habitat-induced variation and will require further investigations. The main thesis of the research is that populations of this commercially important species are likely sustained by resilience to exploitation caused by plasticity in life-history traits. The existence of spatial variability in some parameters (e.g. fecundity and size at maturity) and functions (e.g. niche breadth and growth) requires that scientific management of stocks be based on spatially explicit models that use these parameters.

CHAPTER ONE

INTRODUCTION

1.1 Background of the study

Exploitation of fish stocks may affect local community structure in the short term and life-history traits on an evolutionary time-scale (Rodhouse *et al*., 1998). All fisheries are, to a greater or lesser extent, selective in terms of the size, age, sexual maturity and, in some instances, the sex of the catch (Law, 1991). In the short term, selectivity at high rates of exploitation can radically change the age/size structure and breeding structure between exploited populations, whereas in the long term, mortality caused by harvesting may act as an artificial selection process driving evolution of life-history traits of fish populations (Rodhouse *et al*., 1998). Thus, the life-history traits of fished populations may vary spatially in response to fishing through two pathways; direct environmental effects manifested as phenotypic plasticity (production of different phenotypes by the same genotype under different conditions, *sensu* Morita & Morita, 2002) or through evolutionary selection (Dieckmann & Heino, 2007). Phenotypic and evolutionary changes can co-occur in harvested fish populations, although they may operate on different time scales, at different rates and even in different directions (Sharpe & Hendry, 2009).

Phenotypic changes in life-history traits (e.g. growth, maximum sizes, length-at-first maturity defined as minimal size attained at maturity or the size at which 50% of the fish at that size are mature, Beacham, 1983) can occur in space following reduction of population density in exploited stocks (Heino & Godo, 2002; Jennings & Kaiser, 1998). Evolutionary change occurs when fast-growing individuals are exploited more than those with slow growth hence causing reduction in the average growth rate (defined as the rate in change in length per unit time) and size at maturation of fishes (Law, 2000; Stearns, 1992). Changes in demographic traits of fish such as growth and length at maturity has been shown among fish stocks including; Atlantic Cod on the Scotian Shelf (Beacham, 1983), Atlantic Salmon in North America (Schaffer & Elson, 1975), North-east Arctic Cod (Jørgensen, 1990) and for other fish stocks in the North-west Atlantic (Trippel, 1995). Despite this documentation, little evidence of spatial change in demographic traits in fishes due to differences in fishing mortality or environmental variability is available for the most of the tropics and especially in Western Indian Ocean (WIO) region. This study aimed at bridging this information gap by studying possible variation in life-history traits of the marbled parrotfish (*L. vaigiensis*, Plate 1-1) among fished coral reef sites in coastal Kenya.

Fishes may change their life-history attributes through mechanisms such as phenotypic plasticity thereby making them resilient to the effects of fishing (Candolin, 2009) or environmental variability (Gomes & Monteiro, 2007). Phenotypic plasticity or variance is also associated with niche expansion or ‘ecological release’ (described as the process in which species gain access of resources that may have otherwise been depleted or monopolized by competitors (Bolnick *et al*., 2010; van Valen, 1965). Although the relationship between intraspecific competition and niche expansion is known from theory (Roughgarden, 1976; Wilson & Turelli, 1986), there has been little empirical proof that niches diversify in response to variation in intra- or interspecific competition that may be mediated by drivers like fishing effort. In fishes, niche breadths defined in terms of range of prey organisms found in the guts (Cohen & Lough, 1983), are affected by several factors including food diversity (Layman *et al*., 2007), competition (Svanback & Bolnick, 2005), seasonal changes in resource availability (Tanimata *et al*., 2008) and environmental conditions (Laidre & Heide-Jørgensen, 2005). Niche breadths of fishes may vary in space in response to variable fishing pressure (Layman *et al*., 2007), however, this has not been tested for most of the coral reef species.

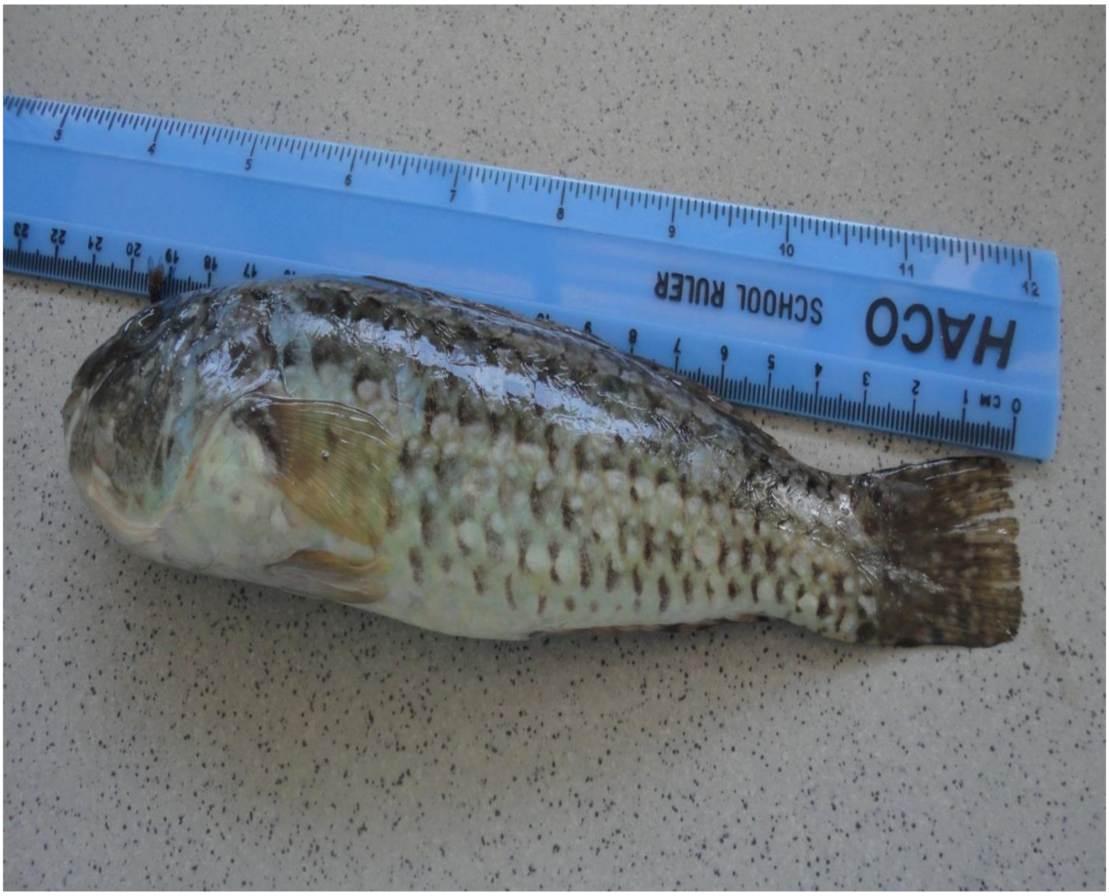

Plate 1.1: The marbled parrotfish (*Leptoscarus vaigiensis*) whose life-history traits were compared among reefs exposed to varied fishing pressure in coastal Kenya.

The marbled parrotfish has a wide geographical distribution extending from the northern end of Red Sea to the WIO region and further to subtropical region (Bellwood, 1994). *Leptoscarus vaigiensis* has socio-economic importance in artisanal fisheries in Kenya and most of the WIO countries. Additionally, the species plays a significant role in coral reef ecosystems by shaping the distribution, community structure, standing crop biomass and production rates of benthic algae on coral reefs (Russ, 2003). The species is sedentary in nature (Kaunda-Arara & Rose, 2004b) making site-specific variations in fishing effects to likely cause spatial variation in its population structure. In this thesis, changes in reproductive traits (fecundity defined as number of eggs per female, egg size, length-at-first maturity), feeding (diet and niche breadth), growth and mortality parameters of the marbled parrotfish are compared between six Kenyan reefs exposed to varying levels of fishing pressure. In the Kenyan context, the protected reefs are also designated as ‘‘Marine Parks’’ and exclude extractive exploitation of resources, “Marine Reserves” or partially protected reefs are buffer areas adjacent to the parks that allow regulated fishing with “traditional” methods that include baited fish traps, fish trapping fences and cast nets, while “non-protected” reefs are open access sites with no formal regulatory framework (McClanahan & Obura, 1995).

This study therefore aimed to test the hypothesis of spatial variation in reproductive, niche breadth, growth and mortality parameters of the marbled parrotfish (*L. vaigiensis*) in coastal Kenya. The results presented in this thesis could form a basis for future efforts to partition spatial differences in life-history traits of fishes to various causal factors in addition to testing ecological theories useful for managing species of socio-economic importance

.

1.2 Statement of the problem

Fishing pressure through its selective tendency and sometimes through destruction of benthic habitats, has significant effects on the abundance of species, often resulting in major shifts in community and trophic structure in time and space (Koslow *et al*., 2000). In Kenya and most of the WIO region, the marbled parrotfish, *Leptoscarus vaigiensis*, is among the heavily fished (catches constituting 18.6% of total catches by number and 16.6% by weight in coastal Kenya) reef fishes (Hicks & McClanahan, 2012). This is mostly because the species is less mobile and often site attached as is the case for many coral reef fishes (Sale, 2002a) making it highly predisposed to fishing mortality. However, despite the heavy fishing pressure on the reefs in Kenya (McClanahan & Mangi, 2004; Kaunda-Arara *et al*., 2003) and most of the tropics, populations of reef fishes tend to persist in viable numbers on the reefs (Jennings & Kaiser, 1998) and have continued to sustain artisanal fisheries.

The mechanisms by which coral reef fishes including the marbled parrotfish avoid overfishing extinctions are not well understood but could relate to resilience mediated by phenotypic plasticity or divergence. Spatial variation in life-history attributes among coral reef fishes due to phenotypic plasticity could create resilience to the effects of fishing allowing species to sustain populations and coral reef functions. Considering that the life-history traits of fished populations may change in response to fishing among other factors (Law, 2000), the present study aimed at testing the hypothesis of phenotypic plasticity in the reproductive traits and growth parameters together with spatial variation in niche breadth of the marbled parrotfish across six reefs of varying fishing intensity in coastal Kenya. Understanding the mechanisms of population maintenance or depletion is important for management of fisheries. The Kenyan dichotomy of protected and non-protected reefs provided an opportunity to test the hypothesis of fisheries induced phenotypic plasticity in the life-history traits of fishes.

1.3 Justification of Study

Characterization of life-history traits such as age or size at maturity as well as growth rate among natural populations of fish stocks is important because they influence population dynamics and resilience to overexploitation (Heino & Godo, 2002). Growth for instance, is an important factor in the life history of fish since other vital rates such as mortality and fecundity largely depend on it (Wootton, 1990). An understanding of growth attributes (e.g. asymptotic length defined as the length reached by fish if they were to grow indefinitely, instantaneous growth rate) is important in determining fish productivity (Qasim, 1973) useful for fisheries management programs (Wootton, 1990; Pitcher & Hart, 1993). Additionally, knowledge of niche breadth and diet variations in fishes based on stomach content analysis (as done in this study) is important in giving insight into factors that may affect spatial variability in population dynamics and food web structure (Pitcher & Hart, 1993). Further, information on fish diets represent an integration of many important ecological components including behavior, condition, habitat use, energy intake, and inter/intra specific interactions (Mohamed, 2004). These data are useful in building trophic and meta-population models necessary for understanding multi-species fisheries and for informing ecosystem approach to fisheries management.

Studies on phenotypic plasticity are important because they embrace different aspects of biology including genetics, development, ecology, evolution, physiology and behavioural science (Dewitt & Scheiner, 2004). Phenotypic plasticity is a powerful means of adaptation with broad significance and enables individual organisms to diminish the effect of environmental degradation by changing their life-history traits such as age/size at maturity (Goto, 1993), patterns of reproductive investment (Iguchi & Tsukamoto, 2001) and timing of migration (Quinn & Adams, 1996).

The results of this study will be useful in providing insights that could enable the use of spatial variability in life-history traits of coral reef organisms as indicators of environmental stress thereby assisting in supporting conservation efforts and management of coral reefs in the WIO region. The results further provide, for the first time in the WIO region, a theoretical framework of understanding spatial structure of exploited coral reef fish species.

1.4 Hypotheses

This study was guided by the following null statistical hypotheses:

1. There is no significant difference in reproductive traits (fecundity and size-at-first maturity) of *L. vaigiensis* among reefs of different protection levels in coastal Kenya.
2. There is no significant difference in the diet composition and niche breadth of *L. vaigiensis* among reefs of different protection levels in coastal Kenya.
3. There is no significant variation in growth parameters of *L. vaigiensis* among reefs of different protection levels in coastal Kenya.

1.5 Objectives

1.5.1 General objective

To examine variation in life-history traits of the marbled parrotfish, *Leptoscarus vaigiensis*, on six reefs exposed to varying fishing pressures in coastal Kenya in order to inform scientific management and conservation of fisheries resources in coastal Kenya.

1.5.2 Specific objectives

The specific objectives of this study were:

1. To perform a retrospective analysis of fish landings (1978-2007) in coastal Kenya as a basis of describing status of fish stocks.

2. To compare reproductive traits (fecundity, egg sizes and size-at-first maturity) of *L. vaigiensis* between protected and fished reef sites in coastal Kenya.
3. To compare niche breadth (variety of food items consumed) of *L. vaigiensis* among reefs of varying protection levels in coastal Kenya.
4. To assess growth parameters (instantaneous growth rate, Kyr^{-1}, and asymptotic length, $L\infty$, cm) of *L. vaigiensis* between protected and fished reef sites in coastal Kenya.

CHAPTER TWO

LITERATURE REVIEW

2.1 Oceanographic conditions and seasonality on the Kenyan coast

The Kenyan coast, like other parts of Western Indian Ocean, is marked by monsoonal seasonality driven by the north-south migration of the Inter-Tropical Convergence Zone (ITCZ) where winds from the north and southern hemisphere converge (Johnson *et al*., 1982). Subsequently, Kenyan coast experiences seasonality caused by both northeasterly and southeasterly monsoon winds. The northeast monsoon season (NEM, November–March) is a period of calm seas, elevated sea surface temperatures (SSTs), higher salinities and low primary productivity, while, the southeast monsoon season (SEM, April–October) is characterized by rough seas, cool weather, lower salinities and higher primary productivity (McClanahan, 1988). Monsoonal seasonality therefore not only drives productivity and other ecological processes in the marine environment but also the biological cycles of marine organisms including reproduction in fish and invertebrates (McClanahan, 1988).

The key oceanographic processes that influence ecology and thus ecological services on the Kenyan coast include ocean currents, monsoon winds and tides. Currents along the Kenyan coast are affected by a number of factors including wind pattern, the continental landmass and the Coriolis force (McClanahan, 1988). The main current experienced on the coast is the East African Coastal Current (EACC) which moves from south to north throughout the year. During the NEM season, the changing wind slows the northerly flowing current thereby reversing the movement to form the Somali Counter Current (SCC). The SCC can reach as far as 4^0S during years when it is strong, before leaving the coast (Johnson *et al*., 1982). During the NEM season, the EACC leaves the coast from Northern Kenya and slight upwelling could occur there (Kabanova, 1968). In the SEM season, the ITCZ shifts further north within the Indian Ocean region than in most tropical areas due to the low pressure belt created on the Asian continent during the northern hemisphere summer (McClanahan, 1988). The shift in ITCZ is responsible for the greater seasonality experienced in East Africa including the Kenyan coast (McClanahan, 1988). Variations in currents speed and directions, up and downwelling, water temperatures and nutrients cause a north-south dichotomy between ecosystems along the coast (McClanahan, 1988). The southern section of Kenyan coastline is predominated by coral reefs and benthic productivity associated with warm low-nutrient waters whereas the northern section has cooler nutrient-rich waters and a greater predominance of planktonic productivity (McClanahan, 1988).

The tidal range on the Kenyan coast is 4 m, which is relatively large for a tropical coastline (Brakel, 1982). As it is the case for equatorial regions, most extreme tides on the coast occur around equinoxes or intermonsoon periods whereas the less extreme ones during solstices thereby affecting rates of emersions duration, growth and distribution for intertidal organisms on a seasonal basis (McClanahan, 1988). Spring and extreme spring tides result in periodic nutrient inputs from estuarine areas on a lunar and annual basis (Brakel, 1982; McClanahan, 1988).

2.2 Biology and ecology of the Scaridae

The Scaridae to which the marbled parrotfish belong, is a diverse family of parrotfishes comprising of 83 species belonging to nine genera world-wide (Hawaii Cooperative Fishery Research Unit, HCFRU, 2008). The bumphead parrotfish (*Bolbometopon muricatu*) is the largest species of Scaridae and inhabits a wide area in the Pacific and Indo-Pacific (WildEarth, 2009). The marbled parrotfish, *Leptoscarus vaigiensis* is the only member of the genus *Leptoscarus* (Bruce & Randall, 1985). Its distribution ranges from the Red Sea in west to Easter Island in east, and Japan in north to New Zealand and South Africa in south (Bruce & Randall, 1985).

Parrotfishes play a significant role in coral reef ecosystems throughout the tropics, functioning as algal consumers and bioeroders (Bellwood *et al*., 2004). As an algal grazer, parrotfishes play a significant role in coral reef ecosystems by shaping the distribution, community structure, standing crop biomass and production rates of benthic algae on coral reefs (Russ, 2003). Massive consumption of coralline algae by parrotfishes makes them both dependent on, and keystone species within coral reef ecosystems. Groups of parrotfish are important in producing coral sands and may enable ecosystem resilience through their feeding (WildEarth, 2009). As herbivores, parrotfishes function as useful linkage between primary producers and predatory consumers on the coral reefs (Moksnes *et al*., 2008) thus acting as key conduits for the transfer of energy in ecosystem processes through both upward and downward cascades in the food web systems (Gullstrom *et al*., 2011). An understanding and management of parrotfish community structure is therefore important in maintaining overall coral reef health throughout the tropics (Howard, 2008).

2.2.1 Reproductive biology of Scarids

Scarids have complex socio-sexual systems that are key to their life-histories and demographic structures (HCFRU, 2008). They are generally sequential protogynous hermaphrodites, initially beginning as females and later changing to males in life (Choat & Robertson, 1975). Since individuals primarily begin life as females and only some individuals change sex, populations of sequential hermaphrodites have female-biased sex ratios (Howard, 2008). There are, however, variations of this pattern where some individuals begin life as males (diandry) and do not change sex (Robertson & Warner, 1978).

The marbled parrotfish, *L. vaigiensis* is the only species of the Scaridae that is gonochoristic (described as the state of having just one of at least two distinct sexes in any one individual fish, Bellwood, 1994) and inhabits seagrass beds or hard substrates heavily covered by macroalgae (Ohta & Tachihara, 2003). Unlike other parrotfishes, both sexes of the marbled parrotfish look alike and do not change sex (Kuiter & Tonozuka, 2001). The species mostly occur in small groups and spawns in shallow water above grass flats on the falling tide (Bruce & Randall, 1985). Like adult stages, the larvae of the marbled parrotfish are associated with drifting algae (Ohta & Tachihara, 2003). Fecundity (number of eggs per female) and length-at-first maturity in *L. vaigiensis* has been shown to vary with level of fishing pressure or level of site protection (Locham *et al*., 2015a). Higher fecundities and lengths-at-first maturity of *L. vaigiensis* have been found to occur at protected or less fished sites relative to intensely fished sites (Locham *et al*., 2015a).

Seasonal reproductive pattern is displayed by tropical scarids including *Scarus rivulatus* and *S. schlegeli* (Lou, 1992). Although spawning among the two species occur year round, the proportion of reproductively active individuals within the population varies over time with most individuals of *S. Schlegeli* spawning during the Austral Winter (May-September) and those of *S. rivulatus* having a pronounced spawning period extending from September to January (Lou, 1992). In Kenya and most of WIO region, reproduction information of marbled parrotfish across reef sites exposed to varying fishing pressure is limited hence the basis for one of the objectives of the present study.

2.2.2 Growth of Scarids

Parrotfishes are believed to grow at rates comparable to or even higher than those of carnivorous coral reef fish despite the relatively low nitrogen content of their diet (Munro & Williams, 1985; Russ & St. John, 1988). Even among herbivorous fish, adult parrotfishes have been found to grow significantly faster than the adult surgeonfishes consistent with Randall’s (1962) conclusion that the parrotfishes growth is fastest among coral reef fishes (Lou, 1992). Additionally, growth in Scarids has also been found to vary with local environmental conditions (Clifton, 1995) and sexual orientation identity (van Rooij *et al*., 1995).

Scarids have shorter life spans (5-20 years) compared to other herbivores like acanthurids (more than 20 years) (Choat *et al*., 1996). The long lived scarids include, *Chlorurus sordidus,* the daisy or bullethead parrotfish, *Scarus frenatus,* the bridled parrotfish and *S. niger,* the dusky parrotfish, (Choat *et al*., 1996). Like other protogynous coral reef fishes, scarids are characterized by different investment in gonad tissue (Choat *et al*., 1996). Gonads of terminal male scarids are usually much smaller than those of females and primary males (Robertson & Warner, 1978) and could be associated with different growth patterns amongst the sexes (van Rooij *et al*., 1995).

Generally, however, published data on the growth of herbivorous reef fish including parrotfishes are scarce (Horn, 1989) and even scarcer is information on growth variation in the group at sites exposed to differential fishing pressure. This study therefore attempted to bridge this information gap.

2.2.3 Feeding ecology of Scarids

Scarids display a wide variety of feeding strategies (Bellwood, 1985). Adult scarids are grazing animals, feeding on the close-cropped algal and bacterial mat covering dead corals or rocks, seagrasses and by crushing bits of coral that may contain invertebrate prey while their juvenile feed on small invertebrates (Choat & Bellwood, 1998). The ingested material alongside sand ingested while feeding is ground in pharyngeal mill resulting into the production of substantial quantities of sand dominated sediments (Choat & Bellwood, 1998). Consequently, scarids have large amounts of carbonate materials and sediments in the gut (Russ & St. John, 1988). Scarids have a short sacculated gut (Bellwood, 1985) compared to acanthurids which have a relatively longer gut and a more complex endoflora ofen with a gizzard and caeca (Clements, 1991). Like acanthurids, parrotfishes form large feeding groups, sometimes with multiple species, to overwhelm territorial fishes and deter predators (Hoey & Bellwood, 2008; Hughes *et al*., 2007). The grazing activities of Scarids make them some of the ecologically most important fishes on coral reefs (Hughes, *et al*., 2007).

The marbled parrotfish exploits a variety of marine flora on Kenyan reefs with the most important being the seagrass, *Thalassodendron ciliatum* and the seaweeds; *Enteromorpha* spp. (green algae) and *Sargassum* spp. (brown algae) (Almeida *et. al*. 1999; Locham *et al*., 2015b). Its grazing action likely explains in part, the observed resilience of some Kenyan coral reefs from the effects of coral bleaching (McClanahan *et al*., 2004; Obura, 2005) or resistance to out-competition by benthic algae (McClanahan & Shafir, 1990).

2.3 Influence of fishing pressure on community structure

On a global scale, increases in fishing pressure has resulted in severe reduction in the abundance of fish stocks (Roberts & Polunin, 1993), shifts in trophic structure (Jennings & Polunin, 1996) and interruption of key ecological processes (Bellwood *et al*., 2004). Fishing also has a detrimental effect on the environment via the use of habitat destructive techniques (Dayton *et al*., 1995; Jennings & Polunin, 1996) or removal of functionally important species (Dulvy *et al*., 2004; Hughes, 1994). Further, fishing may cause habitat loss indirectly by modifying habitat characteristics through cascading processes. For example, the feeding of grazing parrotfish on reefs shifted reefs from coral to macroalgae-dominated benthic assemblages throughout the Caribbean (Bellwood *et al*., 2004; Hughes, 1994). Loss of habitat, directly and indirectly through fishing, poses a major threat to the continued existence of many marine species (Roberts & Hawkins, 1999; Rodwell *et al*., 2003), particularly those that are already endangered (Wilcove *et al*., 1998). Indeed, fishing exploitation is believed to have caused 55% of marine extinctions, while habitat degradation explains a further 37% (Dulvy *et al*., 2003), emphasizing the importance of these two processes for both conservation and sustainability of marine resources (Wilson *et al*., 2010).

In East Africa, the lagoon based artisanal fisheries is thought to have resulted in near over-exploitation of coral reef fisheries mainly due to increases in fishing effort and competition for dwindling resources (McClanahan & Obura, 1995). Over-exploitation of fisheries resources is further exacerbated by among others, the notion that fisheries resources are unlimited, inadequate resources available to management agencies and increasing human population (Brochman, 1984). However, there is limited data on exploitation rates of coral reef fisheries in the tropics largely as a consequence of inadequate landing statistics (United Nations Environment Program, UNEP, 1998).

In Kenya, the true status of marine resources is not known since the last resource assessment was done in 1980s (Fondo, 2004). In general, however, approximately 80% of the total marine products come from shallow coastal waters and coral reefs, while only 20% is from off-shore fishing (Fondo, 2004). Recorded fish catches (landings) are thought to only comprise 5% of total catches, most of which by artisanal fishers, who exploit near shore resources on the continental shelf (Fondo, 2004). The main reef associated families constituting fish landings in coastal Kenya include; Lethrinidae (the emperors), Lutjanidae (the snappers), Siganidae (the rabbitfishes), Scaridae (the parrotfishes), Acanthuridae (the surgeonfishes) and Serranidae (the groupers). Earlier reviews of coral reef fish yields indicated the Siganidae and the Lethrinidae to be forming the bulk (~40%) of the artisanal landings in coastal Kenya before their declines in the 1990s (Kaunda-Arara *et al*., 2003). Declines in other major demersal fish families (e.g. Lutjanidae, Acanthuridae and Serranidae) have occurred over the last decades. Increases in human population in Kenya (≈ 2.70% per year) have likely increased the demand for marine food fish (United Nations Department of Economic and Social Affairs, 2015) considering the over-dependence of Kenyan coastal community on fish as source of animal protein (King, 2000). In the past decade, many marine fisheries resources have declined (Food and Agriculture Organization, FAO, 1995) mainly due to overfishing (Hutchings, 2000; Rose *et al*., 2000). Growth overfishing reduces the size and yield of target species (Munro, 1983; Russ, 1991), recruitment overfishing reduces the recruitment success of populations (Jennings & Lock, 1996), while ecosystem overfishing alters species interactions and habitat quality (McClanahan, 1995).

Fishing gears select catch by size and species (Dalzell, 1996; MacLennan, 1992) thereby influencing catch composition and the size frequencies of target species (Gobert, 1994; Stergiou *et al*., 1996). For instance, gears such as seine nets may take a wide variety of sizes and species with only the smallest individuals avoiding capture (Dalzell, 1996; Gell & Whittington, 2002) whereas gill nets selectively take a wide variety of species of a relatively narrow range of lengths dependent on the size of the mesh (Acosta, 1994). Gear type and use can therefore affect the efficiency of fish capture, the selectivity and composition of fish resources (McClanahan & Mangi, 2004). A well-managed fishery is therefore expected to use gear that catches most of the available species at sizes that do not undermine sustainability (McClanahan & Mangi, 2004). One suggested way of enabling national government to minimize adverse impacts of fishing gear selectivity on fish stocks is by formulating regulations that reduce overlap in the selectivity among gears, the size of fish caught as well as promoting understanding of fishing gear traditions (McClanahan & Mangi, 2004).

2.4 Phenotypic plasticity

Phenotypic plasticity is the environmentally sensitive production of alternative forms of behaviour, physiology and morphology by single genotype (Holopainen *et al*., 1997). It is a powerful means of adaptation with broad significance and appeal because it embraces different aspects of biology including genetics, development, ecology, evolution, physiology and behavioural science (Dewitt & Scheiner, 2004).

Like other organisms, fishes may change their life history attributes such as age/size at maturity (Goto, 1993), patterns of reproductive investment (Iguchi & Tsukamoto, 2001) and migration timing (Quinn & Adams, 1996) through phenotypic plasticity, thereby diminishing the adverse effect of environmental changes (Hutchings, 1996). Through phenotypic plasticity, fished stocks increase individual growth (Policansky, 1993) hence maturing at younger ages (Heino & Godo, 2002; Kuparinen & Merila, 2007) possibly as an adaptive strategy to enhance their resilience to fishing pressure thereby sustaining local populations (Locham *et al*., 2015a). Phenotypic plasticity or variance is also associated with species niche expansion or character release (Bolnick, 2001), polymorphism or adaptive radiation (Bolnick, 2001). In fishes, for example, possession of a generalist (broad) niche is regarded as an adaptive strategy against unpredictable availability of food resources (Dill, 1983) or a necessary precaution for variable environments (Sternberg *et al.,* 2008).

Variable exploitation pressure may contribute to phenotypic plasticity or divergence in life-history traits due to spatial heterogeneity in population densities (Hutchings & Baum, 2005). Fishing may drive life history changes via at least two different mechanisms in addition to the immediate numerical effects of mortality (Dieckmann & Heino, 2007). The two mechanisms include; firstly, direct effects manifested as phenotypic plasticity or divergence, and secondly, through evolutionary selection (Dieckmann & Heino, 2007). Changes in life history traits may result in declines in population size resulting in increased individual growth rates of the survivors following relaxation of intraspecific competition and into maturation at younger ages (Heino & Godo, 2002; Kuparinen & Merila, 2007). Evolutionary (or genetic) changes on the other hand occur through two different mechanisms. One mechanism is an increase in total mortality as a result of added fishing mortality to natural mortality hence selection for earlier maturity and therefore a smaller size at maturity (Reznick & Ghalambor, 2005). A second mechanism is size-selective mortality that occurs because various fishing methods can be biased toward the capture of certain phenotypes (Stokes *et al*., 1993). The sedentary nature of *L. vaigiensis* (Kaunda-Arara & Rose, 2004b), made it suitable for testing the hypothesis of phenotypic divergence in phenotypes in this study as fishing may cause spatially distinct variations in population structure. In the following sections, literature is reviewed on how fishes show phenotypic plasticity in different life-history attributes.

