

**SPATIAL VARIATION IN GROWTH AND MORTALITY PARAMETERS OF THE
MARBLED PARROTFISH, *LEPTOSCARUS VAIGIENSIS* (QUOY AND GAIMARD, 1824)
ON DIFFERENT REEFS ALONG THE KENYAN COAST**

A. G. Locham¹, J. G. Wakibia², B. Kaunda-Arara³ and S. Muya²

¹Kenya Wildlife Service, Mombasa, Kenya

²School of Biological Sciences, Jomo Kenyatta University of Agriculture and Technology, Nairobi, Kenya.

³Department of Fisheries and Aquatic Sciences, University of Eldoret, Eldoret, Kenya.

E-mail: josephwakibia@yahoo.com

Abstract

Growth and mortality variations of *Leptoscarus vaigiensis* (Quoy and Gaimard, 1824) was studied among six reef sites exposed to different fishing pressure in coastal Kenya in order to test the hypothesis of phenotypic plasticity. Monthly fish samples were obtained from marine parks (protected or no-take areas), marine reserves (partially protected areas) and non-protected reefs from May 2011 to April 2013. Measurements for total lengths (cm) and body weights (g) were recorded. Growth (K, L_{∞}) and mortality (Z, M, F) parameters of the species were determined using the ELEFAN I program and compared between sites. Results showed higher asymptotic length (L_{∞}) estimate (~ 31 cm) for parrotfish from the reserve site and lowest estimate (26-27 cm) from the marine park site indicating that the potential for growth is influenced by factors other than levels of protection. Fish from park sites had equal but lowest growth rates ($K \text{ yr}^{-1}$) of 0.46 compared to 1.73 ± 0.11 and 1.36 ± 0.84 for fish from non-protected and reserve sites, respectively. As expected, total mortality estimates ($Z \text{ yr}^{-1}$) 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. This study showed divergence of growth parameters of a coral reef fish exposed to different levels of fishing pressure, thereby providing insights into the possibility of utilizing the parameters as indicators of environmental stress.

Key words: Fishing pressure, marine protected areas, phenotypic plasticity, resilience

1.0 Introduction

Spatial variation in exploitation rates and environmental variability may influence demographic rates of fishes and hence affect population structure and processes (Jennings and Kaiser, 1998). Variable exploitation pressure may contribute to phenotypic divergence in life-history traits due to spatial heterogeneity in population densities (Hutchings and Baum, 2005). Fishing may drive life history changes via at least two different mechanisms (Dieckmann and Heino, 2007) in addition to the immediate numerical effects of mortality. The mechanisms include direct effects manifested as phenotypic plasticity or divergence, and through evolutionary selection (Dieckmann and Heino, 2007). Phenotypic plasticity (production of different phenotypes by the same genotype under different conditions, *sensu* Morita and Morita, 2002) may cause spatial variation in life history attributes thereby making populations to be resilient to the effects of fishing (Candolin, 2009). Spatio-temporal changes in demographic traits such as growth and length at maturity has been found in many fish stocks including the Atlantic cod on the Scotian Shelf (Kelly *et al.*, 2009), Atlantic Salmon in North America (Dumas and Prouzet, 2003) and for other fish stocks in the North-West Atlantic (Enberg *et al.*, 2009). Besides fishing, environmental variables such as sea surface temperature rise has served to induce changes in life-history traits particularly age and size at maturation (Cardinale and Modin, 1999).

In the present study, we tested the hypothesis of phenotypic divergence in growth and mortality parameters of the marbled parrotfish (*Leptoscarus vaigiensis*) on Kenyan reefs exposed to varying fishing intensity. 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 including baited fish traps, fish trapping fences and cast nets, while ‘non-protected’ reefs are open access sites with no formal regulatory framework (McClanahan and Obura, 1995). The hypothesis was that growth and mortality will vary between fished sites (with presumably high total mortality mediated by fishing pressure) and protected sites (with lower total mortality rates since fishing is absent). The marbled parrotfish is an economically important fish in lagoon coral reef fisheries of the Western Indian Ocean (WIO) region. It 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 sedentary nature of the species (Kaunda-Arara and Rose, 2004), makes it suitable for testing the hypothesis of phenotypic divergence in growth as fishing may cause spatially distinct variations in population structure.

2.0 Material and Methods

2.1 Study Area

The study was carried out on six reef sites of different exposure to fishing pressure; two protected (or marine parks), two partially protected (or marine reserves) and two non-protected reefs (Figure 1). Samples of *Leptoscarus vaigiensis* were obtained from the protected (Malindi and Watamu Parks), marine reserves (adjacent to Malindi and Watamu Marine Parks) and non-protected (Vipingo and Kanamai) reef sites (Figure 1). Kenyan reefs are predominantly shallow (~10-12 m at high tide) lagoon fringing reefs that run parallel to the coastline with a mosaic of substrata (seagrass beds, seaweeds, sand, rubble, live corals, etc.) as described in Kaunda-Arara and Rose (2004) and which are common to all reefs. The coast experiences seasonality caused by both northeasterly and southeasterly monsoon winds as detailed in McClanahan (1988).