2.4.1 Variation in reproductive life history traits of fishes in space

Size at maturity is one of the most important life-history traits affecting animal fitness (Stearns, 1992). In fish, body size determines numerous reproductive traits including spawning intensity, quality of eggs, duration and time of offspring production (Berkley *et al*., 2004; Kjesbu *et al*., 1998; Trippel, 1998). Early maturation decreases fishing mortality before maturation and decreases the generation time (lifespan), whereas delayed maturation increases body size at maturity, which in turn increases fecundity. Fishing and other ecological processes therefore trigger a trade-off between early and delayed maturation in fishes (Stearns, 1992).

Fishing is one of the main reasons for declines in size and age at maturation in exploited fish stocks (Kuparinen & Merila, 2007; Law, 2000; Olsen *et al*., 2004). Since fishes live in spatially and temporally heterogeneous environments, age and size at maturity can vary among individuals in space due to phenotypic plasticity (Morita & Morita, 2002). Fishing, especially when size-selective, shifts the population's age and size distributions towards younger ages and smaller sizes through demographic truncation effects (Trippel *et al*., 1997). Evidence for size selective nature of fishing is plentiful (Fenberg & Roy, 2008; Trippel, 1995). In most cases, a fishing gear removes the largest (and fastest growing) individuals of a cohort at the time they enter the harvested part of the stock (Marteinsdóttir & Pardoe, 2008). Commonly also, large individuals are specifically targeted to maximize yield per unit effort. Even if size selective harvesting is not intentional, intensive exploitation will always lead to truncation of age and size structures since members of a cohort are not allowed to survive and attain old age (Marteinsdóttir & Pardoe, 2008). Therefore, an indication of over-harvesting is truncation in the age structure of a stock (Marteinsdóttir & Thorarinsson, 1998) or declines in average age and size of spawners (Marteinsdóttir & Pardoe, 2008).

Variation in annual fecundities as influenced by differential exploitation has been shown among several fish stocks in the North Sea including the Haddock (Hislop & Shanks, 1979), Whiting (Hislop & Hall, 1974), Witch (Bagenal, 1965), Plaice (Horwood *et al*., 1986), Dab (Lee, 1972), Halibut (Haug & Gulliksen, 1988) and Long rough dab (Ntiba, 1989). In this study, variation in fecundity and size-at-first maturity of the marbled parrotfish was compared among reefs of differential fishing pressure in coastal Kenya.

2.4.2 Spatial variation in foraging characteristics of fishes

Fishing pressure through destruction of benthic habitats could result in major shifts in foraging characteristics of benthic feeders like the marbled parrotfish and other species (Koslow *et al*., 2000; Munro *et al*., 1987). Besides fishing effects, other factors including food diversity (Layman *et al*., 2007), competition (Svanback & Bolnick, 2005), seasonal changes in resource availability (Tanimata *et al*., 2008) and environmental variability (Laidre & Heide-Jørgensen, 2005) can affect trophic ecology of fishes in space and time. Optimal foraging theory (MacArthur & Pianka, 1966) and the niche variation hypothesis, NVH, (van Valen, 1965) provide a framework for understanding among-individual variation in diet and the resulting changes in niche breadth of populations (Bolnick *et al*., 2010; Svanback & Bolnick, 2005) as may be modified by fishing pressure, environmental variability and biological interactions.

The niche variation hypothesis proposes constrained niche breadths when populations are exposed to strong inter-specific competition and broader niche breadths when released from inter-specific competition to intra-specific competition (Bolnick *et al*., 2010, van Valen, 1965). The optimal foraging theory on the other hand, asserts that a foraging activity will be maintained if the gains from it are greater than the costs, including missed opportunity costs (MacArthur & Pianka, 1966). Greater fitness by foraging individuals are derived when the energy gains per unit time of foraging are maximized (Stephens & Krebs, 1986; Svanback & Bolnick, 2005). Local environmental factors such as relative abundance of food sources, quality of food and predation risk (e.g. fishing pressure) can affect prey handling time and search time thereby altering the energy income rate hence causing alternate foraging strategies to be favoured with varying local conditions (Svanback & Bolnick, 2005). The optimal foraging theory assumes that individuals act to maximize their rate of energy intake (Stephens & Krebs, 1986) by ignoring certain food types when the time required to consume them could be more profitably spent searching for more valuable food items (Bolnick *et al*., 2003). A demonstration that local environmental conditions can affect the foraging strategy and therefore diet of individuals is required from more studies (Abbey-Lee, 2012) including WIO.

Resource competition as may be modified by fishing pressure has been proposed to promote ecological and phenotypic variation (Bürger & Gimelfarb, 2004; Diekmann *et al*., 2004). Intra-specific competition for instance, is thought to maintain intra-specific variation (Bolnick, 2004; Bürger & Gimelfarb, 2004), trophic polymorphism (Smith & Skulason, 1996) or even drive speciation (Dieckmann *et al*., 2004; Rosenzweig, 1978). Niche breadth differences among species are also thought to be underpinned by genetic trade-offs between the capacity of species to exploit a range of resources and their performance in utilizing resources (Scheiner, 1998; van Tienderen, 1997). Accordingly, a specialist species (with low diet diversity or narrow niche breadth) may outperform a generalist one (with a diverse diet or broad niche) on a subset of resources but cannot maintain that greater performance on a broader range (Caley & Munday, 2003). A generalist species, may outperform a specialist species given a greater range of resources but cannot achieve the performance of a specialist on any of the resources if scarce (Caley & Munday, 2003). In fishes, possession of a generalist feeding mode (broad niche breadth) is regarded as an adaptive strategy against unpredictable availability of food resources (Dill, 1983) or a necessary precaution in variable environments (Sternberg *et al*., 2008; Locham *et al*., 2015b).

Niche breadth expansion can also be associated with an increase in phenotypic variance or character release (Bolnick, 2001), polymorphism or adaptive radiation (Bolnick, 2001). Although the relationship between intra-specific competition and species diversification is known from theory (Roughgarden, 1976; Wilson & Turelli, 1986), there has been little empirical proof that niche breadth diversify in response to intra- or inter-specific competition (Blanchard, 2001) that may be mediated by drivers like fishing effort or resource availability. Therefore, one objective of the present study is, to provide information on the changes in diet and niche breadth of the marbled parrotfish at reefs exposed to different fishing pressure as a measure of phenotypic plasticity.

2.4.3 Spatial variation in growth parameters in fishes

Spatial variation in exploitation rates and environmental variability may influence demographic rates of fishes and hence affect population structure and processes (Jennings & Kaiser, 1998). Spatio-temporal changes in demographic traits such as growth and length at maturity have been found in fish stocks including the Atlantic cod on the Scotian Shelf (Beacham, 1983), Atlantic Salmon in North America (Schaffer & Elson, 1975) and for other fish stocks in the North-West Atlantic (Trippel, 1995). Besides fishing, environmental variables such as sea surface temperature rise have served to induce changes in life-history traits particularly age and size at maturation (Cardinale & Modin, 1999).

Fish have also been shown to achieve greater asymptotic size, higher growth rates, and slightly lower natural mortality in higher productive subregion of the western Santa Barbara Channel (SBC) than fish in the low productivity subregion of the SBC (Wilson *et al*., 2012). Also, population size structure and maximum age have been shown to be greater in the high productivity zone relative to low productivity zone (Wilson *et al*., 2012).

Scarids, although relatively large fish, have rapid growth rates and relatively short life spans than Acanthurids such as the *Acanthurus* and *Ctenochaetus* species which have relatively slow growth rates and extended life spans (Lou, 1992). As a distinct group of herbivorous reef fishes with fast growth rate, Scarids reach sexual maturity at the relatively younger age of 2 years (Lou, 1992). As indicated by the faster growth rate and the relatively short lifespan (compared with the Acanthurids), the turnover rate of Scarid population is relatively high (Lou, 1992). One objective of the present study is to generate information on growth parameters of the marbled parrotfish at reefs of differential fishing pressure in coastal Kenya.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study Area

Coral reefs in Kenya can be divided into three conservation categories depending on their level of exposure to fishing pressure and include: protected (or marine parks), partially protected (or marine reserves) and unprotected reefs. There is therefore a gradient in protection level. Extractive exploitation of resources is prohibited on protected coral reefs in Kenya, also designated as marine parks. “Reserves” or partially protected reefs (in the Kenyan context) are buffer areas adjacent to the marine parks and in which regulated fishing is allowed with “traditional” methods that include baited fish traps, fish trapping fences and cast nets. “Unprotected” coral reefs are open access sites with no formal regulatory framework (McClanahan & Obura, 1995).

This study was done in two protected reefs (Malindi and Watamu Marine Parks), the ‘‘Marine Reserves’’ adjacent to these parks, and in the un-protected reefs (Vipingo and Kanamai) (Fig. 3-1). The Kenyan coral reefs are described as predominantly shallow (~10-12 m at high tide) lagoonal fringing reefs that run parallel to the coastline and have a mosaic of substrata (seagrass beds, sand, rubble, live coral, etc.) common to all coral reefs in the country. The Kenyan coast (≈ 640 km long) experiences seasonal weather caused by both north-easterly and south-easterly monsoon winds described by McClanahan (1988). Samples of *Leptoscarus vaigiensis* (Plate 1-1) were obtained from the protected Malindi and Watamu Marine Parks, the Reserves adjacent to these marine parks and from the unprotected (Vipingo and Kanamai) reefs (Figure 3-1). The samples were obtained on a monthly basis from May 2011 to April 2013.

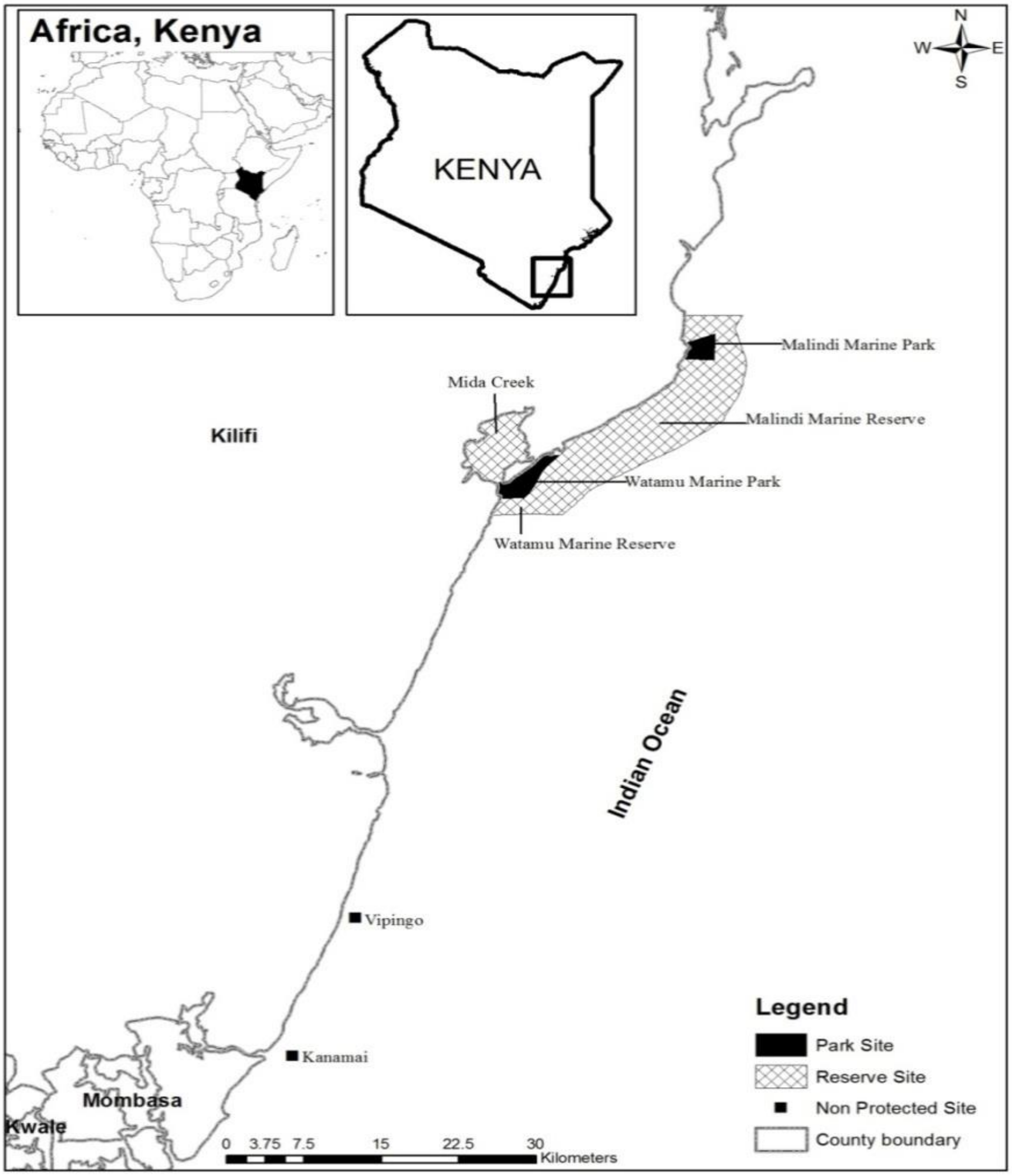

Figure 3-1: A map of Kenyan coastline showing the sampling sites for the marbled parrotfish, *Leptoscarus vaigiensis*, from May 2011 to April 2013.

3.2 Selection of the study specimen

The marbled parrotfish was selected for this study because of their ecological importance as grazers (Russ, 2003), their socio-economic importance in commercial and artisanal fisheries worldwide (Jennings *et al*., 1999) and the paucity of scientific information on this species, particularly in Kenya and most of WIO countries. The sedentary nature of *L. vaigiensis* (Kaunda-Arara & Rose, 2004), made it suitable for testing the hypothesis of phenotypic divergence in phenotypes in this study as fishing may cause spatially distinct variations in population structure.

3.3 General field and laboratory procedures

Samples of *L. vaigiensis* were caught within protected sites (Malindi and Watamu Parks and their reserves, Figure 3-1) on a monthly basis from May 2011 to April 2013 using local traps called *Demas* (Plate 3-2). The traps, adopted from Kaunda-Arara and Ntiba (1997) are pentagonal in shape measuring approximately 1.5 × 1.3 × 0.6 m high. They were constructed of metal frames and covered with a wire mesh of 1 cm stretch length. Each *Dema* trap had a single top-side funnel door made out of bamboo reeds through which the fish enters and an underside aperture for removing the catch (Plate 3-1).

At each site, monthly fishing lasted 4.7 days. On each sampling day, 3-5 *Dema* traps were deployed in park and reserve sites during low tide and retrieved during the subsequent low tide period of the following day having soaked for about 12 hours. Prior to deployment, *Dema* traps were baited with approximately 0.5 kg of a mixture of green and brown benthic algae and mashed tissues of the mangrove gastropod, *Terebralia palustris.*

1 cm mesh sized nylon net Trap entrance

Plate 3.1: A Dema trap used to catch the marbled parrotfish (*Leptoscarus vaigiensis*) in Malindi and Watamu Marine Parks and their Reserves in coastal Kenya during the study.

In the non-protected sites (Vipingo and Kanamai, Figure 3-1), samples were obtained monthly, during the same period, from fishers fishing these sites using cast nets and spear guns. Arrangement was made with specific fishers to obtain samples from them for an average of 4 consecutive days every month. Effort was made to obtain a wide size range of the specimen from fishers. All monthly specimens of *L. vaigiensis* were preserved in ice and taken to the Kenya Marine and Fisheries Research Institute laboratory for further processing.

In the laboratory, the total lengths (TL) and standard lengths (SL) of the specimens were measured to the nearest millimetre and total weights taken to the nearest 0.1 g. The specimens were analysed to produce site-specific information on the following parameters: i) reproductive attributes (fecundity, egg size and length-at-first maturity), ii) feeding attributes (diet and niche breadth) and iii) growth and mortality parameters (asymptotic lengths, instantaneous growth and mortality rates). The details of specimen treatment and data generation for the above attributes are described below.

3.3.1 Reproductive attributes

In order to examine site-specific reproductive attributes, the fish were cut open and sex and maturity stages determined visually following Bagenal (1978) maturation scheme as: I- immature; II- immature; III- maturing; IV- mature; V- active; and VI- spent. The gonads were then weighed to the nearest 0.001 g using a Metler electronic balance. In order to determine fecundity of fish specimens, portions cut from all mature and active ovaries (stages IV-V) obtained monthly were weighed to the nearest 0.001 g on the electronic balance and stored in Gilson’s fluid for at least 2 months with frequent shaking in order to aid in the release of eggs from the ovarian wall as described by Kaunda-Arara and Ntiba (1997). The ovarian portions were derived from left or right lobe following a preliminary analysis of variance that showed no significant difference in egg size distribution along the antero-posterior axis of the either lobes of the ovary. Fecundity was then determined following the volumetric method as described in

Bagenal (1978). Briefly, the contents of each bottle containing the ovarian portions were poured into a Petri dish and the eggs washed repeatedly in tap water. The clean and separated eggs were transferred to a 1-litre beaker containing a known volume of water. A plastic ruler was used to stir the eggs suspension to ensure an even distribution of eggs in the suspension column. After 15 strokes of the ruler, a 5 ml sub-sample was taken by a Labsystem finelet pipette. The eggs in this aliquot were examined, counted and their diameters measured along a horizontal axis using a calibrated eye-piece graticule under a standard dissecting microscope at ×40 magnification.

3.3.2 Diet and niche breadths

Stomachs of fish from sites were preserved in 10% formalin. Contents of the preserved stomachs were observed under a light microscope and the food items in each stomach identified to the lowest taxon using different identification keys (e.g. Bolton *et al*., 2007; Oliveira *et al*., 2005). The Point method as described by Mohammed (2004) was used to quantify the food items in fish stomachs. Briefly, the method involved counting of individual food types in each stomach and allotment of certain number of points to each food type based on its proportion by volume as measured in a graduated cylinder. The diet item with the highest volumetric proportion was given a maximum of 16 points. Every other food type was awarded 8, 4, 2 or 1 points depending on their relative proportional abundance in the stomach. Care was taken to count only the material that appeared whole or partially digested in order to minimize the possibility of double counting. A total of 978 stomachs from the 6 sites were analysed for diet and niche breadth of the fish using this methodology.

3.3.3 Growth and mortality parameters at sites

To describe the growth parameters of *L. vaigiensis* at all the six sites, total (measurement from snout tip along the midline to the posterior edge of the caudal fin, Allen, 1997) and standard (measurement from snout tip along the midline to the anterior edge of the caudal finfold, Allen, 1997) lengths of all specimens obtained from the sites were measured (to the nearest millimetre) from monthly specimens. Monthly length frequency data at sites were used to estimate growth and mortality parameters of the fish using the Electronic Length Frequency Analysis (ELEFAN I) computer program incorporated in FAO-ICLARM Stock Assessment Tool II (FISAT II) software as described in section 3.3.4.

3.4 Data analyses

The data for retrospective fish landings, reproduction and feeding parameters were first entered in MS-EXCEL 2010 spreadsheet before their analysis using SPSS (version 16.0) software package, whereas the growth and mortality parameters data were captured and analysed using FAO-ICLARM Stock Assessment computer program (FISAT II).

3.4.1 Catch trends from landings data (1978-2007)

Landing data derived from Annual Statistical Bulletins of the State Department of Fisheries from 1978 to 2007 were analyzed for the dominant demersal coral reef fish families (Lethrinidae, Lutjanidae, Siganidae, Scaridae, Acanthuridae, Mullidae) in order to examine temporal trends. Catches of pelagic families (mostly Clupeidae and Carangidae) and those under ‘mixed’ or ‘other’ category were excluded from analysis. Fish landings were first standardized for years and fishing effort (number of fishers that fished during the year) in order to allow annual comparison of landing rates (tons fisher^{-1} year^{-1}). Time series of total landings (in tons/year) were used to examine temporal trends in catches of the major demersal families of coral reef fish (Lethrinidae, Lutjanidae, Siganidae, Scaridae, Acanthuridae, Mullidae). A locally-weighted scatterplot smoother (LOWESS) (Cleveland, 1979) was used to fit smoothed trend lines to the full data series using the SigmaPlot package. The LOWESS is based on a weighted least squares algorithm that gives local weights the most influence while minimizing the effects of outliers (Cleveland, 1979). A smoothness parameter (f) of 0.3 was found to adequately smooth the data without distorting the main temporal patterns (Kaunda-Arara *et al*., 2003). The landing rates (tons fisher^{-1} year^{-1}) of the dominant reef fish groups were log transformed before their comparison using one-way analysis of variance (ANOVA) to check for significant differences at a decadal scale. A Student–Newman–Keuls (SNK) test was used to partition the significant differences between decadal intervals.

3.4.2 Reproduction

3.4.2.1 Sex ratio

The sex ratio (male to female) was estimated for the samples caught during the study period before being tested for the expected ratio of 1:1 by chi-square (χ^2) analysis (Zar, 1999).

3.4.2.2 Fecundity

From the counts of eggs in the sub-samples (see section 3.2.1), the fecundity (F) for each active/mature female fish was estimated following Bagenal (1978) as follows:

$$F = V/V_1N \times W/W_1 \text{ .... Equation 1}$$

Where N is number of eggs in a sub-sample, V is the volume of egg suspension; V_1 is volume of sub-sample; W is weight of the whole ovary; and W_1 is weight of the portion of ovary fixed in Gilson's fluid.

Fecundities at sites were log (x + 1) transformed in order to satisfy analysis of variance (ANOVA) assumptions of homoscedasticity (Zar, 1999), and then compared between sites using one-way ANOVA. A Student–Newman–Keuls (SNK) test was performed in order to identify significantly different means (Zar, 1999).

Relationships between fecundity (F) and standard length (SL) at park, reserve and non-protected sites were estimated using regression analysis (Zar, 1999) based on the following formula:

$$F = aSL^b \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Equation 2}$$

Where **a** and **b** are derived from least-squares regression of the log-transformed variables

The length exponent (b) was compared between sites using Analysis of Covariance (ANCOVA) with log standard length as the covariate. Further, multidimensional scaling (MDS) ordination analysis was used to examine the similarity of sites based on fecundity estimates. The spawning period of the species at sites was determined from the monthly distribution of the maturity stages.

3.4.2.3 Egg size and gonado-somatic index

Mean egg diameters at the active stage V were compared between sites using one-way ANOVA after log (x + 1) transformation of the data, and size-frequency distribution of these eggs examined using graphical plots. A MDS analysis was used to examine associations of sites based on gonadosomatic index (GSI) values for both male and female individuals. Gonad weights were related to total lengths to examine variation of gonadal development with fish size at sites.

3.4.2.4 Length at first maturity

The length-at-first maturity (L_{50}) of the species was determined from samples from the sites by calculating the proportion of mature (stages IV-V) individuals for each length class as described by King (1995). The percentage of mature fish by length class at sites were fitted to a logistic function using least-squares regression method implemented by the SOLVER routine in Microsoft™ Excel as follows:

$P(L) = 1/1+e^{-(a+bL)}$ ……………………………………………….........Equation 3

Where, P(L) is the proportion of mature individuals at length **L**, and **a** and **b** are parameters of the logistic equation.

The length at which 50% of fish were mature (stage IV to V) was regarded as the size at first maturity. Non-parametric bootstrapping technique (Efron & Tibshirani, 1993) was used to resample lengths with replacement at sites to form three subsets of the length dataset. The L_{50} was estimated separately for each of bootstrapped length subsets following the procedure described above and true range of L_{50} were inferred from confidence intervals resulting from estimated L_{50} for length subsets. L_{50} for males was not computed mostly due to small sample sizes of the mature gonads at non-protected sites and also because of inherent difficulty in estimating their maturity stages.

3.4.3 Diet and niche breadth variation

3.4.3.1 Spatial variation in diet

The monthly frequency of occurrence of the food items (defined as a percentage of stomachs containing a certain food item in relation to the total number of stomachs examined) was computed following Hyslop (1980) as follows:

$F_i = \frac{100n_i}{n}$ ………………………………………………………... Equation 4

Where, F_i is frequency of occurrence of i^{th} food item in the monthly samples; n_i the number of stomachs in which the i^{th} item is found; and n the total number of stomachs with food in the monthly samples.

The Shannon-Wiener diversity index (H) was used to describe diversity of food items in the diet of fishes from sites following Magurran (1988) as follows:

$H = \sum_{i=1}^{s} P_i \, lnP_i$ ………………………………................................ Equation 5

Where, Pi is the proportion of individuals of one particular species found in the diet.

Diversity estimates at sites between months in each season were then compared using one-way ANOVA. SNK test was performed in order to identify significantly different means (Zar, 1999).

Hierarchical cluster analysis based on group's complete linkage (Landau & Everitt, 2004) was performed to examine association of different food items in the diet of the parrotfish. Numerical abundance of food items at each site were square root transformed in order to down play the influence of most dominant items.

3.4.3.2 Food preference and niche breadth at sites

The Index of Relative Importance (IRI) was used to estimate the importance of each food item in the diet of fish from different sites. The index was obtained separately for each food item following Pinkas *et al*. (1971) as follows:

$$IRI_i = (\%N_i + \%V_i)\ \%O_i \quad \text{……………………………..………………. Equation 6}$$

Where, N_i, V_i and O_i represent percentage composition of the i^{th} food item by numbers, volume, and its frequency of occurrence, respectively.

In order to determine niche breadth of the fish at each site, Levins' measure of niche breadth (B) (Levins, 1968) was derived as follows:

$$B = 1/\Sigma p_i^2 \quad \text{…………………………………………………….…. Equation 7}$$

Where, $\mathbf{p_i}$ is the proportion of diet by volume that is represented by food item of category **i**. The index has a minimum at 1.0 when only one prey type is found in the diet and a maximum at **n**, where **n** is the total number of prey categories, each representing an equal proportion of the diet. The effect of season and site on niche breadths of the species was tested using a two-way ANOVA after conversion to log (x+1) to satisfy

ANOVA assumptions of homoscedasticity. The SNK test was then performed as a *post-hoc* test (Zar, 1999).

The Correspondence analysis (CA) as described by Landau and Everitt (2004) was further used to examine possible diet differentiation with sites based on log (x+1) transformed food abundance at sites. The CA was based on 22 selected food items whose numerical abundance was $\geq 0.1\%$ in order to ease interpretation of the plots.

3.4.3.3 Feeding intensity at sites

Feeding intensity (FI) of the fish at sites was derived following Hyslop (1980) as follows:

FI = weight of food items in stomach/weight of Fish×100………….. Equation 8

The monthly mean feeding intensities at sites (y) were then related to niche breadths (x) using the non-linear second order polynomial regression of the following form:

$y = a_0 + a_1 + a_2x^2 + \varepsilon$………………...…………………………....... Equation 9

3.4.4 Growth and mortality parameters

3.4.4.1 Growth parameters

The length-frequency distribution of fish at each of the six sites was examined for skewness (defined as the degree of departure from symmetry of a distribution) using Pearson's skewness coefficient formula (Zar, 1999) as follows:

Skewness index (Sk) = 3(mean-median)/standard deviation……… Equation 10

The Skewness indices were then used to determine levels of gear selectivity at sites and hence the comparability of length distributions. Analysis for growth parameters was based on length-frequency analysis (LFA) of the monthly data grouped into 2 cm length classes. The Electronic Length Frequency Analysis (ELEFAN I) computer program incorporated in FAO-ICLARM Stock Assessment Tool II (FISAT II) (Gayanilo *et al*., 1996) was used to estimate asymptotic length ($L\infty$, cm) and instantaneous growth rate (Kyr^{-1}). The modified Powell-Wetherall Plot (Pauly, 1986) was used to obtain preliminary estimate of $L\infty$ as a validation of the ELEFAN I outputs. This method is based on the right-descending part of the length-frequency curve and calculates the regression equation of the descending arm as follows:

$$Lmean - L' = a + bL' \qquad \text{Equation 11}$$

Where, Lmean is the mean length of fish of length L' and longer, where L' is some length for which all fish of that length and longer are under full exploitation (Pauly, 1986). Thus, plotting Lmean – L' against L' gives a linear regression from which “a” and “b” can be estimated and hence $L\infty$ and Z/K (ratio of mortality and growth) derived from the relationship (Pauly, 1986):

$$Z/K = -(1+b)/b \text{ and } L\infty = -a/b \qquad \text{Equation 12}$$

The final estimate of the growth parameters ($L\infty$, K and t_0) was based on the von Bertalanffy growth formula (VBGF) (Sparre & Venema, 1998) expressed as follows:

$$Lt = L\infty\,[1-\exp^{-K(t-t_0)}] \qquad \text{Equation 13}$$

Where, Lt = length (in cm) at age t (in years), $L\infty$ (cm) = asymptotic length or the maximum attainable length if the organism is allowed to grow, $K\ yr^{-1}$ = instantaneous growth coefficient, t_0 = age at which length equals zero, or the birthday of the fish. The parameters were derived by fitting the Von Bertalanffy model (Equation 13) on to the monthly length frequency data using the “surface response option” in ELEFAN I sub-package in FiSAT II, where the parameter combination (K and $L\infty$) outputs with the highest index of fit (Rn, range 0 -1) is selected.

The goodness of fit index (Rn) is defined by the following formulae:

$$Rn = 10ESP/ASP /10 \text{……………………………………………} \text{Equation 14}$$

Where, the ASP ("Available Sum of Peaks") is computed by adding the “best” values of the available “peaks” and the ESP ("Explained Sum of Peaks") is computed by summing all the peaks and troughs "hit" by the Von Bertalanffy growth curve (Gayanilo *et al*., 1996). Since ELEFAN I estimate only two ($L\infty$, K) of the three ($L\infty$, K and t_0) growth parameters, t_0 was subsequently derived following Pauly (1983) equation as follows:

$$t_0 = (-0.3922) - 0.2752 \log L\infty - 1.038 \log K \text{………………………} \text{Equation 15}$$

As direct comparison of the growth parameters (K and $L\infty$) between stocks is not desirable because of their correlation (Sparre & Venema, 1998), the parameters derived for the species at the six reef sites were compared using the similarity of a phi-prime (Φ) index, (also called growth performance index) derived by Pauly and Munro (1984) as follows:

$$\Phi = 2 \log10 L\infty + \log10 K \text{…………………………………………..} \text{Equation 16}$$

The growth curves (or parameters) generated by the VBGF were additionally compared by generating 95% confidence regions around the parameter estimates of K and $L\infty$ for the six sites (Kimura, 1980). The 95% confidence intervals (CI) were determined by bootstrapping K and $L\infty$ values, with replacement, to generate 1000 estimates of these parameters (Efron & Tibshirani, 1993; Kimura, 1980). The parameters and 95% CI for the von Bertalanffy growth equation were calculated as the median, upper and lower percentiles of the 1000 bootstrap estimates. Non-overlapping confidence regions indicate differences in growth parameters between sites and were used to compare similarity of the growth functions of the species from the six reef sites.

3.4.4.2 Mortality parameters derived at sites

A total mortality coefficient (Z yr^{-1}) of the fish at sites was estimated using the length-converted catch curve method (Pauly *et al*., 1984) in the FiSAT program. This method consists of a plot of the natural logarithm of the number of fish in various length groups against their corresponding mid-length values. A regression analysis is done on the descending right hand arm of the catch curve, and Z estimated as the negative slope of the line (Gayanilo *et al*., 1996). The natural mortality coefficient (M) of the fish at sites was estimated following Pauly's empirical formula (Pauly, 1980), linking natural mortality with the von Bertalanffy parameters, K (yr^{-1}), $L\infty$ (cm) and the mean annual temperature (T ^{o}C) of the water in which the fish stock lives as follows:

$$\text{Log}_{10}(M) = -0.0152 - 0.279 * \log_{10} L\infty + 0.6543 \log_{10} K + 0.463 \log_{10} T \text{......Eq. 17}$$

Where, T is the annual mean sea surface temperature taken as 27^{o}C for the Kenyan coast (Kenya Meteorological Department).

Since fishing is not allowed inside the parks, estimates of Z from the parks were taken to reflect natural mortality. Fishing mortality (F yr^{-1}) was derived from the difference between Z and M at non-protected sites. The exploitation levels (E) of the parrotfish at the different sites were then obtained following Gulland (1971):

$$E = F/Z \text{..Equation 18}$$

Where, E is considered optimal (Eopt) at E = 0.5 and excessive at E > 0.5

The annual recruitment pattern of the fish at sites was estimated by projecting the length-frequency data backward onto the time axis down to zero length, using the von Bertalanffy growth equation and the estimated growth parameters (Pauly, 1982) in the FiSAT program.

CHAPTER FOUR

RESULTS

4.1 Retrospective analysis of coral reef fish landings in coastal Kenya (1978-2007)

Artisanal landings of major demersal fish groups on the Kenyan coast differed over the last three decades (Figure 4.1, Table 4.1). In general, the long-term catch rates (ton fisher^{-1}year^{-1}) of the fishes peaked in 1992 (Siganidae = 0.082; Scaridae = 0.037; Acanthuridae = 0.014; Lutjanidae = 0.032; Mullidae = 0.005; Lethrinidae = 0.08) and 2004 (Siganidae = 0.080; Scaridae = 0.032; Acanthuridae = 0.008; Lutjanidae = 0.030; Mullidae = 0.007; Lethrinidae = 0.08) (Figure 4.1). Among herbivorous group, the rabbitfishes (family Siganidae) landings (ton fisher^{-1}year^{-1}) increased from 0.050 in 1978 to peak level (0.082) in 1992 before decreasing in subsequent period to a low of 0.035 in 2000 (Figure 4.1). The fisher landings for the Siganidae peaked in 1992 (0.082) and in 2004 (0.075). The other herbivorous families (Scaridae and Acanthuridae) also had the same landing trends over the three decadal periods but with lower landings than that of Siganidae (Figure 4.1).

Among the carnivorous families, the emperors (family Lethrinidae) had landings (ton fisher^{-1} year^{-1}) that increased from 0.06 in 1978 to a peak of 0.08 in 1992 before declining to lower level of 0.05 in 1997. The fisher landings (t fisher^{-1} yr^{-1}) for the Lethrinidae increased variedly from 0.045 in 1997 to a peak value of 0.080 in 2004 before declining monotonously in the subsequent period (Figure 4.1). The landing trends of the other carnivorous families (Mullidae and Lutjanidae) were similar to that of emperors (Figure 4.1). Comparison of the landings of the demersal groups across decades indicated significant difference for the Scaridae (ANOVA, F = 4.332, p = 0.024), Acanthuridae (F = 6.198, p = 0.007) and Lethrinidae (F = 5.543, p = 0.010, Table 4.1).

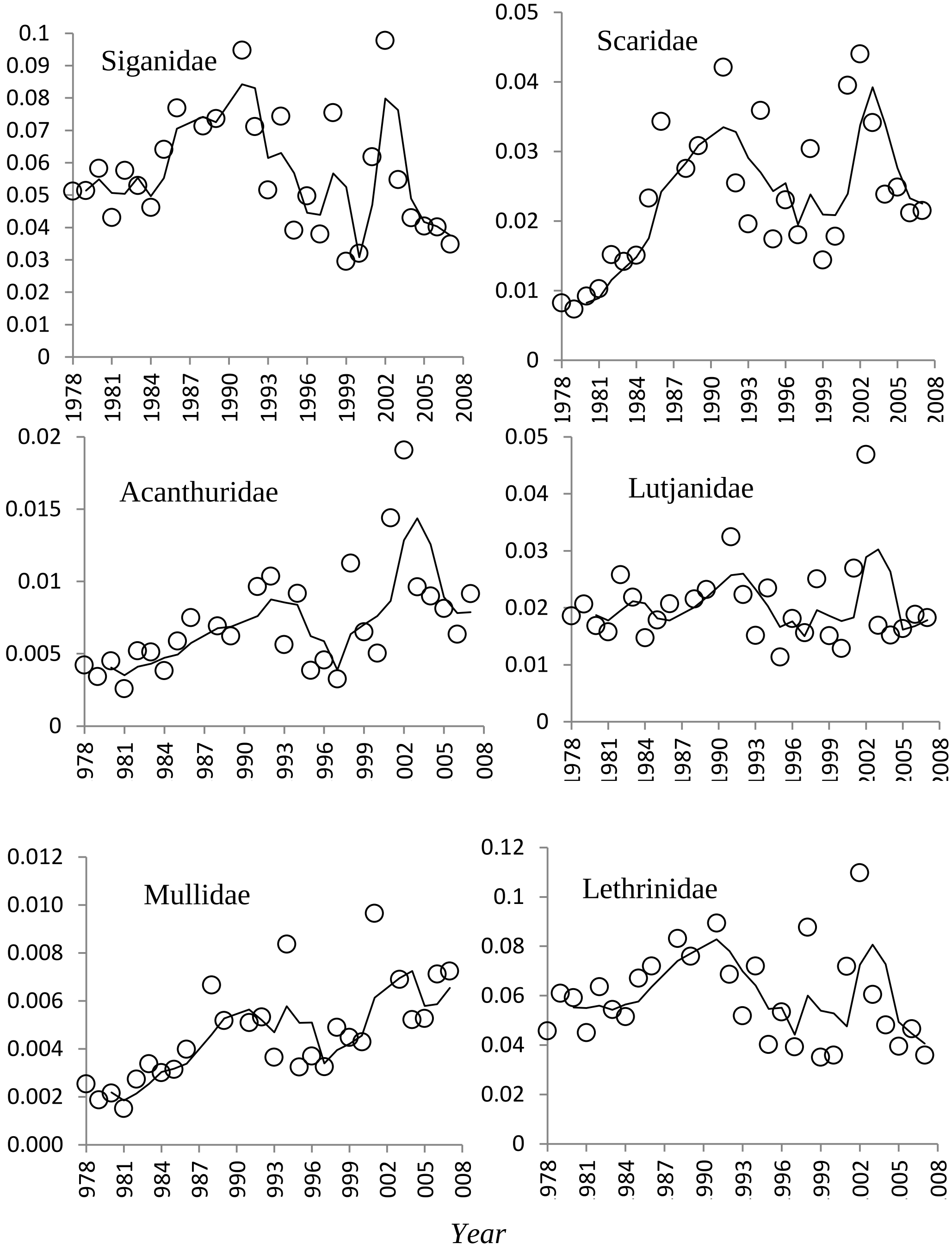

Figure 4.1: Temporal variation in catches of the dominant demersal marine fish families in coastal Kenya from 1978 to 2007. Continuous lines show the locally-weighted scatterplot smoother trend fit to landings, while circles (o), show the actual landings.

Table 4.1: Decadal variation in catch rate (ton fisher-1year-1) of dominant demersal fish families caught in coastal Kenya from 1978-2007. Numbers mean ± standard deviation (SD). Means with different letter superscripts within a row are significantly different as per SNK test.

Families	**Time**			**ANOVA**	
	1978-1988	**1989-1999**	**2000-2010**	**F**	***P***
Siganidae	0.057 ± 0.011	0.060 ± 0.021	0.051 ± 0.022	0.588	0.563
Scaridae	0.017 ± 0.009^{a}	0.026 ± 0.009^{b}	0.028 ± 0.010^{b}	4.332	0.024
Acanthuridae	0.005 ± 0.002^{a}	0.007 ± 0.003^{a}	0.010 ± 0.005^{b}	6.198	0.007
Lutjanidae	0.019 ± 0.003	0.020 ± 0.006	0.022 ± 0.011	0.191	0.828
Mullidae	0.003 ± 0.001	0.005 ± 0.002	0.021 ± 0.040	1.793	0.187
Lethrinidae	0.004 ± 0.001^{a}	0.005 ± 0.002^{a}	0.008 ± 0.003^{b}	5.543	0.010

However, there was no significant difference in the landings of Siganidae (F = 0.588, *p* = 0.563), Lutjanidae (F = 0.191, *p* = 0.828) and Mullidae (F = 1.793, *p* = 0.187) between the decadal periods (Table 4.1). Partitioning of the variance in the landings using SNK test indicated significant difference between landings of Scaridae in 1978-1988 period and 1989-1999/ 2000-2010 periods (Table 4.1). Also, significant difference in landings of Acanthuridae and Lethrinidae were also shown by SNK test between 1978-1988/1989-1999 periods and 2000-2010 period (Table 4.1). There was no significant difference in the landings of Scaridae between 1989-1999 and 2000-2010 periods and also in the landings of Acanthuridae and Lethrinidae in 1978-1988 and 1989-1999 periods (Table 4.1).

The subsequent sets of results explore the general hypothesis that the likely persistence of *L. vaigiensis* (a Scaridae) on Kenyan reefs ($p > 0.05$, Table 4.1) is mediated by phenotypic plasticity in life-history traits despite historical fishing pressure.

4.2 Variation in reproductive traits between reef sites in coastal Kenya

A total of 2701 *L. vaigiensis* were caught during the study period, 1586 (58.7%) during the SEM season and 1115 (41.3%) during the NEM season. There were more males than females at all sites but the overall sex ratio (M:F) of 1.46:1 was not significantly different from unity ($\chi^2 = 43.33$, $p = 0.292$).

4.2.1 Fecundity

The fecundity of *L. vaigiensis* was estimated in 215 active/mature females spread in all the six sites.

Table 4.2: Mean fecundity estimates of *Leptoscarus vaigiensis* caught at protected (Parks), partially protected (Reserves) and non-protected sites in coastal Kenya. Numbers mean ± standard deviation (SD). Means with different letter superscripts are significantly different as per SNK test.

Sites		Mean fecundity (eggs)	No. of ovaries
Watamu Park		$113{,}968 \pm 73{,}253^{b}$	25
Malindi Park		$109{,}840 \pm 48{,}785^{b}$	29
Watamu Reserve		$111{,}879 \pm 44{,}046^{b}$	14
Malindi Reserve		$129{,}353 \pm 85{,}148^{a}$	93
Vipingo (non-protected)		$95{,}928 \pm 69{,}884^{c}$	50
Kanamai (non-protected)		$70{,}418 \pm 55{,}715^{c}$	46
ANOVA	F	4.591	
	p	0.001	
	df	5	

The mean fecundity differed significantly across sites (ANOVA, F = 4.591, df = 5, p = 0.001, Table 4.2). Fecundity estimates in Malindi Reserve (129,353 ± 85,148) and Watamu Park (113,968 ± 73,253) were significantly higher than estimates at the non-protected sites of Vipingo (95,928 ± 69,884) and Kanamai (70,418 ± 55,715) (Table

4.2). Further, partitioning of the variance in fecundity estimates using SNK post-hoc test indicated significant differences in fecundities between Vipingo and Malindi Reserve, Kanamai and all other sites except Vipingo. There was no significant difference in fecundity estimates between park and reserve sites except for Malindi Reserve and also between the non-protected sites of Kanamai and Vipingo (Table 4.2). Values of ‘a’ and ‘b’ parameters of the derived fecundity- standard length relationships varied across sites with higher values of ‘a’ occurring among fish in reserves (a = 528.85) and non-protected (a = 359.88) sites relative to those in park (a = 98.82) sites suggesting higher fecundity unit increase in size for fish in the fished sites (Figure 4.2). Also, the length-fecundity exponents (‘b’ parameter) for fish from the park sites were higher ($b \sim 3$) compared to those from reserve and non-protected sites ($b < 3$) indicating fish at park sites have an isometric length-fecundity relationships relative to other sites (Figure 4.2). However, a comparison of the length exponents (b) from sites by analysis of covariance (ANCOVA) indicated a non-significant interaction between length (covariate) and sampling sites (independent variables) suggesting that effect of length on fecundity is independent of sites, but this could be an artefact of small sample sizes from parks (Table 4.3).

The results of Multidimensional Scaling (MDS) analysis using fecundity data showed no distinct patterns of site similarities; however, the non-protected sites (Kanamai and Vipingo) clustered alongside Watamu Reserve and Malindi Park, while Malindi Reserve and Watamu Park were distinctly separated from the other sites in terms of fecundities (Figure 4.3).

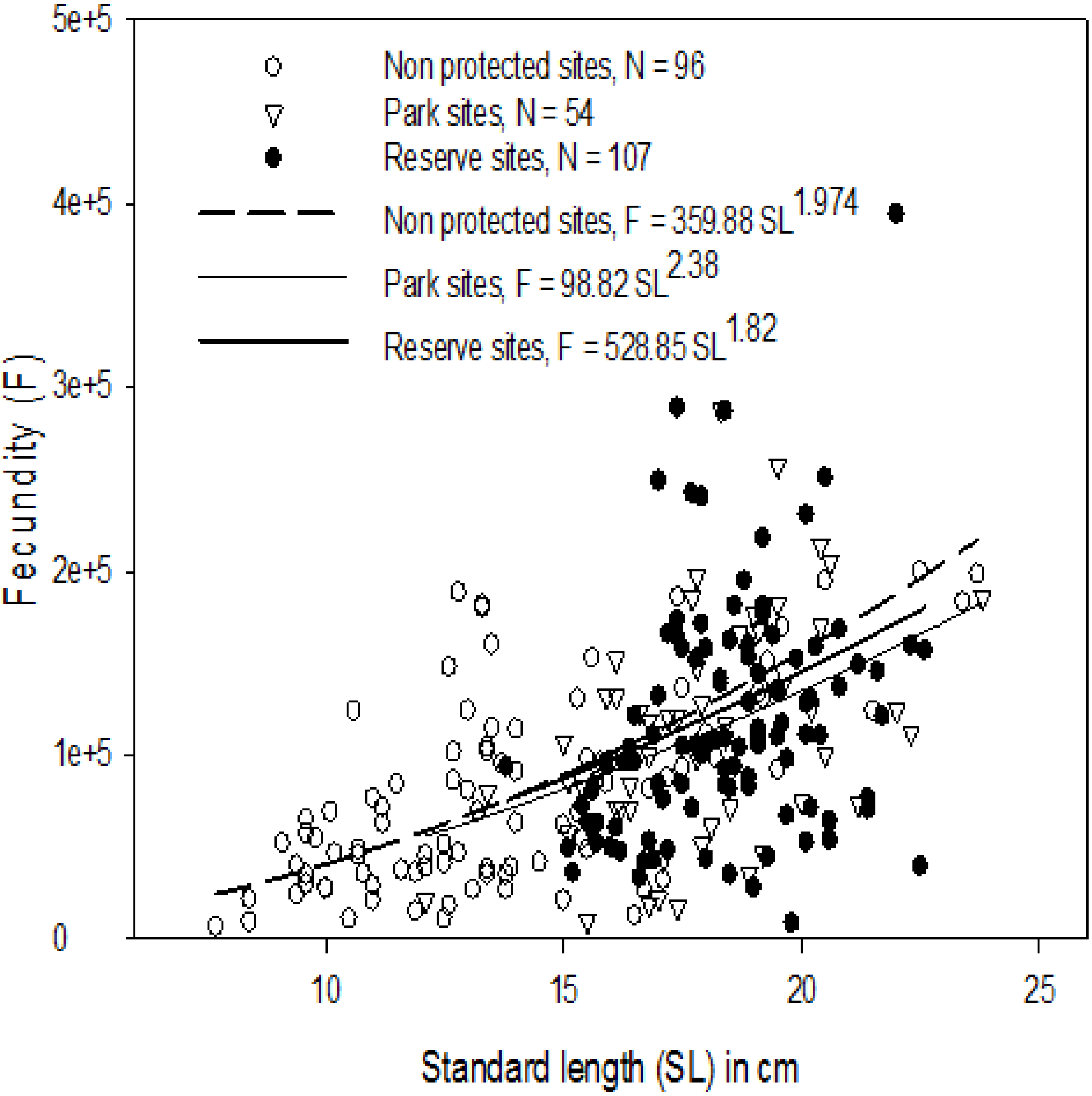

Figure 4.2: Relationships between fecundity (F) and standard length (SL) of *Leptoscarus vaigiensis* at reef sites of different protection levels in coastal Kenya. 'N' denotes number of ovaries examined at sites. 'a' indicates constant (regression intercept) whereas 'b' denotes length exponent.

Table 4.3: Analysis of covariance (ANCOVA) output for the comparison of the slopes of log fecundity and log total length relationships of *Leptoscarus vaigiensis* caught from different reefs in coastal Kenya. 'SL' denotes standard length.

Source of variation	**SS**	**df**	**MS**	**F**	***p***
Sites	0.235	5	0.047	0.641	0.669
SL	2.148	1	2.148	29.235	0.001
Sites*SL	0.214	5	0.043	0.582	0.714

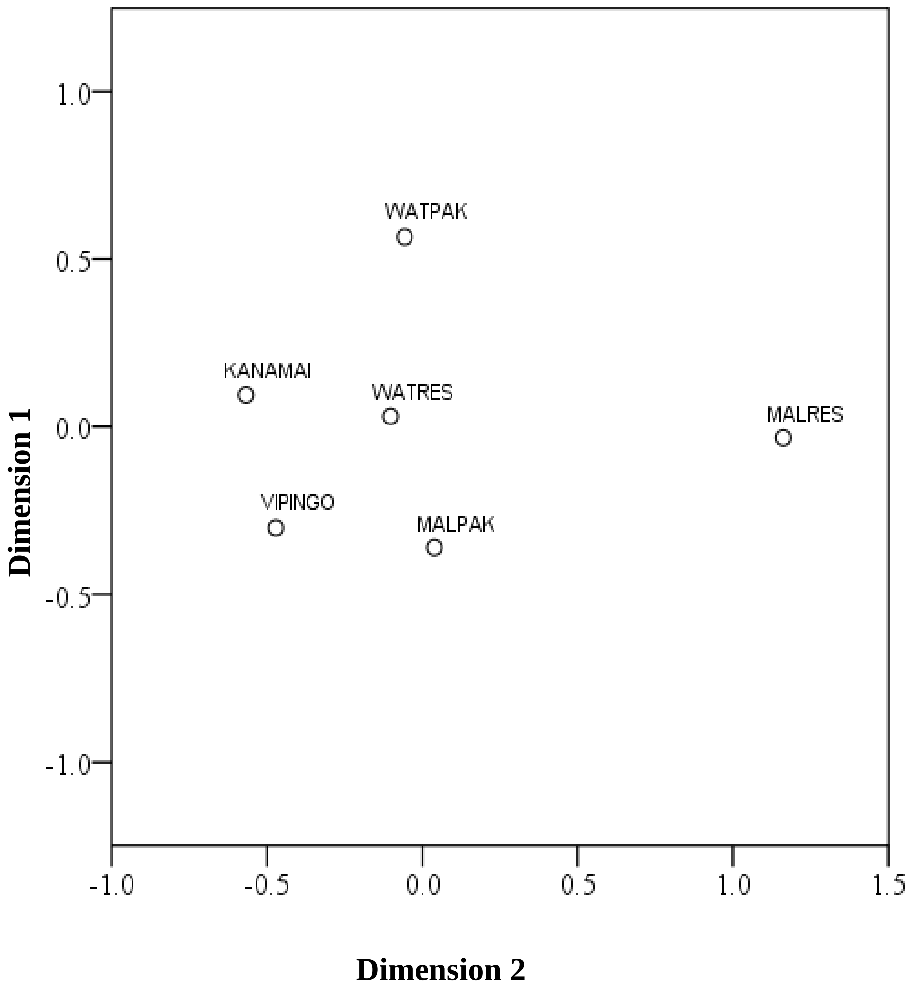

Figure 4.3: Multidimensional Scaling (MDS) ordination plot of fecundity of *Leptoscarus vaigiensis* at reef sites of different protection levels in coastal Kenya. Stress = 0.03875. MALPAK, MALRES, WATPAK and WATRES stand for Malindi Park, Malindi Reserve, Watamu Park and Watamu Reserve, respectively.

4.2.2 Spawning period

Results showed occurrence of mature gonads throughout the study period indicating continuous spawning of the species across sites (Figure 4.4). However, higher percentages of mature gonads (stages IV and V) occurred during the months of April and May in reserve sites, April and July in park sites, June and July in non-protected sites (Figure 4.4). Further, higher percentage of spent gonads (Maturity stage VI) occurred in July among park and reserve sites and in October in non-protected sites (Figure 4.4).

4.2.3 Egg diameters

Egg diameters ranged from 0.04-0.38 mm in Watamu Park to 0.06-0.46 mm in Malindi Park (Table 4.4). Higher mean (±SD) egg diameters (0.26 ± 0.12 mm) occurred in Malindi Park, whereas the smallest eggs (0.20 ± 0.08 mm) occurred in the non-protected Vipingo site (Table 4.4). Mean egg diameter comparison between sites using ANOVA indicated no significant difference in diameters across sites (F = 0.918; df = 5; p = 0.473, Table 4.4).

Size-frequency distribution of egg diameters from sites showed a major mode at 0.22 mm across fished sites and 0.20 mm among protected sites (Figure 4.5). Compared to other sites, the Park sites of Malindi and Watamu had higher percentage size-frequency (26%) at the respective modal diameters (Figure 4.5).

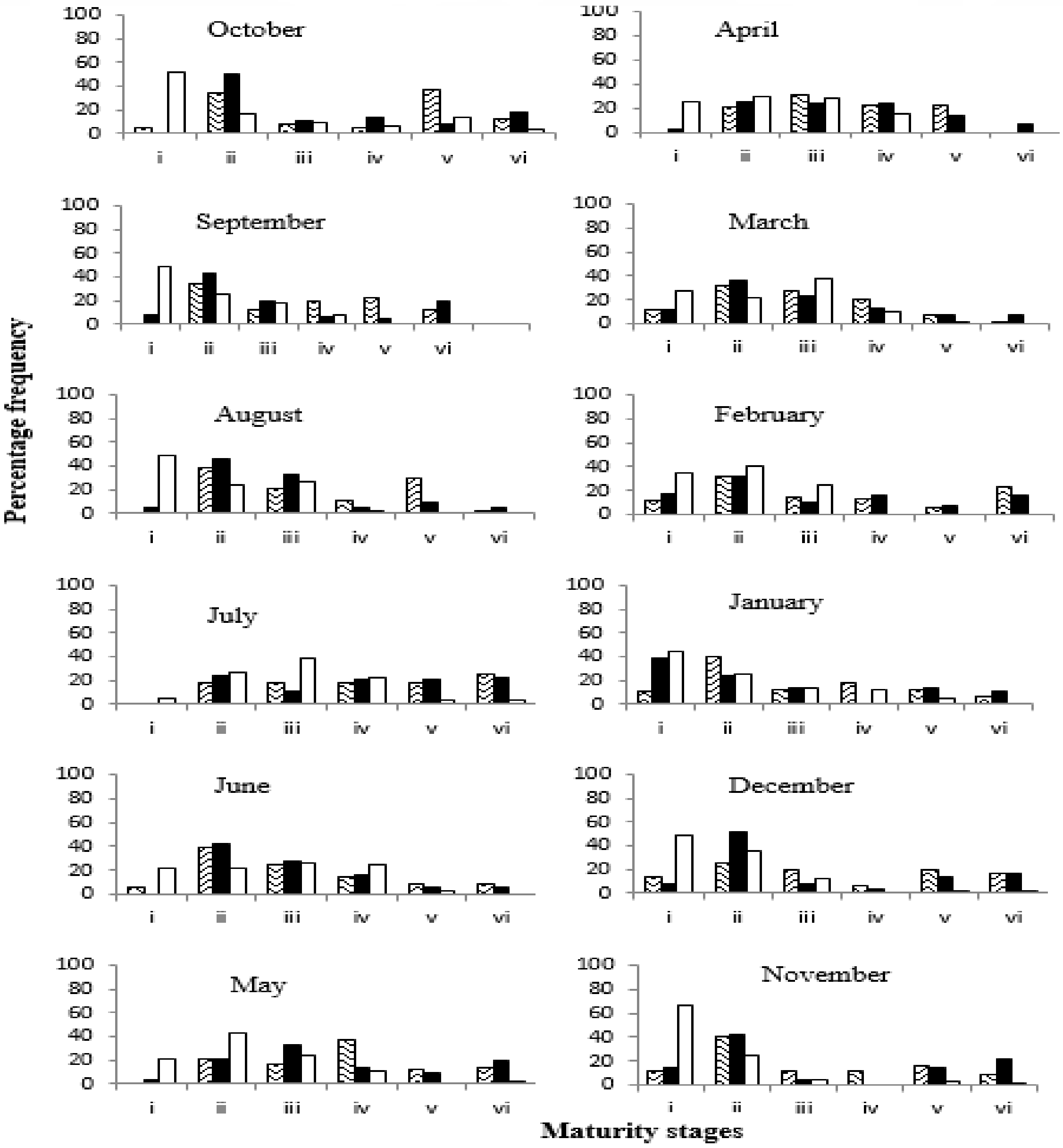

Figure 4.4: Monthly percentage occurrence frequency of the maturity stages of *Leptoscarus vaigiensis* gonads of both sexes across sites of different protection levels (■Parks,▨Reserves, ☐ non-protected) in coastal Kenya from May 2011-April 2013. i & ii = immature; iii = maturing; iv = mature; v = active; vi = spent.

Table 4.4: Egg diameters of active gonads (stage V) in *Leptoscarus vaigiensis* caught on different reefs in coastal Kenya. Numbers mean ± standard deviation (SD). N = number of eggs measured.