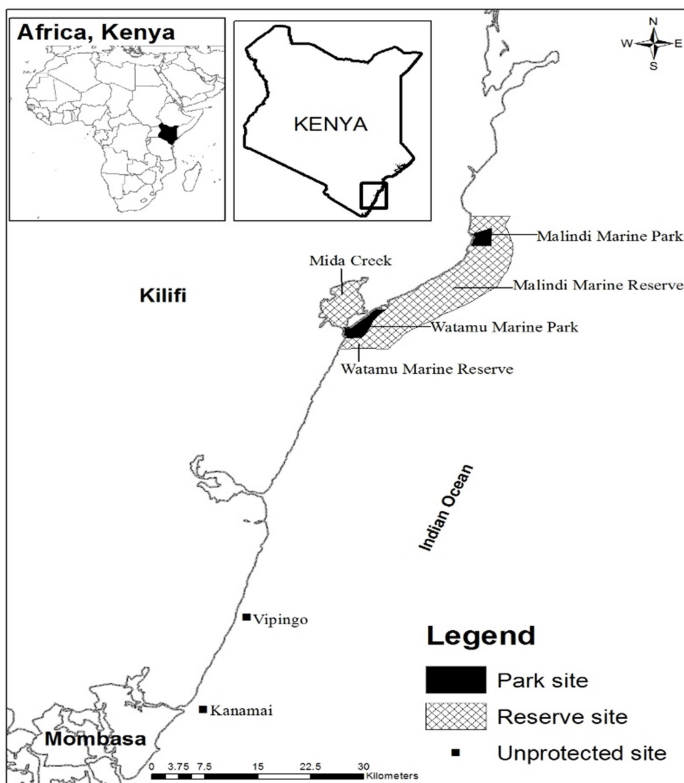


Figure 1: A map of Kenyan coastline showing the sampling sites for the marbled parrotfish, *Leptoscarus vaigiensis*.

The northeast monsoon season (NEM: November–March) is a period of calm seas, elevated sea surface temperatures (SSTs) and higher salinities, while the southeast monsoon season (SEM:

April–October) is characterized by rough seas, cool weather, lower salinities and higher productivity (McClanahan, 1988).

2.2 Field and Laboratory Procedures

Leptoscarus vaigiensis were caught monthly within protected sites (Malindi and Watamu Parks and their Reserves, Figure 1) using local baited traps called ‘*demas*’ from May 2011 to April 2013. The traps, constructed of metal frames and covered with a wire mesh of 1 cm stretch length are pentagonal in shape and measuring approximately 1.5 × 1.3 × 0.6 m high. Each *dema* trap had a single topside funnel door made out of bamboo reeds through which the fish enter and an underside aperture for removing the catch. The baited traps were deployed during low tide and retrieved during the subsequent low tide period of the following day having soaked for about 12 hours. In the non-protected sites (Vipingo and Kanamai, Figure 1), the fish were obtained monthly during the same period from fishers fishing these sites using cast nets and spear guns. Effort was made to obtain a wide size range of the specimens. All specimens of *L. vaigiensis* were preserved in ice and taken to the laboratory, where total lengths (TL) and standard lengths (SL) of specimens were measured (to the nearest millimeter) and weight taken (to the nearest gram).

2.3 Data Analyses

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_{∞} , cm) and instantaneous growth rate ($K \text{ yr}^{-1}$). The modified Powell-Wetherall Plot (Pauly, 1986) was used to obtain preliminary estimate of L_{∞} . 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:

$$L_{\text{mean}} - L' = a + bL' \dots\dots\dots(1)$$

Where, L_{mean} 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 $L_{\text{mean}} - L'$ against L' gives a linear regression from which “a” and “b” can be estimated and hence L_{∞} and Z/K (ratio of mortality and growth) derived from the relationship (Pauly, 1986):

$$Z/K = -(1+b)/b \text{ and } L_{\infty} = -a/b \dots\dots\dots(2)$$

The final estimate of the growth parameters (L_{∞} , K and t_0) was based on the von Bertalanffy growth formula (VBGF) (Sparre and Venema, 1998) expressed as follows:

$$L_t = L_{\infty} [1 - \exp^{-K(t-t_0)}] \dots\dots\dots(3)$$

where, L_t = length (in cm) at age t (in years), L_{∞} (cm) = asymptotic length or the maximum attainable length if the organism is allowed to grow, $K \text{ yr}^{-1}$ = instantaneous growth coefficient, t_0 = age at which length equals zero, or the birthday of the fish. The parameters were derived from 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_{∞}) with the highest index of fit (R_n , range 0 -1) is selected.