Site		**Mean size (mm)**	**Modal size (mm)**	**Size range (mm)**	**No. of eggs**
Kanamai		0.20 ± 0.09	0.22	0.06-0.34	5108
Vipingo		0.20 ± 0.08	0.22	0.08-0.32	2437
Malindi Marine Park		0.26 ± 0.12	0.20	0.06-0.46	8587
Malindi Marine Reserve		0.24 ± 0.12	0.22	0.04-0.44	31146
Watamu Marine Park		0.21 ±0.11	0.20	0.04-0.38	4695
Watamu Marine Reserve		0.22 ± 0.09	0.22	0.08-0.36	3406
ANOVA	F	0.918			
	df	5			
	p	0.473			

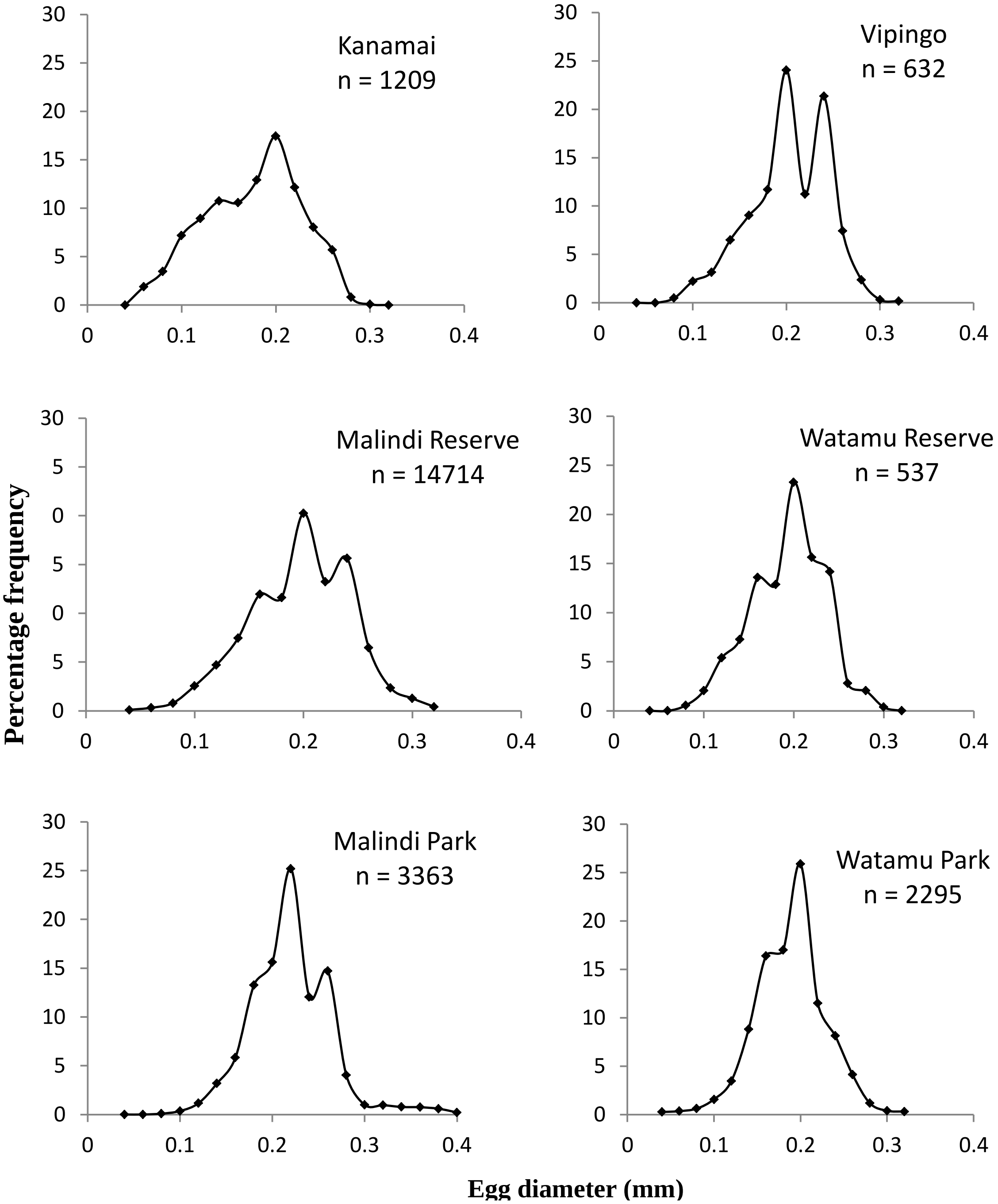

Figure 4.5: Size-frequency distribution of eggs in maturity stage (V) ovaries of *Leptoscarus vaigiensis* caught in different reef sites in coastal Kenya. 'N' denotes number of eggs measured.

4.2.4 Gonad mass variation

Fish in Malindi Park and its Reserve had heavier female gonads per unit total length than those in Watamu Park and its Reserve, whereas fish from Kanamai had heavier gonads than those from Vipingo for similar size (Figure 4.6). Overall, Malindi Reserve had heavier female gonads relative to size compared to other sites (Figure 4.6). For males, fish in Watamu Park and Reserve had heavier gonads than those in Malindi Park and Reserve at similar total lengths (Figure 4.7). Fish in Vipingo had heavier gonads than those from Kanamai site at similar lengths. Generally, Watamu Reserve had heavier gonads relative to other sites at similar lengths of fish (Figure 4.7). A MDS analysis on gonado-somatic indices (GSI, weight of gonads relative to body weight) of female *L. vaigiensis* indicates association of sites based on level of fishing (Figure 4.8a). The marine parks (Watamu and Malindi Parks) and the non-protected (Vipingo and Kanamai) sites formed distinct groupings based on GSI values, while Malindi Reserve associated more closely with park sites (Figure 4.8a). The Watamu Reserve although was separated distinctly from the other sites, was closer to Malindi Park (Figure 4.8a) based on female GSI values. MDS analysis on male GSI values did not indicate association of sites based on their protection levels (Figure 4.8b). All sites grouped together except Watamu Reserve which distinctly separated from the other sites based on male GSI values (Figure 4.8b).

4.2.5 Length at first maturity (L_{50})

A comparison of the estimates of length at first maturity (L_{50}) during the first year pooled for site categories indicated that the lowest L_{50} for female *L. vaigiensis* occurred at non-protected sites (mean 13.4 cm, range,11.8-14.8 cm, 95% CI), and the highest at park sites (mean 17.8 cm, range, 17.5-18.1 cm, 95% CI; Figure 4.9).

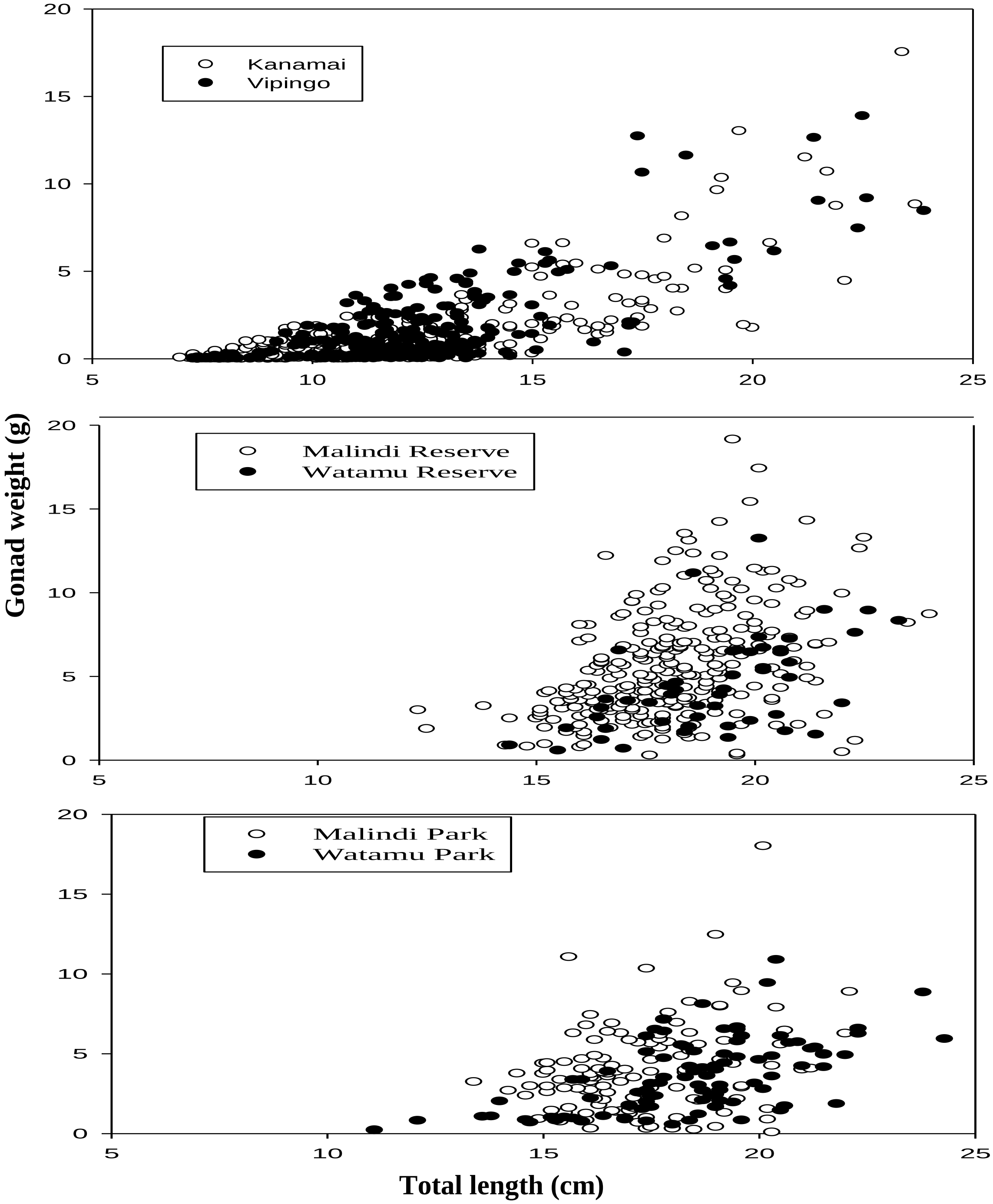

Figure 4.6: Variation of gonad weight with total length of female *Leptoscarus vaigiensis* across site of different protection levels in coastal Kenya.

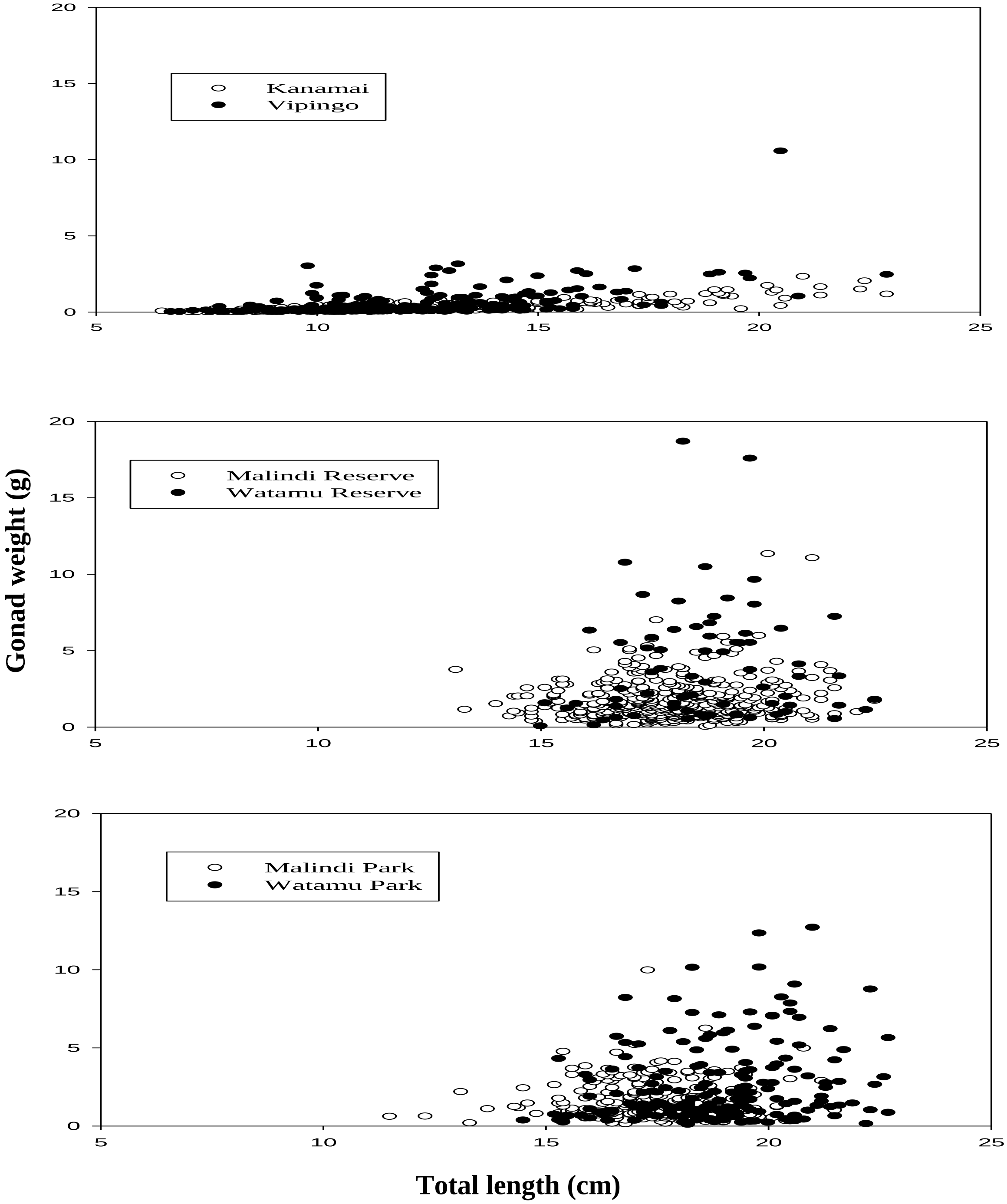

Figure 4.7: Variation of gonad weight with total length of male *Leptoscarus vaigiensis* across sites of different protection levels in coastal Kenya.

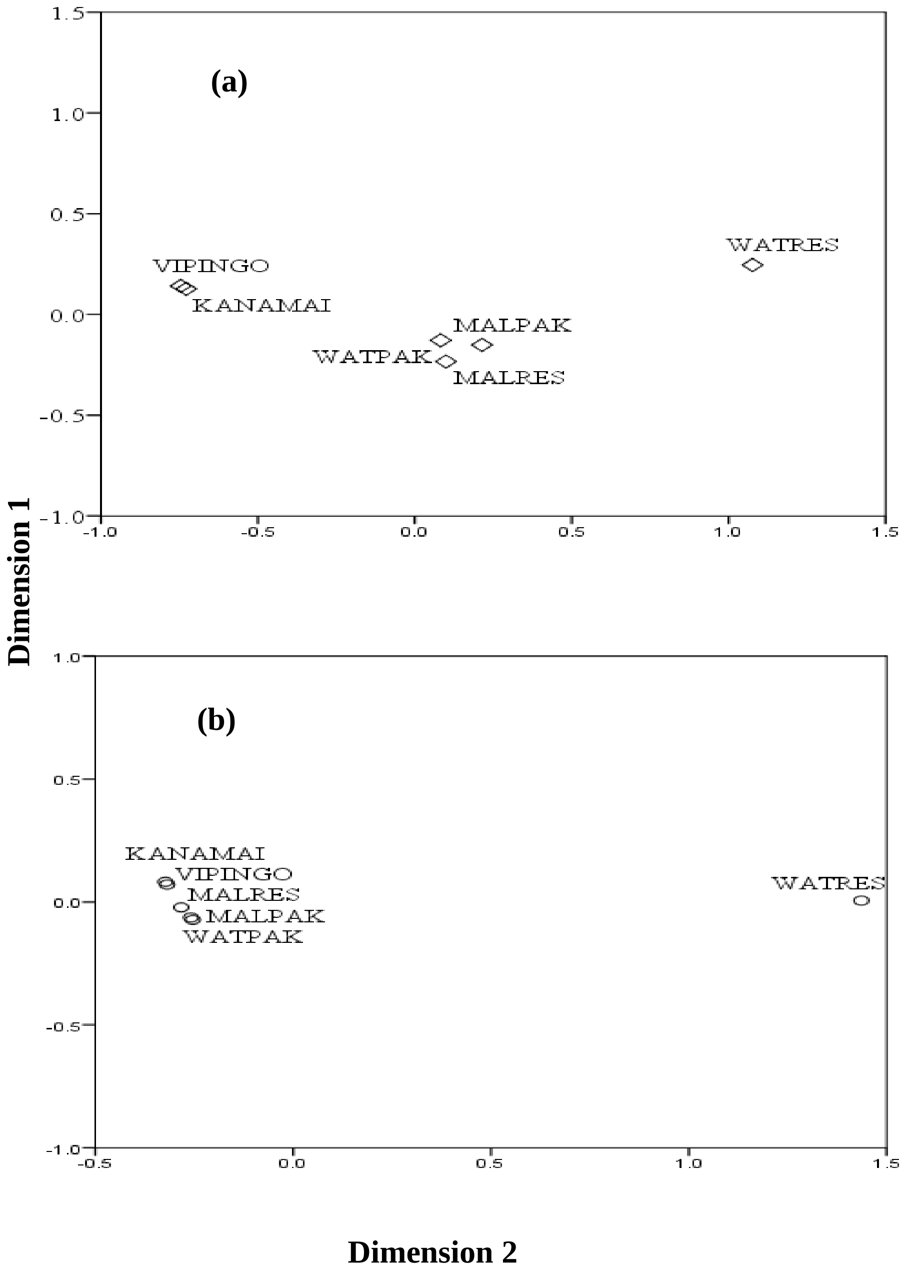

Figure 4.8: Multidimensional Scaling (MDS) ordination plot of gonado-somatic index of (a) female and (b) male *Leptoscarus vaigiensis* at reef sites of different protection levels in coastal Kenya. Stresses: a = 0.00241; b = 0.00105. MALPAK, MALRES, WATPAK and WATRES stand for Malindi Park, Malindi Reserve, Watamu Park and Watamu Reserve, respectively.

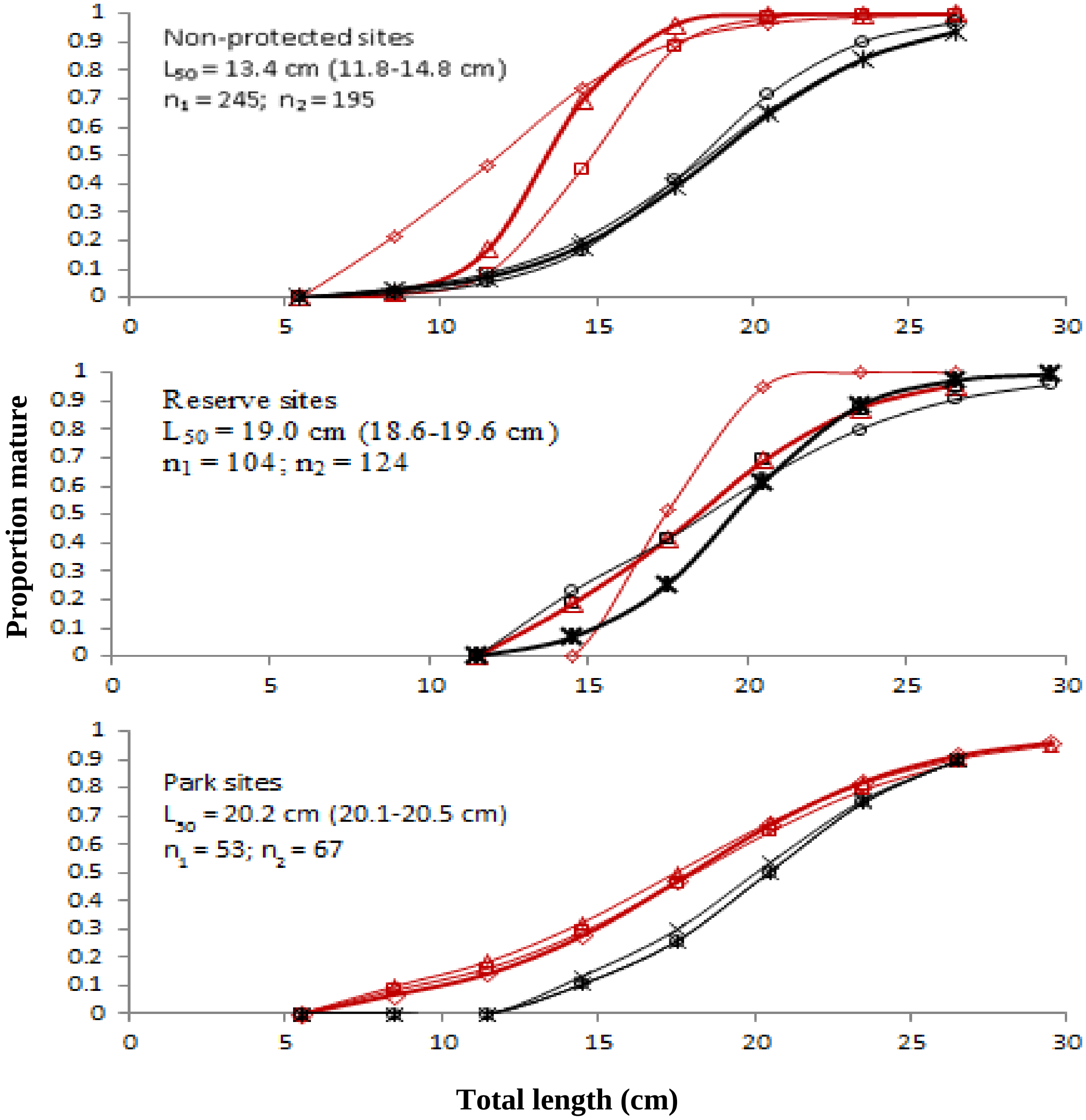

Figure 4.9: Length-at-first maturity ogives (bold dark red/black solid lines) of female *Leptoscarus vaigiensis* caught at sites with different levels of protection in coastal Kenya in the first (dark red lines) and second (black lines) years, respectively. Confidence intervals of the estimates are given in parentheses. The faint dotted/solid lines represent the 95% confidence intervals for lengths at first sexual maturity (L_{50}). n_1 and n_2 are sample size of mature female fish in first and second year of study, respectively.

The L_{50} of female *L. vaigiensis* in the reserve sites was 17.4 cm (range, 16.2-18.4 cm, 95% CI; Figure 4.9) during this period. During the second year, a similar trend of L_{50} for female *L. vaigiensis* was maintained across the sites but with increased L_{50} compared to the first year (Figure 4.9). The lowest L_{50} for female *L. vaigiensis* occurred at non-protected sites (mean 18-6 cm, range 18.3-18.8 cm, 95% CI) and slightly higher at the reserve sites (mean 19.0 cm, range, 18.6-19.6 cm, 95% CI) during the second year (Figure 4.9). The highest L_{50} of female *L. vaigiensis* occurred at park sites (mean 20.0 cm, range, 20.1-20.5 cm, 95% CI, Figure 4.9) during the second year.

4.3 Diet and niche breadth variations between reef sites in coastal Kenya

4.3.1 Spatial variation in diet composition

A total of 42 genera belonging to 21 families of benthic macroalgae and 1 family of seagrasses formed the diet of *Leptoscarus vaigiensis* during the NEM season (Table 4.5). During this season, the diet of the fish at sites consisted mostly of the seagrass, *Thalassodendron ciliatum* (33.3 to 91.3%), the macroalgae; *Enteromorpha* spp. (50 to 77.4%) and *Sargassum* spp. (33.3 to 58.0%) (Table 4.5). Eleven genera of algae were common in the diet across all sites during this season, whereas 16 constituted diet of fish from specific sites (Table 4.5). Fish from the fished sites of Malindi Reserve and Vipingo had the most number of algal genera (n = 10) in their diet, whereas fish from Malindi Park, Kanamai, and Watamu Reserve consumed fewer genera of the flora (n = 3, 2 and 1, respectively) indicating likely mixed effect of protection levels on diet composition (Table 4.5). During the SEM season (Table 4.6), diet of the fish consisted of relatively more genera (n = 48) of benthic macroalgae and seagrasses contained within slightly more families (n = 27) compared to the NEM season.

Table 4.5: Percentage frequency of occurrence of food items in the gut of *Leptoscarus vaigiensis* from reef sites in coastal Kenya during northeast moonson season. Dash (-) represents zero occurrence. 'N' denotes number of stomachs examined at sites.

Food group	**Malindi Reserve N = 131**	**Watamu Reserve N = 6**	**Watamu Park N = 27**	**Malindi Park N = 72**	**Kanamai N = 92**	**Vipingo N = 106**
A: MACROALGAE						
Anadyomenaceae						
Anadyomene spp.	-	-	-	-	-	0.9
Areschougiaceae						
Eucheuma spp.	-	-	-	-	-	0.9
Bachelotiaceae						
Bachelotia spp.	13.0	-	-	11.1	-	6.6
Boodleaceae						
Boodlea spp.	-	-	-	-	-	*1.9*
Champiaceae						
Champia spp.	*0.8*	-	-	-	-	-
Caulerpaceae						
Caulerpa spp.	*0.8*	-	*3.7*	-	*1.1*	*0.9*
Ceremiaceae						
Centroceras spp.	32.1	16.7	11.1	36.1	5.4	4.7
Ceramium spp.	32.1	16.7	14.8	25.0	55.4	37.7
Cladophoraceae						
Chaetomorpha spp.	6.9	16.7	7.4	5.6	6.5	10.4
Cladophora spp.	11.5	-	3.7	1.4	19.6	35.8
Rhizoclonium spp.	-	-	7.4	1.4	-	1.9

Table 4.5 continued

Food group	**Malindi Reserve N=131**	**Watamu Reserve N=6**	**Watamu Park N=27**	**Malindi Park N=72**	**Kanamai N=92**	**Vipingo N=106**
Corallinaceae						
Amphiroa spp.	0.8	-	-	-	-	-
Cheilosporum spp.	6.9	-	-	1.4	7.6	-
Haliptilon spp**.**	0.8	-	-	-	5.4	-
Jania spps.	35.9	16.7	18.5	22.2	26.1	15.1
Cystocloniaceae						
Hypnea spp.	-	-	-	1.4	-	-
Dasyaceae						
Dasya spp.	8.4	-	-	8.3	23.9	5.7
Heterosiphonia spp**.**	-	16.7	-	-	-	-
Dasycladaceae						
Bornetella spp.	-	-	-	-	-	0.9
Neomeris spp.	-	-	-	-	2.2	0.9
Delesseriadeceae						
Vanvoorstia spp.	-	-	-	1.4	-	-
Galaxauraceae						
Actinotrichia spp.	1.5	-	-	2.8	-	-
Galaxaura spp.	0.8	-	-	-	-	-
Rhodomelaceae						
Chondrophycus spp.	32.1	16.7	14.8	48.6	5.4	20.8
Amansia spp.	2.3	-	3.7	2.8	12.0	0.9
Dipterosiphonia spp.	-	-	-	-	2.2	-
Herposiphonia spp.	20.6	16.7	14.8	6.9	20.7	17.9
Laurencia spps.	1.5	-	-	1.4	1.1	-

Table 4.5 continued

Food group	**Malindi Reserve N=131**	**Watamu Reserve N=6**	**Watamu Park N=27**	**Malindi Park N=72**	**Kanamai N=92**	**Vipingo N=106**
Leveillea spp.	19.8	16.7	29.6	25.0	15.2	5.7
Lophosiphonia spp.	10.7	-	3.7	2.8	-	0.9
Polysiphonia spp.	2.3	-	-	2.8	3.3	0.9
Rutaceae						
Murrayella spp.	-	-	-	-	1.1	-
Sargassaceae						
Sargassum spp.	58.0	33.3	51.9	52.8	55.4	55.7
Solieraceae						
Solieria spp.	1.5	-	-	-	-	-
Scytosiphoniaceae						
Rosenvingea spp.	-	-	-	1.4	-	-
Spyridiaceae						
Spyridia spp.	3.8	-	-	1.4	1.1	2.8
Ulvaceae						
Enteromorpha spp.	55.0	50.0	55.6	61.1	72.8	77.4
Ulva spp.	35.1	33.3	18.5	23.6	32.6	34.9
Valoniaceae						
Valonia spp.	0.8	-	-	-	-	-
Valoniopsis spp.	-	-	-	-	-	0.9
B: SEAGRASSES						
Cymodoceaceae						
Cymodocea spp.	1.5	-	-	-	1.1	0.9
Thalassodendron spp.	77.9	33.3	59.3	68.1	91.3	88.7

Table 4.6: Percentage frequency of occurrence of food items in the gut of *Leptoscarus vaigiensis* from reef sites in coastal Kenya during southeast monsoon season. Dash (-) represents zero occurrence. 'N' denotes number of stomach examined at sites.

Food group	**Malindi Reserve N = 142**	**Watamu Reserve N = 17**	**Watamu Park N = 100**	**Malindi Park N = 125**	**Kanamai N = 96**	**Vipingo N = 64**
A: MACROALGAE						
Acinetosporaceae						
Hincksia spp.	-	-	1.0	-	-	-
Bachelotiaceae						
Bachelotia spp.	6.3	-	5.0	4.0	2.1	4.7
Bonnemaisoniales						
Asparagopsis spp.	0.7	-	-	-	-	-
Boodleaceae						
Boodlea spp.	0.7	-	-	-	1.0	1.6
Cladophoropsis spp.	-	-	1.0	-	-	3.1
Champiaceae						
Champia spp.	0.7					
Caulerpaceae						
Caulerpa spp.	9.9	17.6	11.0	11.2	16.7	6.3
Ceremiaceae						
Centroceras spp.	19.0	-	-	7.2	-	4.7
Ceramium spp.	40.8	41.2	42.0	22.4	44.8	48.4
Cladophoraceae						
Chaetomorpha spp.	4.2	-	5.0	2.4	1.0	1.6
Cladophora spp.	19.7	11.8	16.0	20.8	17.7	15.6
Corallinaceae						

Table 4.6 continued

Food group	**Malindi Reserve N = 142**	**Watamu Reserve N = 17**	**Watamu Park N = 100**	**Malindi Park N = 125**	**Kanamai N = 96**	**Vipingo N = 64**
Amphiroa spp.	-	-	1.0	-	-	-
Cheilosporum spp.	14.8	17.6	14.0	14.4	7.3	1.6
Haliptilon spp.	-	-	2.0	-	-	-
Jania spps.	66.2	64.7	26.0	14.4	17.7	25.0
Cystocloniaceae						
Hypnea spp.	-	-	-	1.4	-	-
Dasyaceae						
Dasya spp.	17.6	-	14.0	20.0	16.7	32.8
Dictyurus spp.	-	-	-	-	1.0	-
Heterosiphonia spp.	0.7	-	0.2	-	-	-
Dasycladaceae						
Bornetella spp.	-	-	1.0	-	2.1	-
Delesseriadeceae						
Vanvoorstia spp.	-	-	-	-	1.0	1.6
Galaxauraceae						
Galaxaura spp.	-	-	1.0	-	-	-
Gracilariaceae						
Gracilaria spp.	2.1	-	-	1.6	-	1.6
Lomentariaceae						
Gelidiopsis spp.	-	-	-	0.8	-	1.6
Rhodomelaceae						
Chondrophycus spp.	12.0	11.8	5.0	11.2	3.1	7.8
Amansia spp.	2.1	-	-	-	1.0	-
Dipterosiphonia spp.	0.7	-	-	0.8	-	-

Table 4.6 continued

Food group	**Malindi Reserve N = 142**	**Watamu Reserve N = 17**	**Watamu Park N = 100**	**Malindi Park N = 125**	**Kanamai N = 96**	**Vipingo N = 64**
Chondria spp.	-	5.9	1.0	-	-	1.6
Herposiphonia spp.	9.9	11.8	19.0	11.2	22.9	14.1
Laurencia spps.	3.5	5.9	1.0	0.8	-	6.3
Leveillea spp.	23.9	23.5	24.0	6.4	8.3	12.5
Lophosiphonia spp.	8.5	5.9	-	4.8	1.0	3.1
Polysiphonia spp.	4.2	5.9	5.0	1.6	1.0	6.3
Rhodymeniaceae						
Botryocladia spp.	0.7	-	-	-	-	-
Rutaceae						
Murrayella spp.	1.4	-	-	-	-	-
Sargassaceae						
Hormophysa spp.	0.7	-	-	2.4	-	-
Sargassum spp.	78.9	88.2	75.0	60.0	57.3	78.1
Siphonocladaceae						
Chamaedoris spp.	0.7	-	-	-	-	-
Sphacelariaceae						
Sphacelaria spp.	0.7	-	-	-	1.0	-
Spyridiaceae						
Spyridia spp.	2.1	-	-	2.4	8.3	6.3
Ulvaceae						
Enteromorpha spp.	83.8	88.2	70.0	74.4	84.4	87.5
Ulva spp.	34.5	35.3	31.0	29.6	22.9	40.6
Valoniaceae						
Valonia spp.	0.7	-	-	-	-	-

Table 4.6 continued

Food group	**Malindi Reserve N = 142**	**Watamu Reserve N = 17**	**Watamu Park N = 100**	**Malindi Park N = 125**	**Kanamai N = 96**	**Vipingo N = 64**
***Valoniopsis* spp.**	0.7	-	-	-	-	-
Wrangeliaceae						
Griffithsia spp.	-	5.9	1.0	-	-	-
Tiffaniella spp.	-	-	-	0.8	-	-
B: SEAGRASSES						
Cymodoceaceae						
Cymodocea spp.	0.7	5.9	1.0	-	-	-
Thalassodendron spp.	88.0	88.2	80.0	79.2	86.5	87.5

Similar to the NEM season, diet of the parrotfish at sites during SEM season consisted mostly of the seagrass, *Thalassodendron ciliatum* (79.2 to 88.2%), the macroalgae, *Enteromorpha* spp. (70.0 to 88.2%) and *Sargassum* spp. (57.3 to 88.2%,) but at higher proportions (Table 4.6). Thirteen genera of algae were common in the diet across all sites during this season, whereas 14 constituted diets of fish from specific sites (Table 4.6). As in the NEM season, fish from the fished Malindi Reserve had the highest number of algal genera (n = 7) in their diet, whereas those from Watamu Park, Kanamai and Malindi Park consumed a lower number of genera (n = 4, 2 and 1, respectively) (Table 4.6).

Diversity of food items (as measured by Shannon-Weiner Index, H) consumed by the fish differed significantly across sites during the NEM and SEM seasons (Table 4.7). During the NEM season, there was no significant difference in diversity of food items in the guts of fish from sites of same protection level except for the Reserves (Table 4.7). The diversity of diet for fish from Watamu (H= 0.87 ± 0.31) and Malindi (H = 0.87 ± 0.33) Parks were significantly higher than those from reserve and non-protected sites

(Table 4.7) indicating likely influence of seasonality and protection levels on diet diversity. Partitioning of the variance in the diversity estimates using SNK test indicated significant differences in diet composition between fish from Park sites and all other sites; Kanamai and other fished sites of Vipingo and Reserve sites during the NEM season (Table 4.7). There was no significant difference in composition of diet of fish from Park sites and also between those from Reserve sites and non-protected site of Vipingo (Table 4.7). Unlike in the NEM season, there were differences in the diet composition between sites of the same protection level during SEM except for the Reserve sites (Table 4.7).

Table 4.7: Diversity of the diet of *Leptoscarus vaigiensis* caught at sites of different protection levels in coastal Kenya during northeast (NEM) and southeast (SEM) monsoon seasons as estimated by the Shannon-Weiner Index (H). Number means ± standard deviation (SD). Means with different superscripts are significantly different as per SNK test.

Sites		H during NEM season	H during SEM season
Watamu Park		0.87 ± 0.31^{a}	0.94 ± 0.25^{e}
Malindi Park		0.87 ± 0.33^{a}	0.78 ± 0.27^{f}
Watamu Reserve		0.73 ± 0.20^{b}	0.99 ± 0.22^{d}
Malindi Reserve		0.79 ± 0.31^{c}	1.02 ± 0.22^{d}
Vipingo (non-protected)		0.74 ± 0.34^{b}	0.95 ± 0.23^{e}
Kanamai (non-protected)		0.65 ± 0.37^{b}	0.80 ± 0.28^{f}
ANOVA	F	3.62	14.24
	df	5	5
	p	0.001	0.001

Fish from Watamu Park had a diet composition (H = 0.94 ± 0.25) that was somewhat similar to those from Vipingo site (H = 0.95 ± 0.24), while those from Malindi Park had a composition (H =0.78 ± 0.27) that was similar to those from Kanamai (H= 0.80 ± 0.28, Table 4.7) indicating no influence of area protection on diet diversity during SEM season. Overall, diet composition from parks was similar to those from the non-protected sites during the SEM season.

The correspondence analysis (CA) was performed to analyse spatial variation of diet with sizes at different maturity stages (Figure 4.10). The results indicated the red algae, *Actinotrichia* spp. associated with diets of all size (maturity) categories of *L. vaigiensis*, while the filamentous green algae, *Cladophora* spp. associated exclusively with diets of immature size groups (Figure 4.10). The genera *Caulerpa* (green algae), *Cheilosporum* (red algae), *Laurencia* (red algae) and *Leveillea* (red algae) exclusively associated with diets of maturing fish, whereas the genera, *Centroceras* (red algae), *Haliptilon* (coralline red algae), *Bachelotia* (brown algae), *Amansia* (red algae) and *Hypnea* (red algae) exclusively associated with diets of mature size categories (Figure 4.10). The groups; *Thalassodendron ciliatum* (seagrass), *Enteromorpha* spp. (green algae), *Sargassum* spp. (brown algae), *Ulva* spp. (green algae) and *Jania* spp., (red algae) associated closely with both maturing and mature size groups than immature size groups (Figure 4.10) indicating variability of diet with maturity stages of the fish.

4.3.2 Diet composition and preferences between reef sites

Hierarchical cluster analysis categorized the food utilized by *L. vaigiensis* across sites into three major groupings (G1, G2 and G3) (Figure 4.11) with G2 breaking into 3 sub-groups, A, B and C.

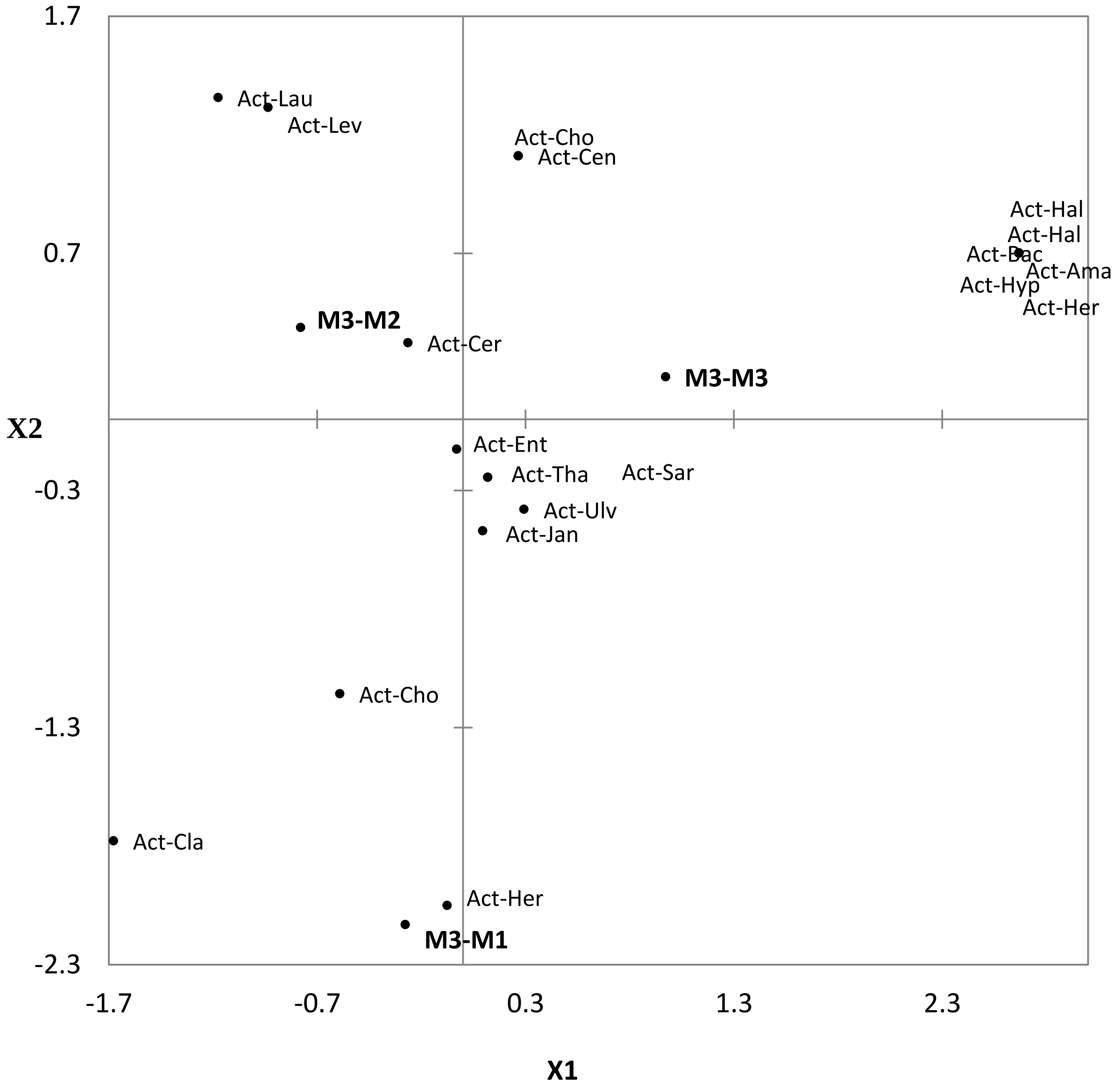

Figure 4.10: Correspondence Analysis (CA) of the association of food items with maturity categories of *Leptoscarus vaigiensis* in coastal Kenya. M1, M2 and M3 stand for immature, maturing and mature size groups, respectively. Names of algal genera are abbreviated to correspond with Table 4.5 and 4.6. Only food items with ≥ 0.1 % numerical abundance were used in the analysis. X1 and X2 denote dimensions 1 (food item types) and 2 (maturity categories, respectively.

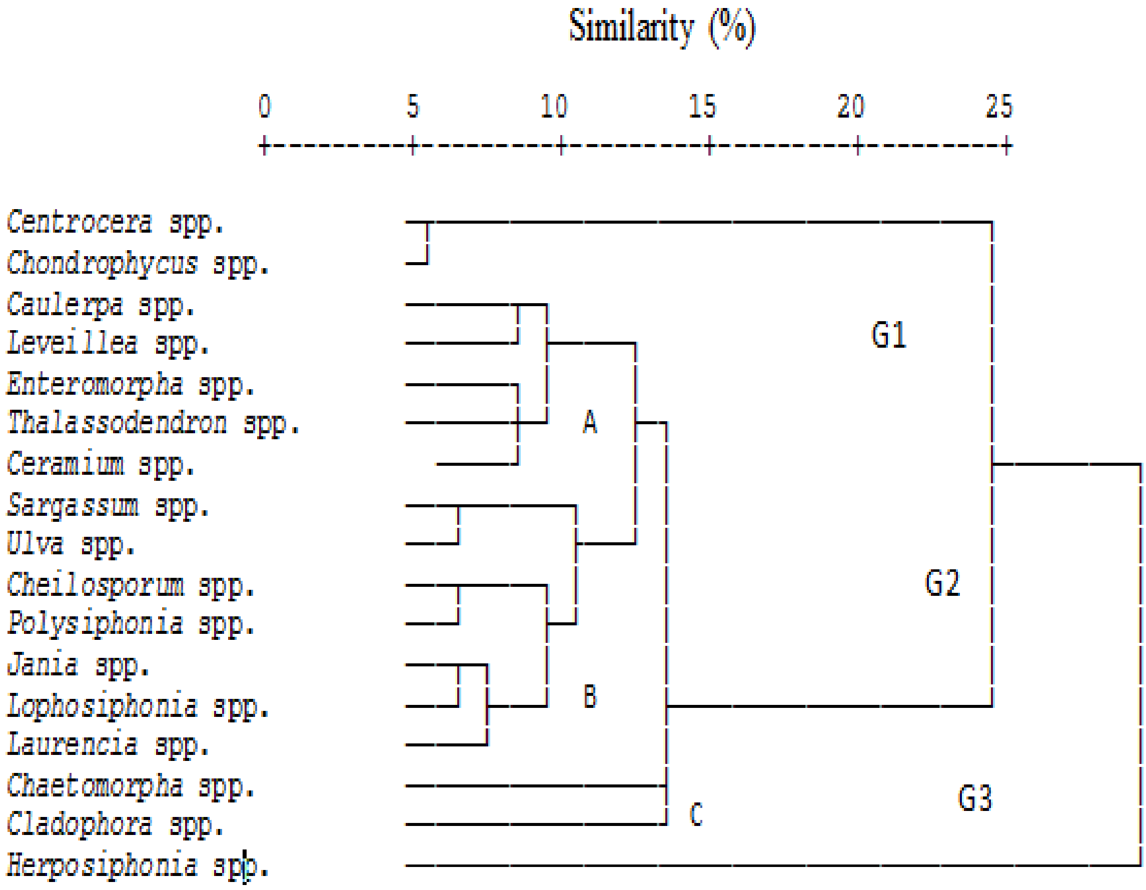

Figure 4.11: A dendrogram of Agglomerative Hierarchical Cluster analysis based on group's complete linkage clustering for the numerically dominant food items utilized by *Leptoscarus vaigiensis* across reef sites of varying fishing intensity in coastal Kenya.

The macroalgae, *Centroceras* and *Chondrophycus* prominently composed diet of fish from Malindi Park and its Reserve forming the distinct group G1 (Figure 4.11, Tables 4.5 and 4.6). The macroalgae *Caulerp*a and *Leveillea* distinctly formed the diet of fish from Watamu Park and its Reserve and clustered together with *Enteromorpha*, *Thalassodendron*, *Ceramium*, *Sargassum* and *Ulva* that were prominent in the diet of fish from the fished sites than the protected sites under sub-group A of the major grouping G2 (Figure 4.11, Table 4.5 and Table 4.6). The macroalgae *Cheilosporum* and *Polysiphonia* constituted diets of fish from both fished and protected sites (Table 4.5 and Table 4.6) and clustered together with *Jania*, *Lophosiphonia* and *Laurencia* that were major components in the diet of fish from reserve sites under sub-group B of the major grouping G2 (Figure 4.11, Tables 4.5 and 4.6). Food items under sub-group C (*Chaetomorpha* and *Cladophora*) composed the diet of fish from both fished and protected sites (Figure 4.11, Tables 4.5 and 4.6). The red algal genus, *Herposiphonia*, primarily formed the diet of fish from Kanamai (Tables 4.5 and 4.6) and clustered isolatedly from other food items under the major grouping G3 (Figure 4.11, Table 4.5 and Table 4.6).

The index of relative importance (IRI) of food items at the sites showed at the seagrass, *T. ciliatum*, the macroalgae, *Sargassum* spp. and *Enteromorpha* spp. to be the most important food items in the diet of *L. vaigiensis* from Parks (*T. ciliatum,* IRI = 1781-1842; *Sargassum*, IRI = 496-828; *Enteromorpha*, IRI = 346-420) and Reserves (*T. ciliatum*, IRI = 1030-1292; *Sargassum*, IRI = 642-946; *Enteromorpha*, IRI = 331-532) sites (Figure 4.12). The green macroalgae *Ulva* spp. was the least important food item in the diet of fish from these sites (Parks, IRI = 25-32; Reserves, IRI = 33-87; Figure 4.12).

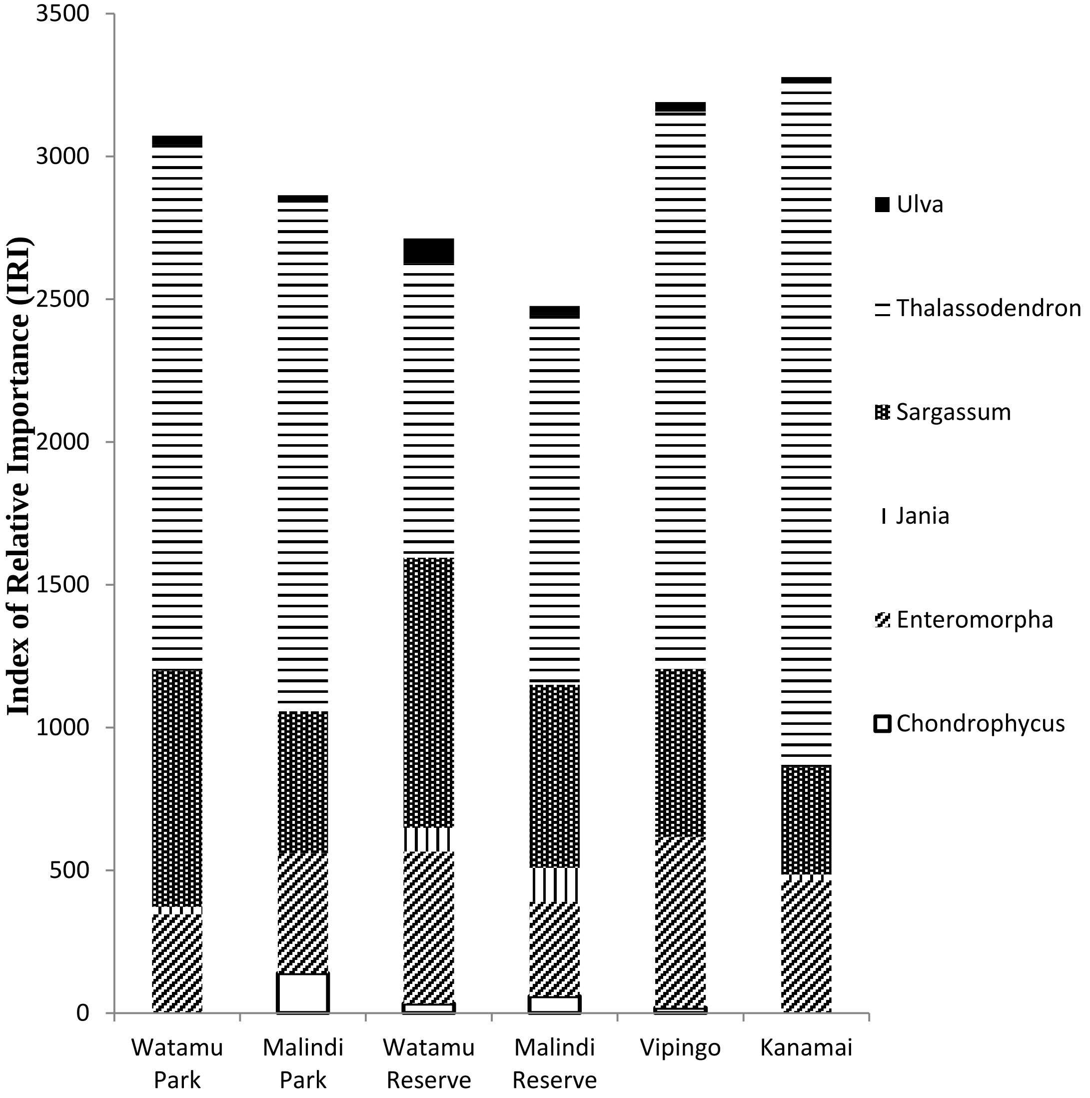

Figure 4.12: Index of Relative Importance (IRI) of main food items in the guts of *Leptoscarus vaigiensis* caught at reef sites of different protection levels in coastal Kenya.

Other food items that were of less importance but constituted diet of fish from specific Park and Reserve sites included the red algae; *Jania* spp. among fish from all the sites except those from Malindi Park, and C*hondrophycus* spp. among fish from Reserve sites (IRI = 33-59) and Malindi Park (IRI = 140) (Figure 4.12). Fish from non-protected areas of Vipingo and Kanamai had the seagrass, *T. ciliatum* (Vipingo, IRI= 1951; Kanamai, IRI = 2394), the seaweeds, *Enteromorpha* spp. (Vipingo, IRI = 598; Kanamai, IRI = 565) and *Sargassum* spp. (Vipingo, IRI = 588; Kanamai, IRI = 377) as the most important constituents of their diets (Figure 4.12). The least important constituent of diet for fish at non-protected sites included the green algae, *Ulva* spp. (IRI = 34) and the red algae, *Chondrophycus* spp. (IRI = 22) that comprised diet of fish from Vipingo (Figure 4.12).

4.3.3 Niche breadth and feeding intensity variation between reef sites

Niche breadths of the fishes from non-protected sites of Kanamai and Vipingo showed a general decline during the calm NEM months (January-March) following a rise during November-December months of the season (Figure 4.13). The niche breadths (mean ± SD) at these sites showed a general increase during the hydrodynamically rough SEM season (April-August) with a peak value during July (2.3 ± 0.6) for Kanamai and August (2.8 ± 0.26) for Vipingo followed by a subsequent decline in the August-November months of this season (Figure 4.13). The long-term average of the niche breath for the fish from non-protected sites of Vipingo (1.9 ± 0.7,) and Kanamai (1.7 ± 0.6) were comparable during the NEM season as was the case during the SEM season (Vipingo = 2.2 ± 0.5; Kanamai = 1.9 ± 0.5).

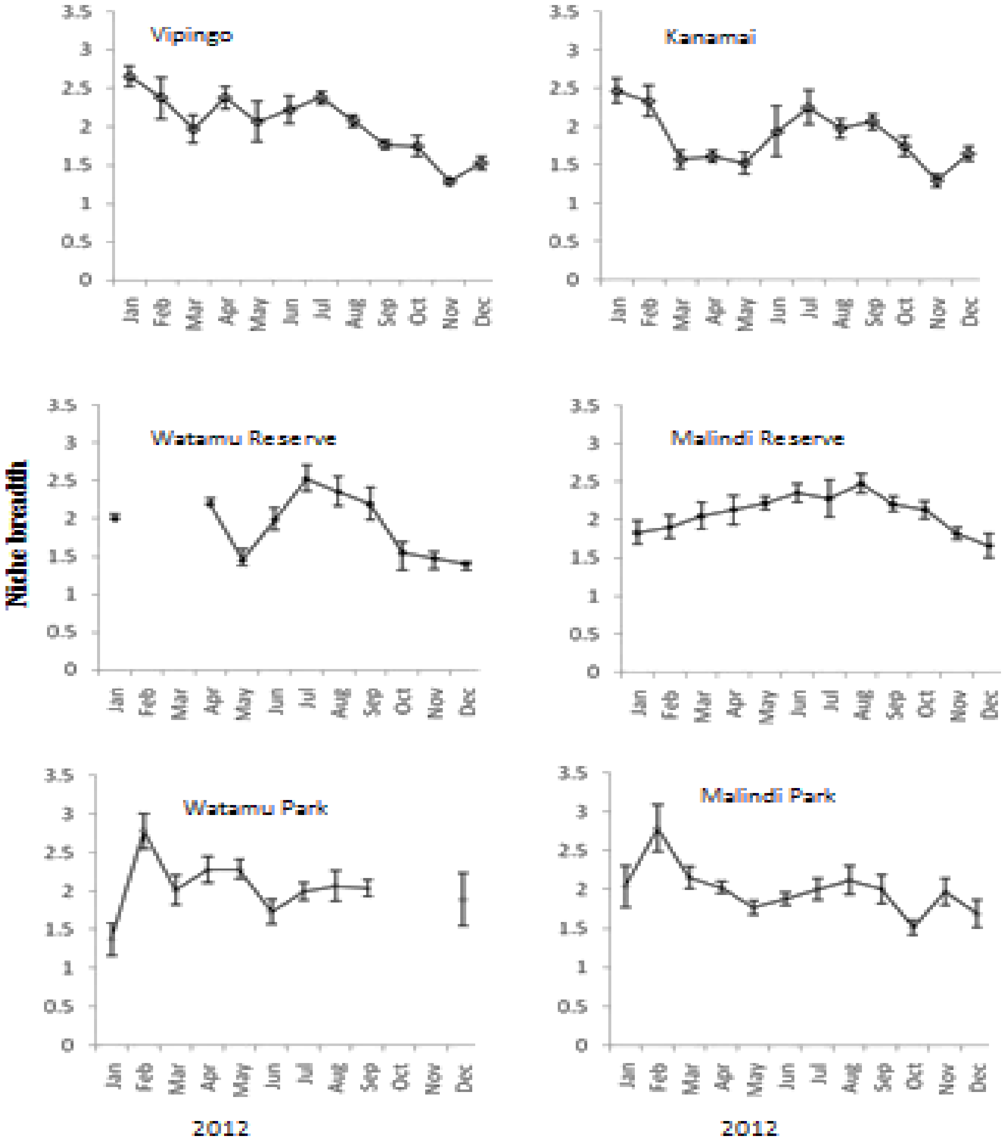

Figure 4.13: Temporal variation in niche breadth of marbled parrotfish, *Leptoscarus vaigiensis*, at reef sites of different protection levels in coastal Kenya during SEM (April-October) and NEM (November-March) seasons. Error bars represent standard deviation.

For the Reserve sites of Watamu and Malindi, niche breadth of the parrotfish showed a general increase in the SEM months of April to August (peaks in July and August for

Watamu and Malindi Reserves, respectively, Figure 4.13), followed by a decline in the NEM months of November-December (Figure 4.13), thereby showing a similar pattern as the non-protected sites (Kanamai and Vipingo). The long-term average of the niche breath (mean ± SE) for the fish from Watamu Reserve (1.6 ± 0.3) was comparable to that of Malindi Reserve (1.8 ± 0.6) during the NEM season as was the case during the SEM season (Watamu Reserve = 2.2 ± 0.5; Malindi Reserve = 2.3 ± 0.5). Unlike the reserve and non-protected sites, *L. vaigiensis* from park sites of Watamu and Malindi showed a general increase in niche breadths during the calm NEM months (January-February) following a decrease during November-December months of the season (Figure 4.13). Temporal patterns of niche breadth variation were therefore seasonally different for the park sites when compared to the non-protected sites and the moderately fished reserve sites.

Overall, mean niche breadths (mean ± SD) of the parrotfish were higher among the Park sites (Watamu Park = 2.02 ± 0.66; Malindi Park = 2.08 ± 0.72) relative to fished sites (1.6-1.9 ± 0.34.0.74) during NEM season, suggesting influence of protection levels on diversity of fish diet (Figure 4.14a). During SEM season, niche breadth values in the Reserve sites of Watamu (2.23 ± 0.54) and Malindi (2.26 ± 0.53) were higher and comparable to those of non-protected site of Vipingo (2.21 ± 0.54) and Watamu Park (2.11 ± 0.53, Figure 4.14b). However, fish from Kanamai (a non-protected site) and Malindi Park had niche breadths values that were lowest (Kanamai = 1.86 ± 0.48; Malindi Park = 1.84 ± 0.82) among the sites, indicating mixed effect of protection levels on niche breadths values during SEM season (Figure 4.14b).