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

$$R_n = 10^{ESP/ASP} / 10 \dots\dots\dots(4)$$

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 growth curve (Gayanilo *et al.*, 1996). Since ELEFAN I estimate only two (L_{∞} , K) of the three (L_{∞} , K and t_0) growth parameters, t_0 was subsequently derived following Pauly (1983) equation as follows:

$$t_0 = (-0.3922) - 0.2752 \log L_{\infty} - 1.038 \log K \dots\dots\dots(5)$$

Since direct comparison of the growth parameters (K and L_{∞}) between stocks is not desirable because of their correlation (Spare and Vanema, 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:

$$\Phi' = 2 \log_{10} L_{\infty} + \log_{10} K \dots\dots\dots(6)$$

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_{∞} for the sites (Kimura, 1980). 95% confidence intervals (CI) were determined by bootstrapping K and L_{∞} values, with replacement, to generate 1000 estimates of these parameters (Kimura, 1980; Efron and Tibshirani, 1993). 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 and were used to compare similarity of the growth functions of the species from the six reef sites.

Total mortality coefficient ($Z \text{ yr}^{-1}$) 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 age groups against their corresponding age. 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, $K \text{ (yr}^{-1}\text{)}$, L_{∞} (cm) and the mean annual temperature ($T \text{ }^{\circ}\text{C}$) of the water in which the fish stock lives as follows:

$$\text{Log}_{10} (M) = -0.0152 - 0.279 * \text{log}_{10} L_{\infty} + 0.6543 \text{log}_{10} K + 0.463 \text{log}_{10} T \dots\dots\dots(7)$$

T - the annual mean sea surface temperature was taken as 27°C for the Kenyan coast (Kaunda-Arara *et al.*, 2005). Since fishing is not allowed inside the parks, estimates of Z from the parks were taken to reflect natural mortality. Fishing mortality ($F \text{ yr}^{-1}$) was derived from the difference between Z and M at non-protected sites. The exploitation level (E) of the parrotfish at the different sites was obtained following Gulland (1971) as follows:

$$E = F/Z \dots\dots\dots(8)$$

E is considered optimal (E_{opt}) at $E = 0.5$ and excessive at $E > 0.5$.

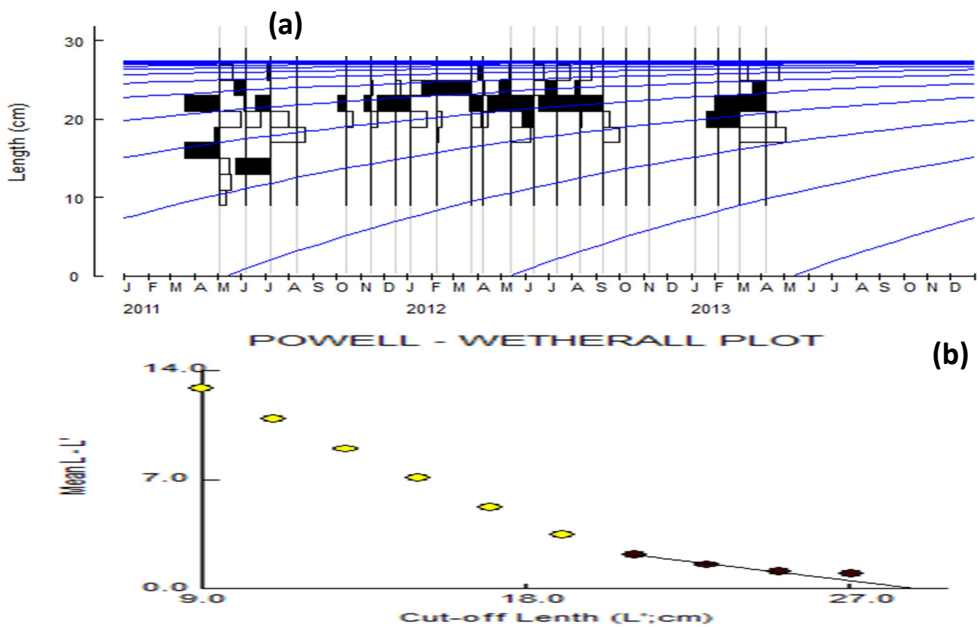
The annual recruitment pattern of the fish at sites was estimated by projecting the length-frequency data backward onto the time axis down to zero length, using the von Bertalanffy growth equation and the estimated growth parameters (Pauly, 1982) in the FiSAT program.