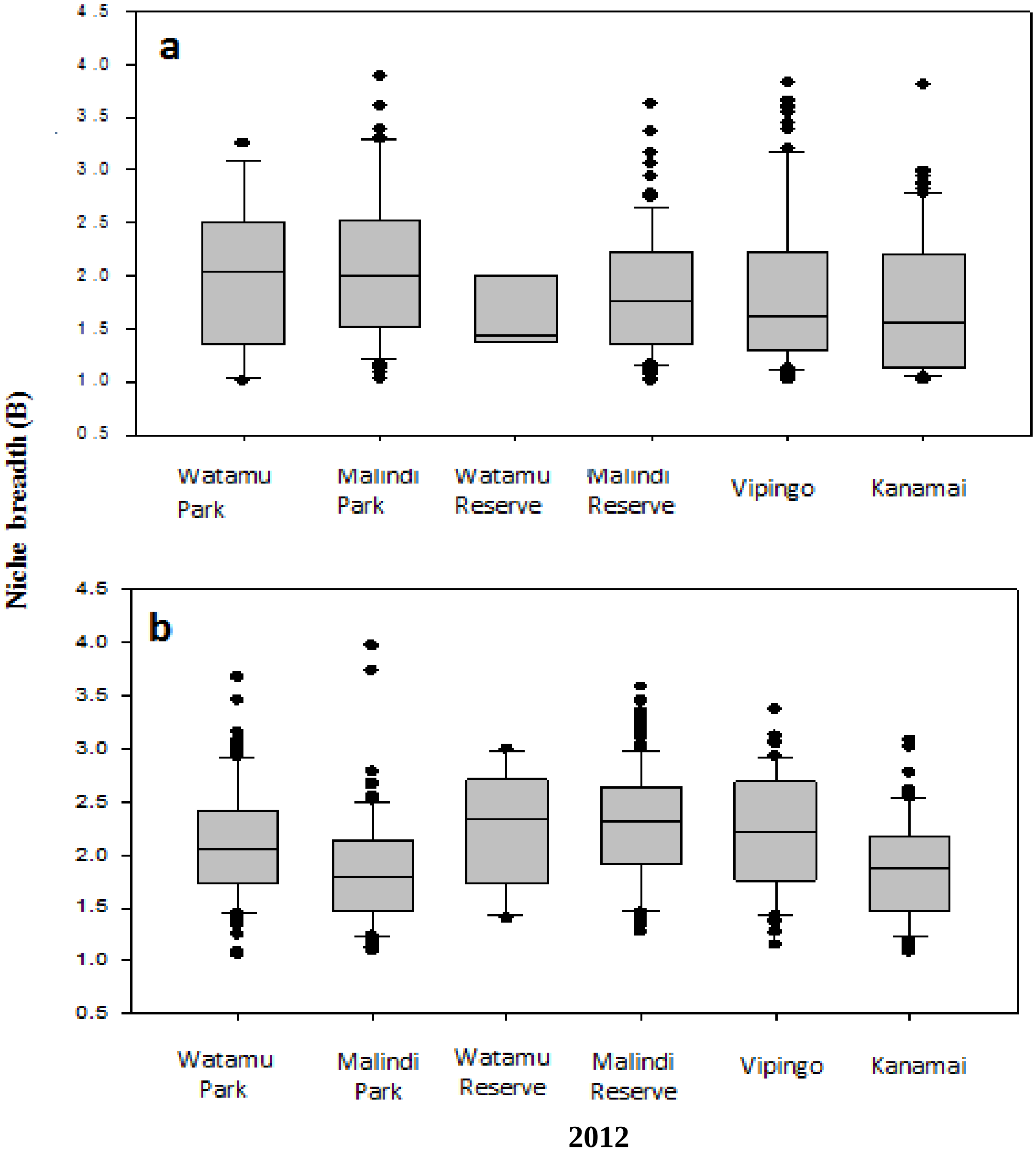

Figure 4.14: Boxplots of seasonal variation (a = northeast monsoon season, b = southeast monsoon season) in niche breadth of *Leptoscarus vaigiensis* caught from reef sites of different protection levels in coastal Kenya in 2012. Error bars represent standard deviation.

Results of two-way ANOVA indicated that both site and season as well as their interaction significantly influenced niche breadths of the parrotfish (sites, F = 5.390, $p < 0.001$; seasons, F = 12.455, $p < 0.001$; sites x season, F = 6.906, $p < 0.001$, Table 4.8).

The relationship between feeding intensity and niche breadth of fishes at the different reef sites showed site specific patterns (Figure 4.15). Fish from the marine park sites had a pattern of variation of niche breadth with feeding intensity that appears to be inverse of each other (Figure 4.15a). Fish from Malindi Park had a positive parabolic relationship between niche breadth and feeding intensity with lowest breadth at a feeding intensity of about 1.8. Fish from Watamu Marine Park had a somewhat inverse relationship (negative parabola) between niche breadth and feeding intensity. The fish from Watamu Park had higher niche breadths than those from Malindi Park at feeding intensities < 1.7 and > 2.1 (Figure 4.15a). The marbled Parrotfish at Watamu Marine Reserve showed a somewhat inverse pattern of variation of feeding intensity with niche breadth, while those at Malindi Reserve had a positive relationship (Figure 4.15b). The pattern of variation at the non-protected sites showed fishes at Kanamai reef to have higher niche breadths than those in Vipingo at a feeding intensity range of 1.35 to 2.25 beyond which the fishes at Kanamai are predicted to have higher niche breadths (Figure 4.15c).

4.4 Variation of growth and mortality parameters between sites

4.4.1 Growth parameter (L_∞ and K) variations

Skewness index (Sk) of the length-frequencies of fish from the sites showed distinct difference in size distribution of fish based on protection levels (Figure 4.16).

Table 4.8: Two-way analysis of variance (ANOVA) results on the influence of sites, season and their interaction on niche breadth of *Leptoscarus vaigiensis* at reef sites of different protection levels in coastal Kenya.

Source of variation	**DF**	**SS**	**MS**	**F**	***p***
Sites	5	0.190	0.038	5.390	0.001
Season	1	0.088	0.088	12.455	0.001
Sites*season	5	0.243	0.049	6.906	0.001

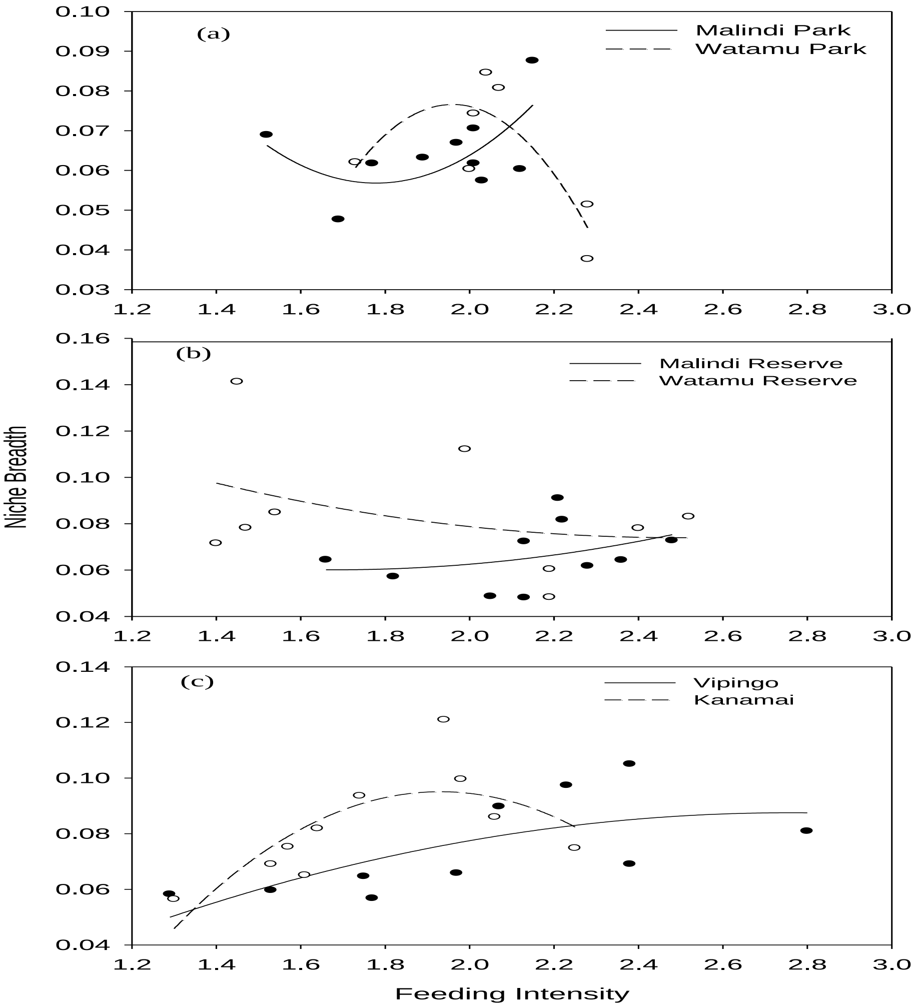

Figure 4.15: Second order polynomial regression of niche breath on feeding intensity of marbled parrotfish, *Leptoscarus vaigiensis*, from reefs of different protection levels in coastal Kenya during 2012.

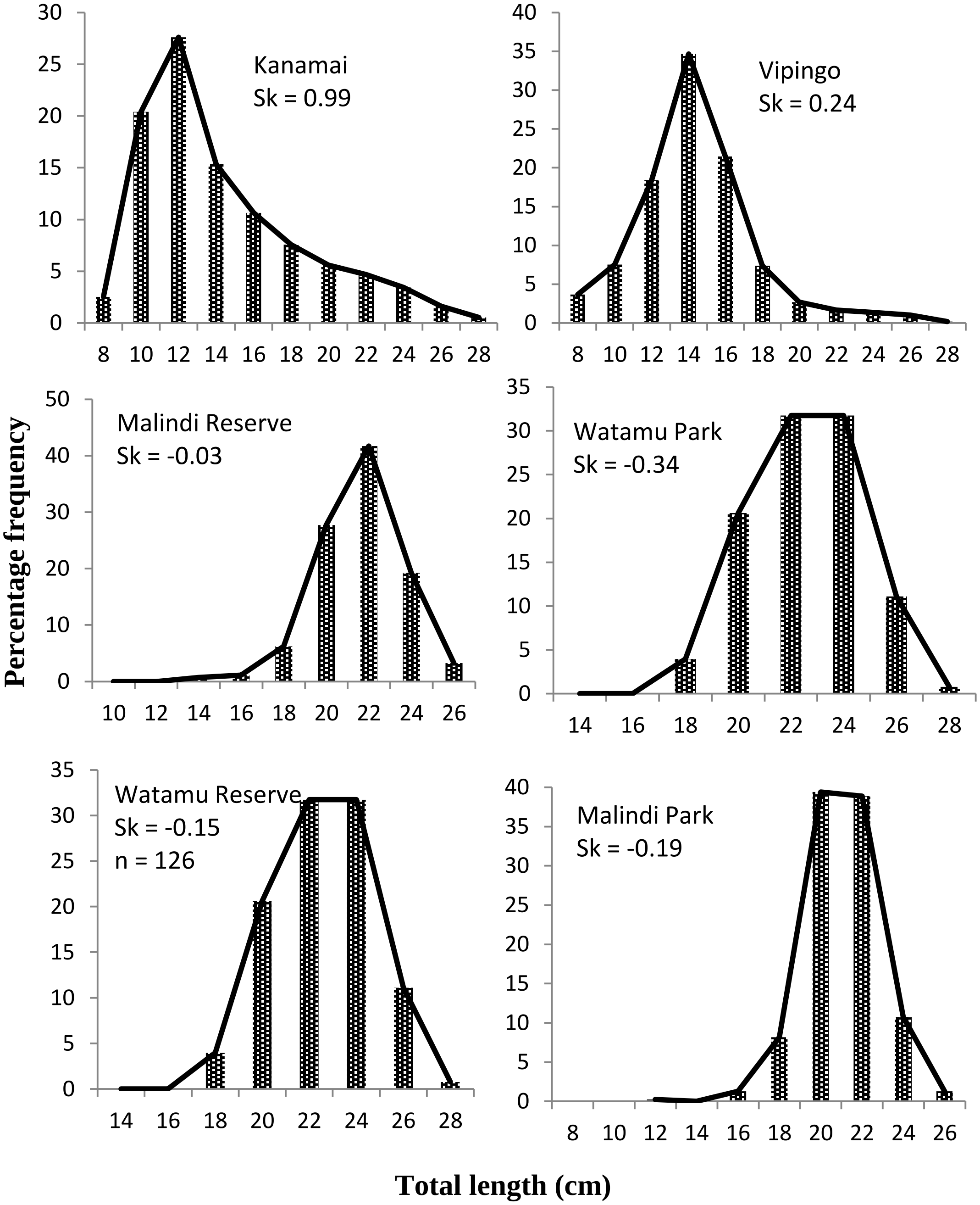

Figure 4.16: Length-frequency distribution of *Leptoscarus vaigiencies* at reefs of different protection levels in coastal Kenya. 'Sk' denotes skewness index and 'n' number of fish measured.

Fish from non-protected sites of Vipingo and Kanamai had positively skewed length frequencies (Sk = 0.24 and 0.99 for Vipingo and Kanamai, respectively) whereas those from Watamu Reserve and Malindi Reserve had length frequencies that were marginally skewed negatively (Sk = -0.15 and -0.03 for Watamu Reserve and Malindi Reserve, respectively) (Figure 4.16). Fish from protected sites of Malindi and Watamu Parks had length frequencies that were of comparatively higher negative skewness (Sk = - 0.19 and - 0.34 for Malindi Park and Watamu Park, respectively) (Figure 4.16) suggesting influence of protection on size structure of fish at sites.

The analysis and outputs from the FiSAT II program obtained for sites based on length frequency distributions are shown in Figures 4.17, 4.18 and 4.19, while the growth estimates are shown in Table 4.9. Although the L∞ estimates obtained through Powell-Wetherall Plot and ELEFAN I were comparable within sites, the ELEFAN I estimates were marginally higher for all the sites except the Malindi Reserve (Table 4.9). Higher L∞ estimate (~ 31 cm) was obtained for Malindi Reserve, while the lowest (26-27 cm) was obtained for Malindi Park. Fish from the two marine parks had equal and lowest growth rates, K yr^{-1} (Malindi Park = 0.46; Watamu Park = 0.46) amongst the sites, while the fish from non-protected sites and Malindi Reserve had the highest growth rates (Vipingo = 1.80 yr^{-1}; Kanamai = 1.65 yr^{-1}; Malindi Reserve = 1.95 yr^{-1}) with those from Watamu Reserve having an intermediate growth of 0.76 yr^{-1} (Table 4.9). Estimates of Phi-Prime (Φ) were comparable between the sites of similar protection level (Table 4.9) suggesting less variability of K and L∞ describing growth curves of the species between sites of similar protection status.

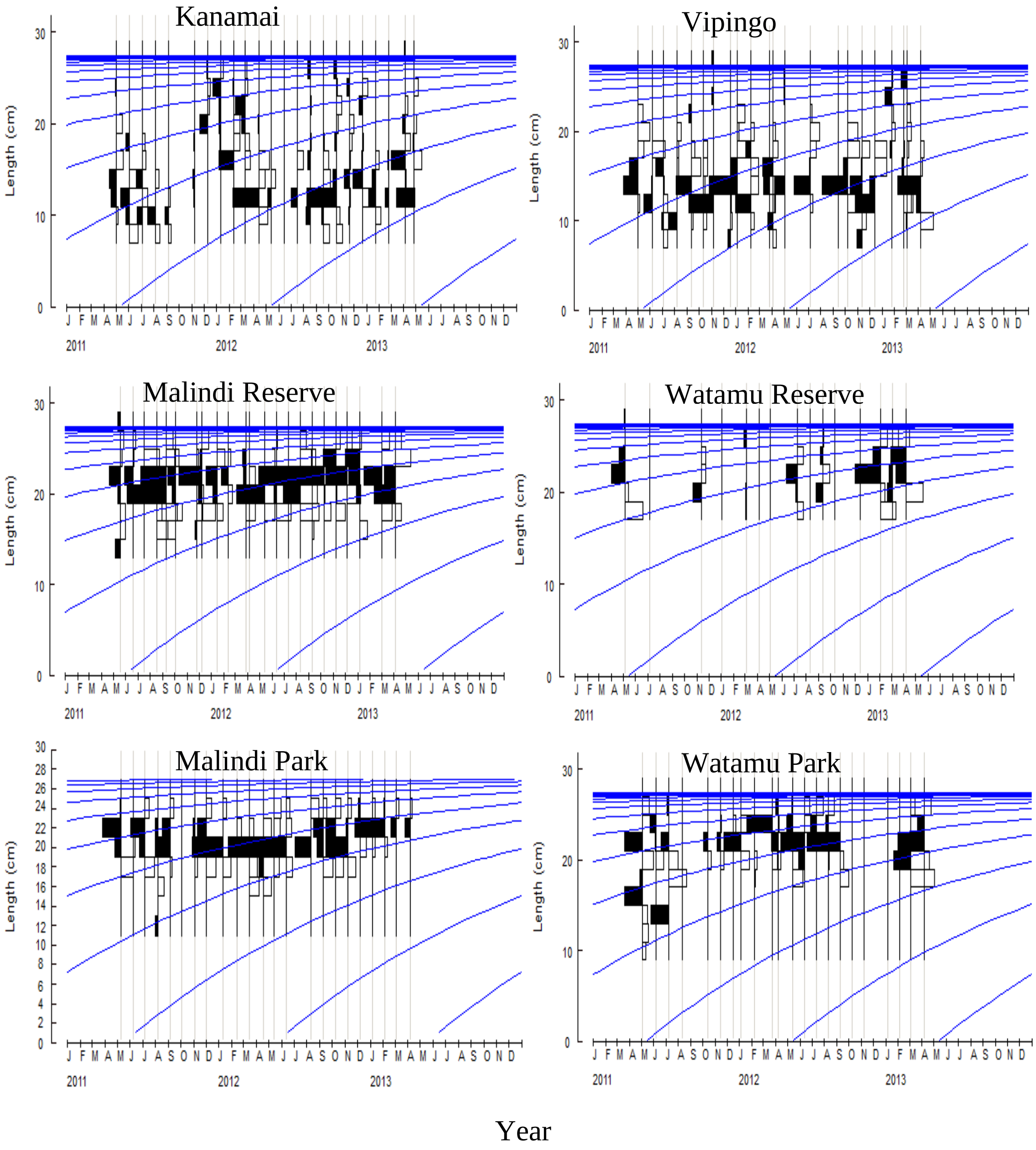

Figure 4.17: von Bertalanffy growth curves (continuous blue lines) of cohorts superimposed over re-structured length frequency data of *Leptoscarus vaigiensis* caught at reef sites of different protection levels in coastal Kenya.Peaks (black) are positive points and troughs (white) are negative points.

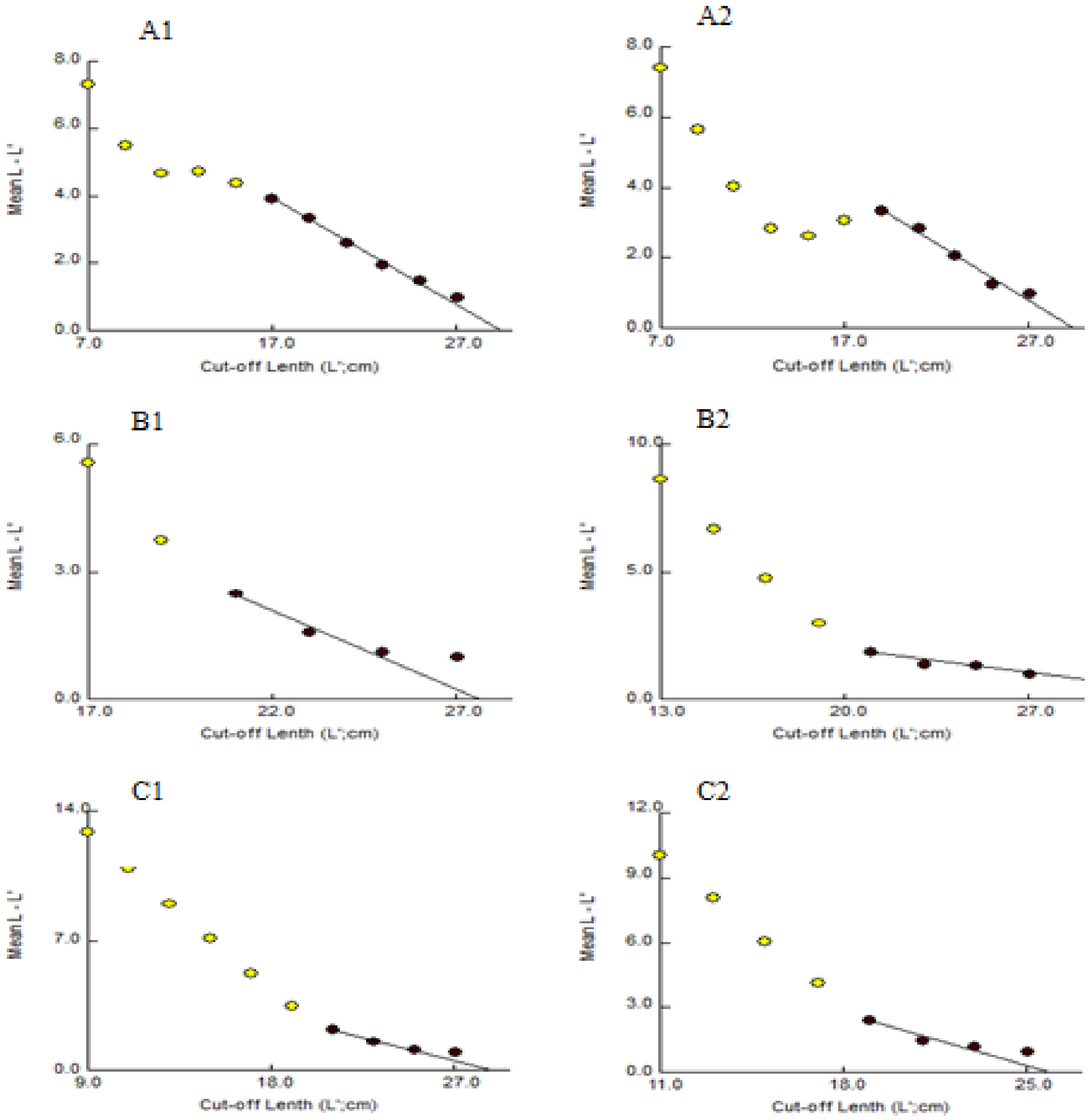

Figure 4.18: Powell-Wetherall plot for estimation of asymptomatic length ($L\infty$) of *Leptoscarus vaigiensis* caught at reef sites of different protection levels in coastal Kenya. Black dots on the right side were used for regression analysis. A1 = Kanamai, A2 = Vipingo, B1 = Watamu Reserve, B2 = Malindi Reserve, C1 = Watamu Park, C2 = Malindi Park.

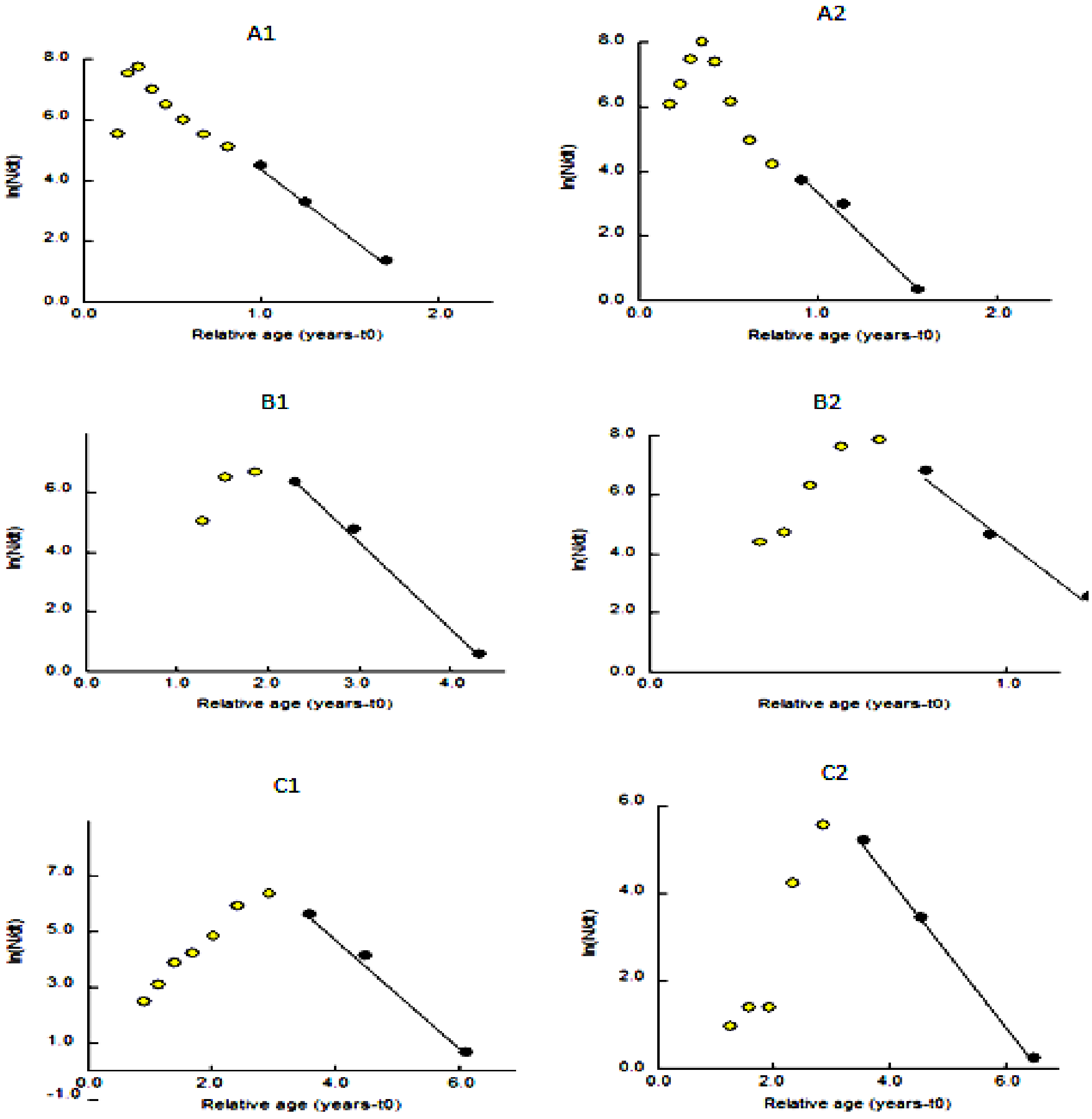

Figure 4.19: Linearized length-converted curve used to estimate instantaneous annual total mortality rate (Z) of *Leptoscarus vaigiensis* from reef sites in coastal Kenya. N is the number of fish in length class i and dt is time needed for fish to grow through the length class. Black circles were used in the regression, yellow circles were not because fish are not fully recruited or are close to L_∞. A1 = Kanamai, A2 = Vipingo, B1 = Watamu Reserve, B2 = Malindi Reserve, C1 = Watamu Park, C2 = Malindi Park.

Table 4.9: The von Bertalanffy growth parameters (asymptotic length, L_∞, cm; instantaneous growth rate, K/yr; age at which length equals zero, t_0), maximum length, Lmax (cm), goodness of fit index (Rn), growth performance index (Φ') of *Leptoscarus vaigiensis* from reefs of different protection levels in coastal Kenya. A dash (-) denotes lack of data.

Site	**Powell-Wetherall plot L_∞ (cm)**	**ELEFAN L_∞ (cm)**	**Lmax (cm)**	**K**	**Rn**	**Φ'**	**t_o**
A: This study							
Malindi Park	25.9	27.4	25.8	0.46	0.14	2.54	-0.44
Watamu Park	28.8	29.8	28.5	0.46	0.24	2.61	-0.45
Malindi Reserve	31.6	30.8	29.0	1.95	0.23	3.27	-1.10
Watamu Reserve	27.6	29.1	27.7	0.76	0.17	2.81	-0.67
Vipingo	29.4	29.8	27.1	1.80	0.13	3.20	-1.06
Kanamai	29.4	29.8	27.8	1.65	0.14	3.17	-1.02
B: Other studies							
Dar-es-Salaam, Tanzania, [a]	-	33.7	35	2.30	-	3.42	-
South coast, Kenya[b]	-	28.9	35	1.50	-	3.10	-
South coast, Kenya[c]	-	34.1	-	1.31	-	3.18	-

[a] Benno (1992); [b] Mwatha (1997); [c]Otieno (2002)

Fewer studies were found with Φ estimates for the species but available values are comparable to the estimates for the non-protected sites in this study ($\Phi \sim 3$, Table 4.9). There was a significant relationship between asymptotic sizes ($L\infty$) of the fish and the growth rates (K) ($L\infty = 2.24K + 26.14$; $r^2 = 0.66$, $p<0.05$).

Comparison of the growth parameters (K and $L\infty$) and hence growth curves or patterns among sites using bootstrapping technique indicated two distinct overlapping groupings of confidence regions between sites (Figure 4.20). One grouping comprised the overlapped confidence regions of the Marine Parks, while the other distinct group comprised the overlapped confidence regions of the non-protected sites of Kanamai and Vipingo as well as that of Malindi Reserve (Figure 4.20). The confidence region for the growth parameters of fish at the partially protected site of Watamu Reserve did not overlap with any of the sites but appeared closer to the confidence regions of the parks (Figure 4.20). Overlapping confidence regions around the growth parameter estimates at sites is taken to indicate similarity of the growth patterns of fish between sites. Hence, sites with overlaps indicate similarity in growth patterns of the marbled parrotfish.

4.4.2 Variation in mortality

The total mortality ($Z\ yr^{-1}$) estimates for *L. vaigiensis* from this study were lower for marine parks (~2) and higher for reserve (3-9) and non-protected sites (4.5) (Table 4.10). The natural mortality ($M\ yr^{-1}$) estimates although different between reserve sites, were comparable among park (~ 1) and non-protected (~2) sites (Table 4.10). Higher fishing mortality ($F\ yr^{-1}$) estimate (6.45) was derived for the partially protected Malindi Reserve, while a lower value (1.39) was obtained for the Watamu Reserve (Table 4.10). Moderate estimates of fishing mortality were obtained for the non-protected sites of Kanamai (1.95) and Vipingo (2.72) (Table 4.10).

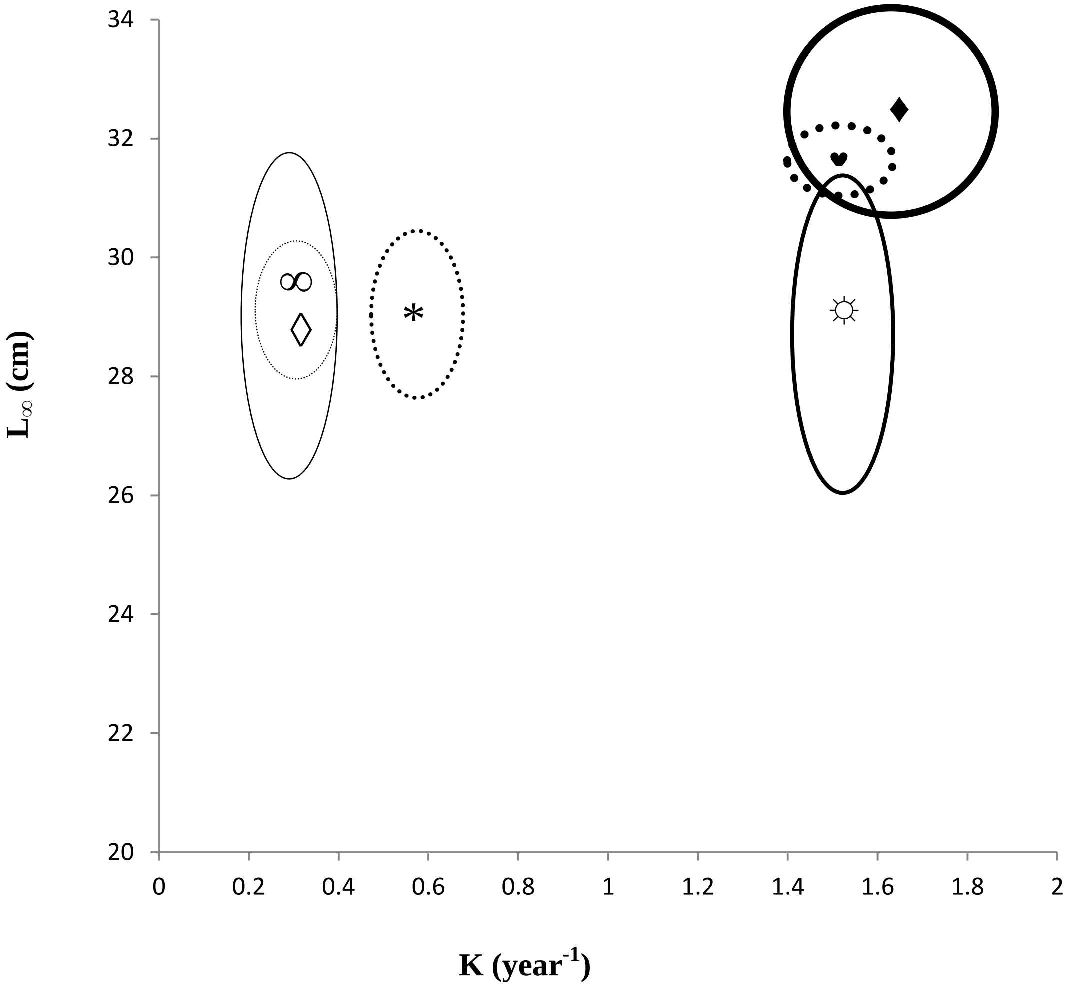

Figure 4.20: Comparison of von Bertalanffy Growth Function (VBGF) parameters, L∞ and K, with 95% confidence regions estimated for *Leptoscarus vaigiensis* at sites of different protection levels in coastal Kenya. Malindi Park (◊, ……), Watamu Park (∞, —), Watamu Reserve (*, ……), Kanamai (☼, —), Vipingo (♥, ……), Malindi Reserve (♦, —).

Table 4.10: Total mortality (Z yr-1), natural mortality (M yr-1), fishing mortality (F yr-1) coefficients and exploitation rate (E) of *Leptoscarus vaigiensis* from six reefs of different protection levels in coastal Kenya. Dash (-) denotes not determined.

Site	**Z**	**M**	**F**	**E**
Malindi Park	1.69	1.08	-	-
Watamu Park	1.96	1.06	-	-
Malindi Reserve	9.15	2.70	6.45	0.71
Watamu Reserve	2.87	1.48	1.39	0.48
Vipingo (non-protected)	5.30	2.59	2.72	0.51
Kanamai (non-protected)	4.39	2.44	1.95	0.44

Exploitation rates (E) of the parrotfish at fished sites were higher for Malindi Reserve (0.71) and lower for the non-protected sites of Kanamai (0.44, Table 4.10) indicating likely ineffectiveness of “reserve” status in protecting fish populations from high fishing mortality.

4.4.3 Variation in relative recruitment patterns

Annual relative recruitment patterns of *L. vaigiensis* (Figure 4.21) show year round recruitment of the fish with multimodal peaks in most sites except in Malindi Reserve where the fish had unimodal recruitment to the fishery (Figure 4.21). Recruitment pattern of fish from the non-protected site of Kanamai showed two uneven pulses (Figure 4.21a), whereas those from Vipingo had three annual recruitment pulses (Figure 4.21b). Fish from reserve sites had variable recruitment patterns with those from Malindi Reserve showing a single peak (Figure 4.21c), while those from Watamu Reserve had two pulses (Figure 4.21d). Recruitment pattern was similar among fish from park sites with two major annual pulses (Figure 4.21e and Figure 4.21f).

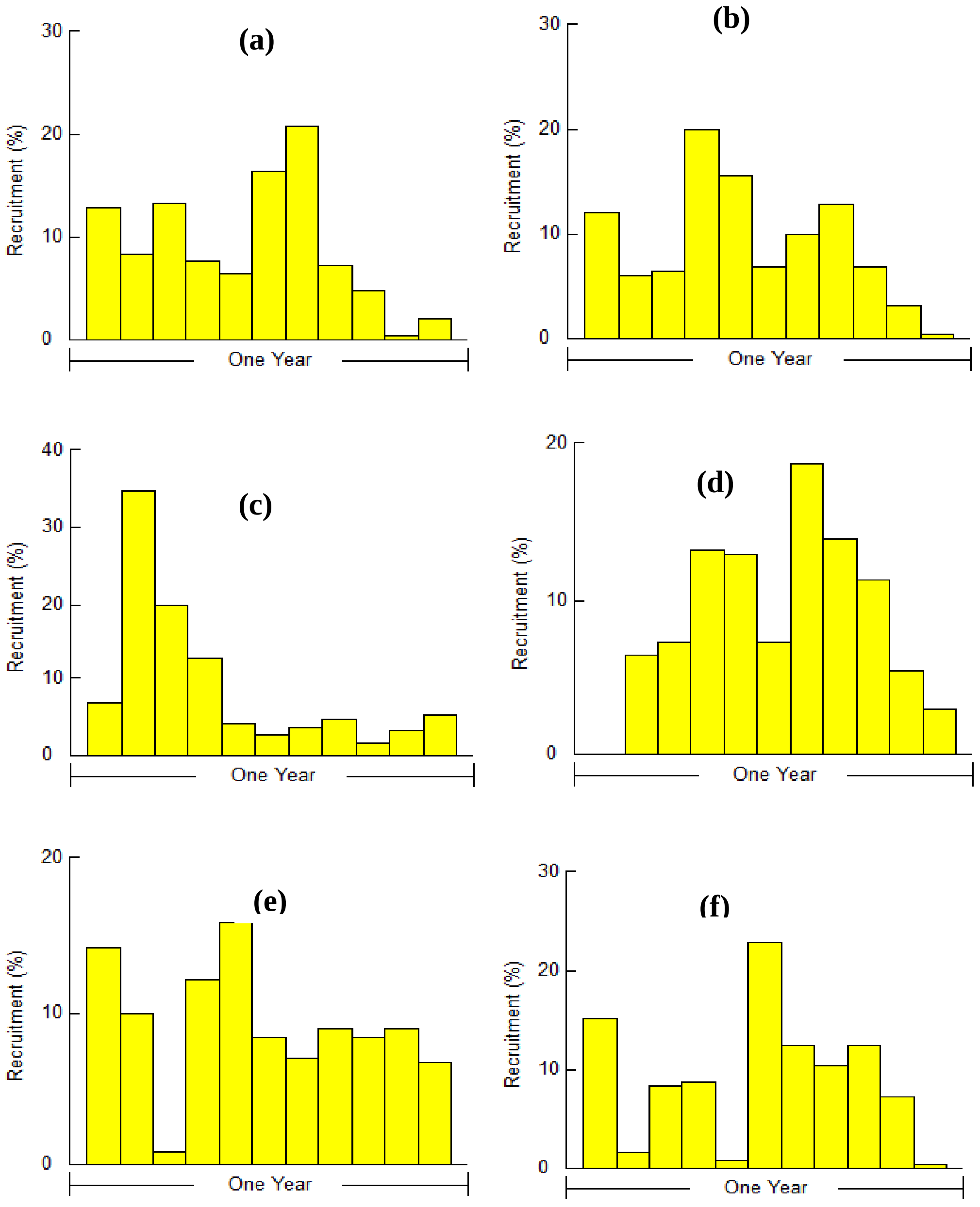

Figure 4.21: Annual relative recruitment pattern of *Leptoscarus vaigiensis* at the six sites of different protection levels in coastal Kenya:a) Kanamai, b) Vipingo, c) Malindi Reserve, d) Watamu Reserve, e) Malindi Park and f) Watamu Park.

CHAPTER FIVE

DISCUSSION

5.1 Catch trends from landing data (1978-2007)

The catch trend analysis indicate decline in the major coral-reef fish landings in coastal Kenya over the last decades. The causes of the declining trends cannot be determined from the present data, but human population driven increase in fishing effort as a result of increased demand for food may have played an important role (Kaunda-Arara *et al*., 2003). The principal commercial reef fishes namely the rabbitfishes (Siganidae) and emperors (Lethrinidae) are likely being exploited beyond optimal levels, and their catch trend forecast predicts a gradual decline in landings in the next decade. However, the family Scaridae to which the marbled parrotfish belong fairly maintained its landing rates during these periods. The marbled parrotfish, *L. vaigiensis* like other many coral reef fishes is a less mobile and often site attached species (Sale, 2002b) hence likely to be predisposed to fishing mortality. The mechanism(s) by which *L. vaigiensis* (Scaridae) avoids depletion despite its exposure to heavy fishing pressure as indicated by sustained landing rate over time, are not well understood but could relate to phenotypic plasticity.

5.2 Variation of reproductive traits between sites

The marbled parrotfish, *Leptoscarus vaigiensis*, is largely a sedentary reef fish thereby precluding the likelihood of mass movements between sites. Fishing selectively removes large and highly fecund individuals from sites (Jennings & Kaiser, 1998), leaving small sized individuals with the reduced fecundity reported in this study and in others (e.g. Jennings & Phillips, 1992; Wilson *et al*., 2010). However, even if harvesting was not size-selective, intensive exploitation will always lead to truncation of age and size structures of fished stocks, since members of a cohort do not survive to attain a relatively old age or large body size (Marteinsdóttir & Pardoe, 2008); this may further explain the lower fecundity of *L. vaigiensis* at the intensely fished and non-protected sites relative to the reserves and marine parks. However, there could be other causes for spatial variation in fecundity, including genotypic variation (Dieckmann & Heino, 2007) and differences in inter- and intra-species interactions at the sampling sites (Law, 2000). Low fecundity at non-protected sites in this study could be a function of the so called 'selfish mothers effect' (Marshall & Uller, 2007). As it is the case in many female insects and birds, fish lay fewer or smaller eggs when such eggs are anticipated to experience higher mortality say through predation from non-commercial (less targeted) species thereby saving energy for somatic growth as opposed to reproductive growth (Jennings & Philips, 1992).

In this study, levels of fecundity of small-sized fish at heavily-fished sites were higher than those of equivalent-sized fish at the less fished and unfished sites. It is likely that this is caused by the early maturation observed at fished sites, possibly mediated by reduced competition between individuals as a result of population declines due to fishing pressure (Heino & Godo, 2002; Kuparinen & Merila, 2007), among other factors. The distance between the heavily fished sites (Kanamai and Vipingo) on the south and the park and reserve sites in the north, together with the sedentary nature of this fish, would isolate these populations from each other and possibly thereby facilitate selection for higher fecundity and earlier maturation at smaller sizes at the fished sites consistent with findings of previous works (e.g. Sharpe & Hendry, 2009).

Population dynamics of marine fishes are characterized by high larval mortality (Werner & Fuiman, 2002) which is predominantly driven by size- and growth-selective processes (Meekan & Fortier, 1996). Higher survival is expected amongst juveniles emanating from large larvae (Raventos & Macpherson, 2005; Tomkiewicz *et al*., 2003) developing from large eggs (Pitcher & Hart, 1993). It is therefore intuitively expected that fish under heavy predation (e.g. fishing pressure) may develop larger eggs relative to those in protected sites (Einum & Fleming, 2000; Heath *et al*., 2003) as a phenotypic response to stress. However, in this study, a higher proportion of small eggs in *L. vaigiensis* were found at fished sites, although the mean egg diameter was not significantly different between sites. It is likely that *L. vaigiensis* at non-protected sites invest more energy into somatic growth to attain maturity faster as a trade-off against larger gonadal development which is energetically more demanding (Jennings & Phillips, 1992). Clearly, studies on predator-prey manipulations would be required to test this hypothesis. Otherwise, predominant production of small sized eggs by *L. vaigiensis* in non-protected sites relative to other sites suggests difference in strategies of reproductive investment between sites.

The earlier maturity of female fish at non-protected sites relative to those in marine parks and reserves is possibly a compensatory response to ensure that fish at fished sites reproduce before capture (Hutchings & Baum, 2005). Fishing has been identified as one of the main factors for declines in size and age at maturation in exploited fish stocks (Jennings & Kaiser, 1998; Kuparinen & Merila, 2007; Olsen *et al*., 2004). Apart from causing a decline in stock biomass, fishing can trigger changes in individual fish growth in response to an increase in per capita food availability (Trippel, 1995) and, hence, enhanced growth rates that result in earlier maturation at fished sites (Haug & Tjemsland, 1986). Conversely, high levels of competition and predation in protected marine parks mediated by the high biomass and diversity of fishes at these sites (McClanahan & Kaunda-Arara, 1996) probably reduces relative growth rates and hence increased size at maturity. Spatial differences in growth rate and maturation may thus be a phenotypic response to changes in food availability and predation pressure. However, it may also develop over evolutionary time-scale in response to selective mortality (Law, 2000).

5.3 Diet and niche breadth variations between sites

The marbled parrotfish exploits a variety of marine flora on Kenyan reefs with the most important being the seagrass, *Thalassodendron ciliatum* and the seaweeds; *Enteromorpha* spp. (green algae) and *Sargassum* spp. (brown algae). These results are similar to the findings on the diet of this species in Mozambique (Almeida *et al*., 1999).

As an algal grazer, the marbled parrotfish therefore likely plays a significant role in Kenyan coral reef ecosystems by shaping the distribution, community structure, standing crop biomass and production rates of benthic macroalgae as documented elsewhere (Russ, 2003). Its grazing action likely explains in part, the observed resilience of some Kenyan coral reefs from the effects of coral bleaching (McClanahan *et al*., 2004; Obura, 2005) or resistance to out-competition by benthic algae (McClanahan & Shafir, 1990).

The results of this study indicated no clear pattern on the effect of protection level on diet composition in the parrotfish. However, in general there was higher diet diversity in park sites during the calm NEM season and in reserve, while non-protected sites were of more diverse diet during the hydrodynamically rough SEM season. Increased fishing activities on the reefs during the calm NEM season (Kaunda-Arara & Rose, 2004) together with increased fishing predation during this season (McClanahan & Shafir, 1990) may cause fish in fished sites (reserves and non-protected areas) to forego foraging opportunities for relative safety as a trade-off between predation and survival. This trade-off may explain the low diversity of food items among fish in fished areas compared to those in protected sites during this period. Conversely, the increased diversity in fish diet especially at fished sites during the SEM season may be due to maximized foraging opportunities by fish during this season when fishing predation is less intensive. This notion is further supported by the general similarity in the relationship between niche breadths and feeding intensity at the reserve and non-protected sites.

The narrower niche breadth among fish from fished sites relative to those from park sites during the calm NEM season suggests that the “niche variation hypothesis” (van Valen, 1965; van Valen & Grant, 1970) that predicts wider niche breadths at low inter-specific competitions as may be expected in fished sites, can be modified by environmental variability (such as monsoon seasonality) and fish behaviour as influenced by fishing pressure. These results are obviously confounded by lack of data on food abundance and distribution on the reefs. Spatial differences in food distribution and abundance may influence diet composition of individuals (O'Brien *et al*., 1990; Semmens *et al*., 2009). The influence of fishing pressure at the non-protected sites on food availability to the parrotfish is unknown but is likely significant as fishing indirectly modifies habitat characteristics through cascading processes (Francii-filho & Moura, 2008).

There was significant influence of site, season and their interaction on the niche breadth of the parrotfish with synchronized timing of peak niche breadths at sites of same protection regime. This synchronized timing likely indicates presence of unifying factors such as fishing pressure and environmental variability among sites. Prohibited fishing at park sites could facilitate conditions for optimal foraging by fish at these sites resulting in broader niche breadths during the calm NEM season.

Results of hierarchical cluster analysis (HCA) indicated clustering of some food items whereas that of correspondence analysis (CA) indicated association of certain food items with the different maturity categories of fish. The HCA results may simply reflect the relative abundance of algal food resource at sites or indicate food partitioning among conspecifics as induced by diversifying force of intra-specific competition or constraining effect of inter-specific competitors (Svanback & Bolnick, 2005; Taper & Case, 1985; van Valen, 1965). Clustering of food items or their association with sites could be a reflection of the assemblage of food items preferred by the fish among sites or simply an artefact of spatial distribution of food items in the environment. On the other hand, association of certain food items with either immature or mature individuals as indicated by CA results suggests ontogenetic differences in diet preference. It is possible that niche breadths will vary with ontogenetic shifts in diet (Rotenberry, 1980). However, spatial analysis at population level likely reduces the influence of ontogenetic shifts on niche breadths especially if the size-frequency distribution does not vary substantially between sites as was in this study. Lack of data on environmental variables such as substrate characteristics, nutrients regime and chemical parameters at sites in this study, constrains robust determination of factors influencing diet and niche breadth variability between sites. Nonetheless, the between-site similarity of patterns of niche breadth variation for sites of same protection level suggests low influence of environmental factors on diet and niche breadth variation; however, this notion will require testing. Indeed the lagoonal reefs sampled in this study have been found to contain grossly similar substrate categories and all experience the monsoonal seasonality (Kaunda-Arara & Rose, 2004; McClanahan & Shafir, 1990).

5.4 Variation of growth and mortality parameters between sites

This study estimated for the first time in the WIO region, the growth parameters of the marbled parrotfish among reefs exposed to different levels of fishing pressure, thereby providing insights into the possibility of utilizing the parameters as indicators of environmental stress. Bootstrapping of the parameters showed distinct spatial variation in growth patterns of *L. vaigiensis* from protected and fished sites, suggesting likely existence of plasticity in the growth of the species perhaps mediated by fishing pressure among other factors. The higher growth rates of fish at fished sites relative to those in protected areas, as found in this study, are consistent with findings of previous work (e.g. Haug & Tjemsland, 1986). The higher growth rate at fished sites may be due to reduced inter- and intra-specific competition as a result of increased availability of food per capita (Trippel, 1995). Higher growth rate may also be a phenotypic response to attain maturity faster in order to maximize reproductive fitness (Law, 2000, Locham *et al.*, 2015a). The two marine reserves (Malindi and Watamu, with partial protection) seem to have different growth patterns (or curves) deduced from the non-overlapping confidence regions of the growth parameters; this variation may suggest differences in effectiveness of the “reserve” status of sites as also reflected in differences in fishing mortality between the reserves.

The marbled parrotfish has been found to mature at smaller sizes at fished sites in this study (also see; Locham *et al.*, 2015a). However, the higher asymptotic sizes at fished sites suggest continued growth after maturation (Heino & Godo, 2002). The causes for the continued growth to higher asymptotic lengths at these sites are not clear but may be mediated by reduced competition for resources. The correlation between $L\infty$ and K suggests that asymptotic size is reached faster after maturation (Heino & Godo, 2002). Fishes at protected sites appear to have smaller growth rates and relatively smaller asymptotic sizes. This finding is not intuitive as fishes are expected to grow to larger sizes in the absence of fishing and this observation will require more investigation. The marbled parrotfish, like other reef fishes, is heavily fished among the coral reef fishes in Kenya and most of the WIO region (Hicks & McClanahan, 2012) but have continued to sustain artisanal fisheries. The mechanisms by which this species avoids overfishing depletions are not well understood but could relate to phenotypic plasticity or divergence as suggested by the results of this study.

Mortality and exploitation patterns of the marbled parrotfish as found in this study appeared to relate to protection status of the sites. In general, total mortality estimates were low among protected sites and higher in fished sites. However, higher estimates of fishing mortality and exploitation rates derived for the reserves relative to non-protected sites indicating that the “reserve” status may not be effective in protecting fish populations from high fishing mortality. Use of different gears at sites (traps in protected sites and cast nets and spear guns in non-protected areas) could also have contributed to the observed results since fishing gears select fish by size and species (Dalzell, 1996). Varied patterns of relative recruitment in the marbled parrotfish at sites may suggest influence of fishing amongst other factors on reproductive output and timing; however, the data generated is inadequate to explain the spatial variability in recruitment as determined.

CHAPTER SIX

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

This study has shown evidence of divergence in the reproductive attributes of *L. vaigiensis* among reefs in Kenya probably induced by fishing pressure. As a likely adaptive strategy to enhance their resilience to fishing pressure, fish from non-protected sites mature earlier and have an equivalent or higher fecundities at smaller sizes relative to larger fish in protected sites.

The present study has confirmed the marbled parrotfish as an algal grazer. As a grazer, the marbled parrotfish therefore likely plays a significant role in Kenyan coral reef ecosystems by shaping the distribution, community structure, standing crop biomass and production rates of benthic macroalgae. The results show interaction of site protection level with seasonality to cause greater diet diversity in non-protected sites during the SEM season and higher niche breadth during the NEM season in protected sites. Spatial variation in food types and environmental variability (e.g. in fishing intensity) likely affects the diet of the species between reefs.

Also, this study has shown spatial variation in growth and mortality parameters of *L. vaigiensis* in coastal Kenya due to variations in fishing pressure, though, the variation cannot be attributed solely to fishing as other covariates may confound the influence of fishing mortality. It is likely that the variation in growth patterns may enhance resilience of the stocks to fishing pressure. This study also generates for the first time in the WIO, the growth and mortality parameters for this commercially important species thereby adding to the scarce database on these parameters (see www.Fishbase.org).

In general, the hypotheses that guided the study are not supported by the results and a broad scale divergence in life-history attributes is concluded to exist for the marbled parrotfish among reefs of various exploitation levels in coastal Kenya. The exact causes of this divergence are unknown but are likely related to spatial variation in fishing pressure.

6.2 Recommendations

Based on the results of this study, the following recommendations are advanced:

1. Additional research is proposed to undertake predator-prey manipulations in order to test the hypothesis that *L. vaigiensis* at non-protected sites invest more energy into somatic growth in order to attain maturity faster as a trade-off between gonadal and somatic growth.
2. A further research is recommended to explore other factors besides fishing mortality that could influence life-history traits (e.g. genetic variability, habitat-induced variations) in order to partition the observed phenotypic divergence of reproductive traits to its causes.
3. There is the potential to apply variability of life-history traits such as high growth rate and early maturation of fish at fished sites as indicator of environmental stress for purposes of fisheries management. Such management applications could include effort control, recommendation on area or seasonal closures amongst others.
4. Fisheries management and conservation programs should be based on spatially explicit population models using growth parameters (instantaneous growth rate and asymptotic length) to avoid poor management decisions based on unifying models. This is because these parameters have been found to vary spatially within a single species. Such models include, for example, the Beverton and Holt Yield per recruit model, the von Bertalanffy growth models, stock-recruitment models amongst others.

REFERENCES

Abbey-Lee, R. (2012). *Relative role of dispersal dynamics and competition in niche breadth.* Unpublished M.Sc thesis, Florida: Florida International University. Retrieved from digitalcommons.fiu.edu/etd.

Acosta, A.R. (1994). Soak time and net length effects on catch rate of entangling nets in coral reef areas. *Fisheries Research*, *19*, 105-119.

Allen, G. (1997). *Marine fishes of the Great Barrier Reef and south-east Asia - afield guide for anglers and divers*. Perth: Western Australia Museum.

Almeida, A.J., Marques, A., & Saldanha, L. (1999). Some aspects of the biology of three fish species from the seagrass beds at Inhaca Island, Mozambique. *Cybium, 23*, 369 - 376.

Bagenal, T.B. (1978). *Aspects of fish fecundity*. In: S.D. Gerking (Ed.), Ecology of freshwater fish production. (3rd ed.). Oxford, England: Blackwell Publishing.

Bagenal, T.B. (1965). The fecundity of long dabs in the Clyde sea area. *Journal of the Marine Biological Association of the United Kingdom, 45*(3), 599-606.

Beacham, T.D. (1983). Variation in length and age at sexual maturity of Atlantic groundfish: a reply. *Environment Biology of Fishes*, *19*, 149-153.

Bellwood, D.R. (1985). *The functional morphology, systematics and behavioural ecology of parrotfishes* (*Scaridae*). Unpublished Ph.D thesis, Townsville, Australia: James Cook University of North Queensland. Retrieved from http://researchonline.jcu.edu.au.

Bellwood, D.R. (1994). A phylogenetic study of the parrotfishes family Scaridae (Pisces: Labroidei), with a revision of genera. *Records of the Australian Museum Supplement, 20*, 1-84.

Bellwood, D.R., Hughes, T.P., Folke, C., & Nystrom, M. (2004). Confronting the coral reef crisis. *Nature, 429*, 827-833.

Benno, B.L. (1992). *Some features of beach seine fishery along the Dar es Salaam coast, Tanzania*. Unpublished M.Sc. thesis, Finland: University of Kuopio.

Berkeley, S.A., Chapman, C., & Sogard. S.M. (2004). Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, *85*, 258-264.

Blanchard, F. (2001). The effect of fishing on demersal fish community dynamics. An hypothesis. *ICES Journal of Marine Science, 58*, 711-718.

Bolnick, D.I. (2004). Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution*, *87,* 608-618.

Bolnick, D.I. (2001). Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature, 410,* 463-466.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., &Forrister, M.L. (2003). The ecology of individuals: incidence and implications of individual specialization. *American Naturalist*, *161*, 1-28.

Bolnick, D. I., Ingram, T., Stutz, W., Snorberg, L., Lau, O., & Paull, J. (2010). Ecological release from interspecific competition leads to decoupled changes in populationand individual niche width. *Proceedings of the Royal Society of London*, *277*, 1789-1797.

Bolton, J.J., Oyieke, H. A., & Gwanda, P. (2007). The seaweeds of Kenya: checklist,history of seaweed study, coastal environment, and analysis of seaweed diversity and biogeography. *South African Journal of Botany, 73*, 76-87.

Brakel, W. H. (1982). Tidal patterns on the East African coast and their implications for the littoral biota. *Proceedings for the Symposium of Coastal and Marine Environment of the Red Sea*, *2*, 403-418.

Brochman, B. S. (1984). *Fisheries development and economy*. In: S.A. Iverson & S. Myklevoll (Eds). Proceedings of Norad-Kenya seminar to review the marine fish stocks and fisheries in eastern Africa. Mombasa, Kenya: Kenya Marine and Fisheries Research Institute.

Bruce, R.W., & Randall, J.E. (1985). *A revision of the Indo-West Pacific parrotfish genera Calotomus* and *Leptoscarus* (Scaridae: Sparisomatinae). Honolulu, Hawaii: Bernice Pauahi Bishop Museum.

Bürger, R., & Gimelfarb, A. (2004*).* The effects of intraspecific competition and stabilizing selection on a polygenic trait*. Genetics, 167,* 1425-1443*.*

Caley, M., & Munday, P. (2003). Growth trades off with habitat specialization. *Proceedings of the Royal Society of London*, *270,* 175-177.

Candolin, U. (2009). Population responses to anthropogenic disturbance: Lessons from three-spined sticklebacks *Gasterosteus aculeatus* in eutrophic habitats. *Journal of Fish Biology*, *75,* 2108-2121.

Cardinale, M., & Modin, J. (1999). Changes in size-at-maturity of Baltic cod (*Gadus morhua*) during a period of large variations in stock size and environmental conditions. *Fisheries Research, 41,* 285-295.

Choat, J., & Robertson, D. (1975). *Protogynous hermaphroditism in fishes of the family Scaridae*. In: R. Reinboth (Ed.), Intersexuality in animal kingdom. Berlin, Germany: Springer-Verlag.

Choat, H., & Bellwood, D. (1998). *Wrasses & Parrotfishes*. In W. Eschmeyer, & J. Paxton, (Eds.), Encyclopedia of Fishes (2nd ed.). California: Academic Press.

Choat, J.H., Axe, L.M., & Lou, D.C. (1996). Growth and longevity in fishes of the Family Scaridae. *Marine Ecology Progress Series*, *145,* 33-41.

Clements, K.D. (1991). *Gut microorganisms of surgeonfishes* (*Family Acanthuridae*). Unpublished Ph.D thesis, Townsville, Australia: James Cook University of North Queensland. Retrieved from http://researchonline.jcu.edu.au.

Cleveland, W. S. (1979) Robust locally weighted regression and smoothing scatterplots. *Journal of the American Statistical Association*, *74,* 829-836.

Clifton, K.E. (1995). Asynchronous food availability on neighbouring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish, *Scarus iserti*. *Marine Ecology Progress Series*, *116,* 39-46.

Cohen, R. E., & Lough, R. G. (1983). Prey field of larval herring, *Clupea harengus* on a continental shelf spawning area. *Marine Ecology Progress Series, 10*, 221-222.

Dalzell, P. (1996). *Catch rates, selectivity and yields of reef fishing*. In: N.V.C. Polunin & C.M. Roberts (Eds.), Reef fisheries. London, England: Chapman and Hall.

Dayton, P., Thrush, S., Agardy, M., & Hofman, R. (1995). Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *5,* 205-232.

DeWitt, T., & Scheiner, S. (Eds.). (2004). *Phenotypic plasticity: functional and conceptual approach*. Oxford, England: Oxford University Press.

Dieckmann, U., & Heino, M. (2007). Probabilistic maturation reaction norms: Their history, strengths, and limitations. *Marine Ecology Progress Series, 225*, 253-269.

Dieckmann, U., Doebeli, M., Metz, J., and Tautz, D. (Eds.) (2004). *Adaptive speciation*. Cambridge, England: Cambridge University Press.

Dill, L. (1983). Adaptive flexibility in the foraging behaviour of fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, *40*, 398-408.

Dulvy, N., Sadovy, Y., & Reynolds, J. (2003). Extinction vulnerability in marine populations. *Fish and Fisheries*, *4*, 25-64.

Dulvy, N., Polunin, N., Mill, A., & Graham, A. (2004). Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Canadian Journal of Fisheries and Aquatic Sciences, 61*, 466-475.

Efron, B., & Tibshirani, R.J. (1993). *An introduction to the bootstrap*. New York: Chapman and Hall.

Einum, S., & Fleming, I.A. (2000). Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature*, *405*, 565-567.

Fenberg, P.B., & Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology*, *17*, 209-220.

Fondo, E. N. (2004). *Assessment of Kenyan marine fisheries from selected fishing areas*. Unpublished final project report, Reykjavik: United Nations University.

Food and Agriculture Organization. (1995). *The state of world fisheries and aquaculture*. Rome, Italy: Food and Agriculture Organization of the United Nations.

Francii-filho, R.B., & Moura, R.L. (2008). Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos bank, eastern Brazil. Aquatic Conservation: *Marine and Freshwater Ecosystems, 18*, 1166 - 1179.

Gayanilo, Jr., Sparre, F., & Pauly, P.D. (1996). *FAO-ICLARM Stock assessment tools (FISAT).* Rome: Food and Agriculture Organisation of the United Nations.

Gell, F.R., & Whittington, M.W. (2002) Diversity of fishes in seagrass beds in the Quirimba Archipelago, northern Mozambique. *Journal of Marine and Freshwater Research, 53*, 115–121.

Gobert, B. (1994). Size structures of demersal catches in a multispecies multigear tropical fishery. *Fisheries Research*, *19,* 87-104.

Gomes, J.L., & Monteiro, L.R. (2007). Size and fecundity variation in populations of *Poecilia vivipara* Block and Schneider (Teleostei; Poeciliidae) inhabiting an environmental gradient. *Journal of Fish Biology*, *71*, 1799-1809.

Goto, A. (1993). Clinal life-history variation in the river-sculpin, *Cottus hangiongensis*: an example of phenotypic plasticity. *Japan Journal of Ichthyology*, *39*, 363-370.

Gulland, J.A. (1971). *The fish resources of the ocean*. London, England: Fishing News (Books).

Gullstrom, M., Berkstrom, C., Ohman, M., Bodin, M., & Dahlberg, M. (2011). Scale-dependent patterns of variability of a grazing parrotfish (*Leptoscarus vaigiensis*) in a tropical seagrass-dominated seascape. *Marine Biology*, *158*, 1483-1495.

Haug, T., & Gulliksen, B. (1988). Fecundity and egg sizes in ovaries of female Atlantic halibut, *Hippoglossus hippoglossus* (L). *Sarsia*, *73*(4), 259-261.

Haug, R., & Tjemsland, J. (1986). Changes in size- and age-distributions and age at sexual maturity in Atlantic halibut, *Hippoglossus hippoglossus*, caught in North Norwegian waters. *Fisheries Research*, *4*, 145-155.

Hawaii Cooperative Fishery Research Unit (2008). *The biology of parrotfish in Hawaii.* Hawaii: Western Pacific Regional Fishery Management Council.

Heath, D.D., Hearh, J.W., Bryden, C.A., Johnson, R.M., & Fox, C.W. (2003). Rapid evolution of egg size in captive salmon. *Science*, *299*, 1738-1740.

Heino, M., & Godo, O. (2002). Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: A new technique illustrated by application to Northeast Arctic cod. *ICES Journal of Marine Science*, *59*, 562-575.

Hicks, C.C., & McClanahan, T.R. (2012). Assessing gear modification needed to optimize yields in heavily exploited, multi-species, seagrass and coral reef fishery. *PLoS One*, *7*(5), 1-12.

Hislop, J.R., & Hall, W.B. (1974). The fecundity of whiting, *Merlangius merlangus* (L.) in the North Sea, the Minch and at Iceland. *ICES Journal of Marine Science, 36*, 42-49.

Hislop, J.R., & Shanks, A.M. (1979). Recent investigations on the reproductive biology of the haddock, *Melanogrammus aeglefinus*, of the northern North Sea and the effects on fecundity of infection with the copepod parasite *Lernacocera branchialis*. *ICES Journal of Marine Science*, *39*, 244-251.

Hoey, A., & Bellwood, D.R. (2008). Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs*, *27*(1), 37-47.

Holopainen, I. J., Tonn, W. M., & Paszkowski, C. A. (1997). Tales of two fish: the dichotomous biology of crucian carp (*Carassius carassius* (L)) in northern Europe. *Annales Zoologici Fennici*, *34*, 1-22.

Horn, M. (1989). Biology of marine herbivorous fishes. *Oceanographic Marine Biology Annual Review*, *27*, 167-272.

Horwood, J. W., Bannister, R.C., Howlett, G.J. (1986). Comparative fecundity of North Sea plaice (*Pleuronectes platessa*). *Proceedings of the Royal Society of London, Series B*, *228*, 401-431.

Howard, K. (2008). *Community structure, life history and movement patterns of parrotfishes: large protogynous fishery species*. Unpublished Ph.D thesis, Manoa: University of Hawaii. Retrieved from hpp://play.google.com.

Hughes, T. (1994). Catastrophes, phase shifts and large scale degradation of a Caribbean coral reef. *Science, 265,* 1547-1551.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., HoeghGuldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology, 17,* 360-365.

Hutchings, J. A. (1996). Adaptive phenotypic plasticity in brook trout, *Salvelinus fontinalis,* life histories. *Ecoscience, 3,* 25-32.

Hutchings, J. A. (2000). Collapse and recovery of marine fishes. *Nature, 406,* 882-885.

Hutchings, J., & Baum, J. (2005). Measuring marine fish biodiversity: Temporal changes in abundance, life history and demography. *Philosophical Transactions of the Royal Society B:Biological Sciences, 360*, 315-338.

Hyslop, E. P. (1980). Stomach contents analysis, a review of methods and their application. *Journal of Fish Biology, 17*, 411-429.

Iguchi, K., & Tsukamoto, Y. (2001). Semelparous or iteroparous: resource allocation tactics in the ayu, an osmeroid fish. *Journal of Fish Biology, 58*, 520-528.

Jennings, M.J., & Phillips, D.P. (1992). Reproductive investment and somatic growth rates in longear sunfish. *Environmental Biology of Fishes*, *35*, 257-271.

Jennings, S., & Polunin, N. (1996). Impacts of fishing on tropical reef ecosystems. *Ambio*, *25*, 44-49.

Jennings, S., & Lock, J. M. (1996). *Population and ecosystem effects of fishing*. In N.V. Polunin & Roberts, C.M. (Eds), Reef fisheries. London,England: Chapman and Hall.

Jennings, S., & Kaiser, M.J. (1998). The effects of fishing on marine ecosystems. *Advances in Marine Biology*, *68*, 201-352.

Jennings, S., Reynolds, J.D., & Polunin, N. (1999). Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conservation biology*, *13(6)*, 1466-1475.

Johnson, D. R., Mutua N. M., & Kimani, E. J. (1982). Response to annually reversing Monsoon winds at the southern boundary of the Somali Current. *Deep Sea Research*, *29*, 1217-1222.

Jørgensen, T. (1990). Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *Journal du Conseil International pour l'Exploration de la Mer., 46*, 235-248.

Kabanova. J. G. (1968). Primary production in the northern part of the Indian Ocean. *Oceanology*, *8*, 214-255.

Kaunda-Arara, B., & Ntiba, M.J. (1997). The reproductive biology of *Lutjanus fulviflamma* (Forsskål,1775) (Pisces: Lutjanidae) in Kenyan inshore marine waters. *Hydrobiologia, 353,* 153-160.

Kaunda-Arara, B., Rose, G.A., Muchiri, M.S., & Kaka, R. (2003). Long term trends in coral reef fish yields and exploitation rates of commercial species from coastal Kenya. *Western Indian Ocean Journal of Marine Science*, *2*, 105-116.

Kaunda-Arara, B., & Rose, G.A. (2004a). Effects of marine reef national parks on fishery CPUE in coastal Kenya. *Biological Conservation*, *118,* 1-13.

Kaunda-Arara, B. & Rose, G.A. (2004b). Out-migration of tagged fishes from marine reef national parks to fisheries in coastal Kenya. *Environmental Biology of Fishes, 70,* 363-372.

Kimura, D.K. (1980). Likelihood methods for the von Bertalanffy growth curve. *FisheryBulletin, 77*, 765-774.

King, M. (1995). *Fisheries biology, assessment and management*. Oxford, England: Blackwell Publishing.

King, A. (2000). *Managing Without Institutions: The Role of Communication Networks in Governing Resource Access and Control*. Unpublished Ph.D thesis, England: University of Warwick. Retrieved from http://wrap.warwic.ac.uk.

Kjesbu, O.S., Witthames, P.R., Solemdal, P., & Greer, W. M. (1998). Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *Journal of Sea Research, 40*, 303-321.

Koslow, J. A., Boehlert, G. W., Gordon, J.D., Haedrich, R.I., Lorance, P., & Parin, N. (2000). Continental slope and deep sea fisheries: implication for a fragile ecosystem. *ICES Journal of Marine Science, 57*, 548-557.

Kuiter, R.H., & Tonozuka, T. (2001). *Pictorial guide to Indonesian reef fishes. Part 2. Fusiliers - dragonets, Caesionidae - Callionymidae. zoonetics.* Seaford, Australia: PT Dive and Dive's.

Kuparinen, A., & Merila, J. (2007). Detecting and managing fisheries-induced evolution. *Trends in Ecology and Evolution, 22*, 652-659.

Laidre, K.L., & Heide-Jørgensen, M.P. (2005). Winter feeding intensity of narwhals (*Monodon monoceros*). *Marine Mammal Science*, *21,* 45-57.

Landau, S., & Everitt, B. (2004). *A handbook of statistical analyses using SPSS*. Florida: Chapman and Hall.

Law, R. (1991). Fishing in evolutionary waters. *New Scientist*, *129,* 35-37.

Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science, 57,* 659-668.

Layman, C.A., Quattrochi, J.P., Peyer, C.M., & Allgeier, J.E. (2007). Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecological Letters*, *10,* 937-944.

Lee, C.K. (1972). *The Biology and Population Dynamics of the Common Dab, Limanda limanda (L.) in the North Sea*. Unpublished Ph.D thesis, England: University of East Anglia. Retrieved from http://www. Amazon.co.uk.

Levins, R. (1968). *Evolution in changing environments: some theoretical explorations*. Princeton: Princeton University Press.

Locham, A.G., Kaunda-Arara, B., Wakibia, J., & Muya, S. (2015a). Phenotypic divergence in reproductive traits of the marbled parrotfish, *Leptoscarus vaigiensis* (Quoy and Gaimard 1824), among reefs of varying protection levels in Kenya. *Western Indian Ocean Journal of Marine Science*, *1*, 69-80.

Locham, A.G., Kaunda-Arara, B., Wakibia, J., & Muya, S. (2015b). Diet and niche breadth variation in the marbled parrotfish, *Leptoscarus vaigiensis*, among coral reef sites in Kenya. *African Journal of Ecology*, *53*, 560-571.

Lou, D.C. (1992). *Age specific patterns of growth and reproduction in tropical herbivorous fishes*. Unpublished Ph.D thesis, Townsville, Australia: James Cook University of North Queensland. Retrieved from http://eprints.jcu.edu.au.

MacArthur, R.H., & Pianka, E.R. (1966). On optimal use of a patchy environment. *TheAmerican Naturalist*, *100*, 603-609.

MacLennan, D.L. (1992). Fishing gear selectivity: an overview. *Fisheries Research*, *13*, 201-204.

Magurran, A. E. (1988). *Ecological diversity and its measurement*. New Jersey: Princeton University Press.

Marshall, D. J., & Uller, T. (2007). When is a maternal effect adaptive? *Oikos 116*, 1957-1963.

Marteinsdóttir, G., & Pardoe, H. (2008). Effects of fishing on inter- and intra-stock diversity of marine resources. *Fisheries for Global Welfare and Environment, World Fisheries Congress*, *5*, 27-43.

Marteinsdóttir, G., & Thorarinsson, K. (1998). Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 1372-1377.

McClanahan, T.R. (1988). Seasonality in East Africa's coastal waters. *Marine Ecology Progress Series*, *44*, 191-199.

McClanahan, T. R. (1995). Fish predators and scavengers of the sea urchin, *Echinometra mathaei*, in Kenyan coral-reef marine parks. *Environmental Biology of Fishes, 43*, 187-193.

McClanahan, T.R., & Shafir, S. H. (1990). Causes and consequences of sea urchins abundance and diversity in Kenyan coral reef lagoons. *Oecologia*, *83*, 362-370.

McClanahan, T.R., & Obura, D. (1995). Status of Kenyan coral reefs. *Coastal Management*, *23*, 57-76.

McClanahan, T.R., & Kaunda-Arara, B. (1996). Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conservation Biology*, *10*, 1187-1199.

McClanahan, T.R., Baird, A.H., Marshall, P.A., & Toscano, M.A. (2004). Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Marine Pollution Bulletin*, *48*, 327-335.

McClanahan, T.R., & Mangi, S.C. (2004). Gear based management of a tropical artisanal fishery based on species selectivity and capture size. *Fisheries Management and Ecology*, *11*, 51-60.

Meekan, M. & Fortier, L. (1996). Selection for fast growth during the larval life of Atlantic Cod, *Gadus morhua*, on the Scotian shelf. *Marine Ecology Progress Series, 137*, 25-37.

Mohamed, K.S. (2004). *Towards ecosystem based management of marine fisheries-building mass balance trophic and simulation models*. In: P.U. Zacharia & K.P. Abdurahiman (Eds.), Methods of stomach content analysis of fishes, technical notes. Kerala, India: Central Marine Fisheries Research Institute.

Moksnes, P.O., Gullstro, M., Tryman, K., & Baden, S. (2008). Trophic cascades in a temperate seagrass community. *Oikos, 117*, 763-777.

Morita, K., & Morita, S., (2002). Rule of age and size at maturity. Individual variation in the maturation history of resident white-spotted charr. *Journal of Fish Biology, 61*, 1230-1238.

Munro, J. L. (Ed.). (1983). *Caribbean coral reef fishery resources*. Manila, Philippines: International Centre for Living Aquatic Resources Management.

Munro, J.L., & Willlams, D. (1985). Assessment and management of coral reef fisheries: biological, environmental and socio-economic aspects. *Proceedings of 5th international Coral Reef Congress*, 4, 44.58

Munro, J. L; Parrish, J. D., & Talbot, F. H. (1987). *The biological effects of intensive fishing upon coral reef communities.* In B. Salvat, (Ed.), Human impacts on coral reefs: facts and recommendations. French Polynesia: Antenne Museum.

Mwatha, G. (1997). *Aspects of the reproductive biology and fishery of the blue marbled parrot fish, Leptoscarus vaigiensis (Quoy and Gaimardi 1824) in Kenya shallow in-shore waters*. Unpublished M.Sc thesis, Nairobi, Kenya: University of Nairobi.

Ntiba, M.J. (1989). *The biology and ecology of the long rough dab, Hippoglossoides platessoides (Fabricius 1780) in the North Sea*. Unpublished Ph.D thesis, England: University of East Anglia. Retrieved from http://www.amazon.co.uk.

O'brien, P.O., Roseman, E.F., Killey, C.S. & Schaeffer, J.S. (1990). Fall diet and bathymetric distribution of deepwater sculpin (*Myoxocephalus thompsonii*) in Lake Huron. *Journal of Great Lake*s, *35,* 464-472.

Obura, D. (2005). Resilience and climate change: Lessons from coral reefs and bleaching in the Western Indian Ocean. *Estuarine, Coastal and Shelf Science, 603*, 353-372.

Ohta, I., & Tachihara, K. (2003). Larval development and food habits for the marbled parrotfish, *Leptoscarus vaigiensis*, associated with drifting algae. *Ichthyological Research*, *51,* 63-69.

Oliveira, C., Österlund, K., & Matern, S. (2005). *Marine plants of Tanzania. A field guide to the seaweeds and seagrasses of Tanzania*. Stockholm: Stockholm University.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B.,…(2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature, 428*, 932-935.

Otieno, A.N. (2002). *Catch assessment on the artisanal fisheries of Mpunguti Marine Reserve, Shimoni and Funzi Bay, southcoast Kenya*. Unpublished M.Sc thesis, Nairobi, Kenya: University of Nairobi.

Pauly, D. (1980). On the interrelationship between natural mortality, growth parameters, mean environmental temperature in 175 fish stock. *Journal du counscil International pour l'Exploration de la Mer, 39,* 175-192.

Pauly, D. (1982). Studying single-species dynamics in a tropical multispecies context. In: D. Pauly., G. Murphy, (Eds.). Theory and practice of tropical fisheries management. *International Centre for Living Aquatic Resources Management Conference Proceedings, 9,* 33-70.

Pauly, D. (1983). Length-converted catch curves: a powerful tool for fisheries research in the tropics- Pt. 1. *Fishbyte*, *1,* 9-13.

Pauly, D. (1986). On improving operation and use of the ELEFAN programs. Pt. II. Improving the estimation of L∞. *Fishbyte, 4*, 18-20.

Pauly, D., & Munro, J.L. (1984). *Once more on growth comparison in fish and Invertebrates.* Manila, Philippines: International Centre for Living Aquatic Resources Management.

Pauly, D., Ingles, J., & Neal, R. (1984). *Application to shrimp stock of objective methods for the estimation of growth, mortality and recruitment related parameters from length frequency data (ELEFAN I and II)*. In: J.A. Gulland,, & B.J. Rothschild (Eds.), Panaeid shrimps- their ecology and management. Farnham, London: Fishing News (Books) Ltd.

Pinkas, L., Olipahnt, M.S.& Iverson, I.L.K. (1971). Food habits of albacore, bluefin tuna, and bonito in Californian waters. California Department of Fish and Game, *Fisheries Bulletin, 152*, 1-105.

Pitcher, T.J., & Hart, P.J. (1993). *Fisheries Ecology. Fishing as a cause of evolution in fishes*. In: T. Stokes, J. McGlade., & R. Law. (Eds.), The exploitation of evolving resources. Washington: Springer-Verlag Berlin Heidelberg.

Policansky, D. (1993). *Fishing as a cause of evolution in fishes*. In T. K. Stokes, J. M.McGlade, & R. Law, (Eds), the exploitation of evolving resources. Washington: Springer-Verlag Berlin Heidelberg.

Qasim, S. Z. (1973). Some implications of the problem of age and growth in marine fishes from the Indian waters. *Indian Journal of Fisheries*, *20,* 351-371.

Quinn, T. P., & Adams, D. J. (1996). Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology, 77***,** 1151-1162.

Randall, J.E. (1962). Tagging reef fishes in the virgin Islands. *Proceedings of Gulf Carribbean Fisheries Institute*, *14*, 201-241.

Raventos, N., & Macpherson, E. (2005). Effect of pelagic larval growth and size-at-hatching on post-settlement survivorship in two temperate labrid fish of the genus *Symphodus*. *Marine Ecology Progress Series*, *285*, 205-211.

Reznick, D., & Ghalambor, C. (2005). Can commercial fishing cause evolution? Answers from guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 791-801.

Roberts, C., & Polunin, N. (1993). Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series, 100*, 167-176.

Roberts, C. M., & Hawkins, J.P. (1999). Extinction risk in the sea. *Trends in Ecology and Evolution*, *14,* 241-246.

Robertson, D.R., & Warner, R.R. (1978). Sexual patterns in the labroid fishes of the western Caribbean 11: The parrotfishes (Scaridae). *Smithsonian contributions to Zoology*, *255*, l-26.

Rodhouse, P.G., Murphy, E.J., & Coelho, M.L. (1998). *Impact of fishing on life histories*. Food and Agriculture Organization Technical Paper No. 376. Rome: Food and Agriculture Organization of the United Nations.

Rodwell, L., Barbier, B., Roberts, C., & McClanahan, T. (2003). The importance of habitat quality for marine reserve fishery linkages. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*, 171-181.

Rose, G. A., deYoung, B., Kulka, D. W., Goddard, S. V., & Fletcher, G. L. (2000). Distribution shifts and overfishing the northern cod (*Gadus morhua*): A view from the ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*: 644-664.

Rotenberry, J. T. (1980). Dietary relationships among shrub steppe passerine birds: competition or opportunism in a variable environment? *Ecological Monographs*, *50*, 93-110.

Roughgarden, J. (1976). Resource partitioning among competing species. A coevolutionary approach. *Theoretical Population Biology*, *9*, 388-424.

Rosenzweig, M.L. (1978). Competitive speciation. *Biological Journal of the Linnean Society*, 10, 275-289.

Russ, G. (2003). Grazer biomass correlates more strongly with production than biomass of algal turfs on a coral reef. *Coral Reefs*, *22*, 63-67.

Russ, G. R. (1991). *Coral reef fisheries*. In: Sale, P.F. (ed.). The ecology of fishes on coral Reefs. California: University of Hawaii Academic Press.

Russ, G.R., & St. John, J. (1988). Diets, growth rates and secondary production of herbivorous coral reef fishes. *Proceedings of 6th International Symposium on Coral Reefs*, *2*, 37-43.

Sale, P.F. (2002b). The ecology of fishes on coral reefs: What has the last decade taught us? *Fisheries Science*, *1*, 113-118.

Sale, P.F. (Ed.) (2002a). *Coral reef fishes, dynamics and diversity in a complex ecosystem*. London, England: Academic Press.

Schaffer, W.M., & Elson, P.F. (1975). The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. *Ecology*, *56*, 577-590.

Scheiner, S. M. (1998). The genetics of phenotypic plasticity. Evolution in a spatially-structured environment. *Journal of Evolutionary Biology*, *11*, 303-320.

Semmens, B.X., Ward, E.J., Moore, J.W., & Darimont, C.T. (2009). Quantifying Inter- and intra- population niche variability using hierarchical Bayesian stable isotope mixing models. *PLoS ONE 4* (7), 1-9.

Sharpe, D.M., & Hendry, A.P. (2009). Life history change in commercially exploited fish stocks: An analysis of trends among studies. *Evolutionary Applications*, *2*, 260-275.

Sparre, P., & Venema, S.C. (1998). *Introduction to tropical fish stock assessment*. Part 1 manual. FAO Fisheries Technical Paper No. 306. Rome: Food and Agriculture Organisation of the United Nations.

Stearns, S. (1992). *The evolution of life histories* (pp. 264). Oxford, England: Oxford University Press.

Stephens, D.W., & Krebs, J.R. (1986). *Foraging theory* (pp. 86). Princeton: Princeton University Press.

Stergiou, K.I., Petrakis, G., & Politou C. (1996). Small scale fisheries in the South Euboikos Gulf (Greece): species composition and gear competition. *Fisheries Research, 26,* 325-336.

Sternberg, D., Balcombe, S., Marshall, J., & Lobegeiger, J. (2008). Food resource variability in an Australian dryland river: evidence from the diet of two generalist native fish species. *Marine and Freshwater Research, 59,* 137-144.

Smith, T. B., & Skulason, S. (1996). Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics, 27,* 111-133.

Stokes, T., McGlade, J., & Law, R. (eds) (1993). *The exploitation of evolving resources*. Berlin, Germany: Springer-Verlag.

Svanback, R., & Bolnick, D.I. (2005). Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evolutionary Ecology Research, 7,* 993-1012.

Taper, M.L., & Case, T.J. (1985). Quantitative genetic models for the coevolution of character displacement. *Ecology, 66,* 355 - 371.

Tanimata, N., Yamamura, O., Sakurai, Y., & Azumaya, T. (2008). Dietary shift and feeding intensity of *Stenobrachius leucopsarus* in the Bering Sea. *Journal of Oceanography, 64,* 185-194.

Trippel, E.A. (1998). Egg size and viability and seasonal offspring production of young Atlantic cod. *Transactions of American Fisheries Society, 127,* 339-359.

Trippel, E.A. (1995). Age at maturity as a stress indicator in fisheries. *BioScience, 45,* 759-771.

Trippel, E.A., Kjesbu, O.S., & Solemdal, P. (1997). *Effects of adult age and size structure on reproductive output in marine fishes.* In: R.C. Chambers, & E.A. Trippel, (Eds.), Early life history and recruitment in fish populations. London, England: Chapman and Hall.

Tomkiewicz, J., Morgan, M.J., Burnett, J., & Saborido-Rey, F. (2003). Available information forestimating reproductive potential of Northwest Atlantic groundfish stocks. *Journal of Northwest Atlantic Fisheries Sciences, 33*, 55-70.

United Nations Department of Economic and Social Affairs (2015). *World population prospects.* New York, USA: Population Division of the Department of Economic and Social Affairs of the United Nations Secretariat.

United Nations Environmental Programme (UNEP) (1998). *Eastern Africa atlas of coastal resources, Kenya*. Nairobi: UNEP.

van Rooij, J.M., Hruggemann, J.H., Videler, J.J., & Breeman, A.M. (1995). Plastic growth of the herbivorous reef fish, *Sparisoma viride*: field evidence for a trade-off between growth and reproduction. *Marine Ecology Progress Series*, *122*, 93-105.

van Tienderen, P. H. (1997). Generalists, specialists, and the evolution of phenotypic plasticity in sympatric populations of distinct species. *Evolution*, *51,* 1372-1380.

van Valen, L. (1965). Morphological variation and width of ecological niche. *The American Naturalist*, *99,* 377-390.

van Valen, L., & Grant, P.R. (1970). Variation and niche width reexamined. *The American Naturalist*, 104, 589-590.

Werner, R.G., & Fuiman, L.A. (2002). *Methodological resources*. In: L.A. Fuiman & R.G.Werner, (Eds.), Fishery science: the unique contributions of early life stages. Oxford, England: Blackwell Science.

Wilcove, D., Rothstein, S., Dubow, J., Phillips, A., & Losos, E. (1998). Quantifying threats to imperiled species in the United States. *BioScience*, *48,* 607-615.

WildEarth, G. (2009). *Petition to list the bumphead parrotfish (Bolbometopon muricatum) under the U.S. endangered species Act,* New Mexico: WildEarth Guardians.

Wilson, D., & Turelli, M. (1986). Stable underdominance and the evolutionary invasion of empty niches. *The American Naturalist*, *127*, 835-850.

Wilson, J.R., Kay, M.C., Colgate, J., & Lenihan, H.S. (2012). Small-scale spatial variation in population dynamics and fishermen response in a coastal marine fishery. *PLoS ONE*, *7*(12), 1-11.

Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A., Dulvy, N.K., Turner, R.A.,… (2010). Habitat degradation and fishing effects on the size structure of coral reef communities. *Ecological Applications*, *20,* 442-451.

Wootton, R. J. (1990). *Ecology of Teleost Fishes* (2nd ed.). London, England: Chapman and Hall.

Zar, J.H. (1999). *Biostatistical analysis* (4th ed.) New Jersey: Prentice-Hall.