3.0 Results

3.1 Growth Parameters

A total of 2701 *Leptoscarus vaigiensis* were caught during the study period, 712 in Malindi Reserve, 126 in Watamu Reserve, 321 in Watamu Park, 391 in Malindi Park, 554 in Kanamai and 597 in Vipingo. Fish lengths from protected areas ranged from 13.0-25.8 cm TL in Malindi Park to 13.0-28.9 cm TL in Watamu Park whereas those from non-protected areas ranged from 8.1-26.5 cm TL from Vipingo to 8.9-27.8 cm TL in Kanamai. Fish from reserve sites had lengths ranging from 13.4-29.0 cm TL in Malindi Reserve to 18.2-27.7 cm TL in Watamu Reserve.

The analysis and outputs from the FiSAT II program obtained for Watamu Marine Park, by way of example of the outputs, is shown in Figure 2, while the growth estimates are shown in Table 1. 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 1). 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 1). Estimates of Phi-Prime (Φ) were comparable between the sites of similar protection level (Table 1) suggesting less variability of K and L_{∞} describing growth curves of the species between sites of similar protection status. 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 1). There was a significant



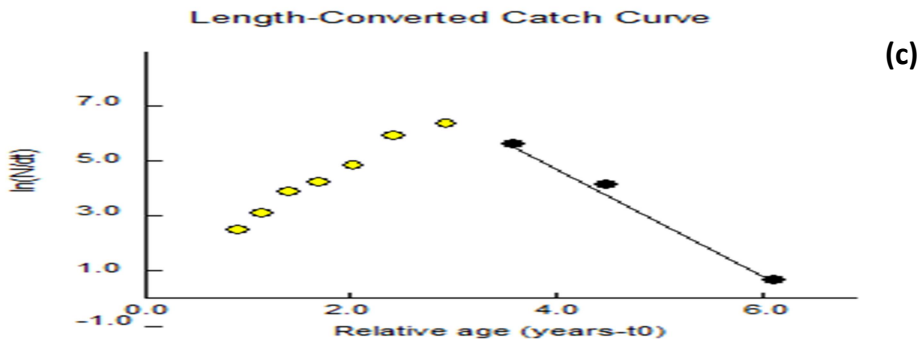


Figure 2: Output of growth parameter analyses for *Leptoscarus vaigiensis* derived by way of example for Watamu Marine Park, Kenya, using the FiSAT II program:

- a) von Bertalanffy growth curves (continuous lines) of cohorts superimposed over re-structured length frequency data. Peaks (black) are positive points and troughs (white) are negative points;
- b) Powell-Wetherall plot for estimation of asymptomatic length (L_{∞}). Black dots on the right side were used for regression analysis;
- c) Linearized length-converted curve used to estimate instantaneous annual total mortality rate (z). N is the number of fish in length class l 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_{∞} .

Table 1: The von Beterlanffy growth parameters (asymptotic length, L_{∞} , cm; instantaneous growth rate, K/yr ; age at which length equals zero, t_0), maximum length, L_{max} (cm), goodness of fit index (Rn), growth performance index (Φ') of *Leptoscarus vaigiensis* from reefs of different protection levels in coastal Kenya. Dash (-) denote lack of data.

Site	Powell-Wetheall plot L_{∞} (cm)	ELEFAN L_{∞} (cm)	L_{max} (cm)	K	Rn	Φ'	t_0
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

Tanzania, Dar-es-Salaam ^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)

relationship between asymptotic sizes (L_{∞}) 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_{∞}) among sites using bootstrapping technique indicated two distinct overlapping groupings of confidence regions between sites (Figure 3). One grouping comprised the overlapped confidence regions of park sites, while the other distinct group comprised the overlapped confidence regions of non-protected sites of Kanamai and Vipingo as well as that of Malindi Reserve (Figure 3). 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 3). Overlapping confidence regions around the growth parameter estimates at sites is taken to indicate similarity of the growth patterns of fish between sites.

3.2 Variation in Mortality

The total mortality ($Z \text{ yr}^{-1}$) estimates for *L. vaigiensis* from this study were lower at marine parks (1-2) and higher at reserves (3-9) and non-protected sites (4-5) (Table 2). The natural mortality ($M \text{ yr}^{-1}$) estimates although different between reserve sites, were comparable among park (~ 1) and non-protected (~ 2) sites (Table 2). Higher fishing mortality ($F \text{ yr}^{-1}$) estimate (6.45) was derived for the partially protected Malindi Reserve, while a lower value (1.39) was obtained for the

Watamu Reserve (Table 2). Moderate estimates of fishing mortality were obtained for the non-protected sites of Kanamai (1.95) and Vipingo (2.72) (Table 2). 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) indicating likely ineffectiveness of “reserve” status in protecting fish populations from high fishing mortality (Table 2).

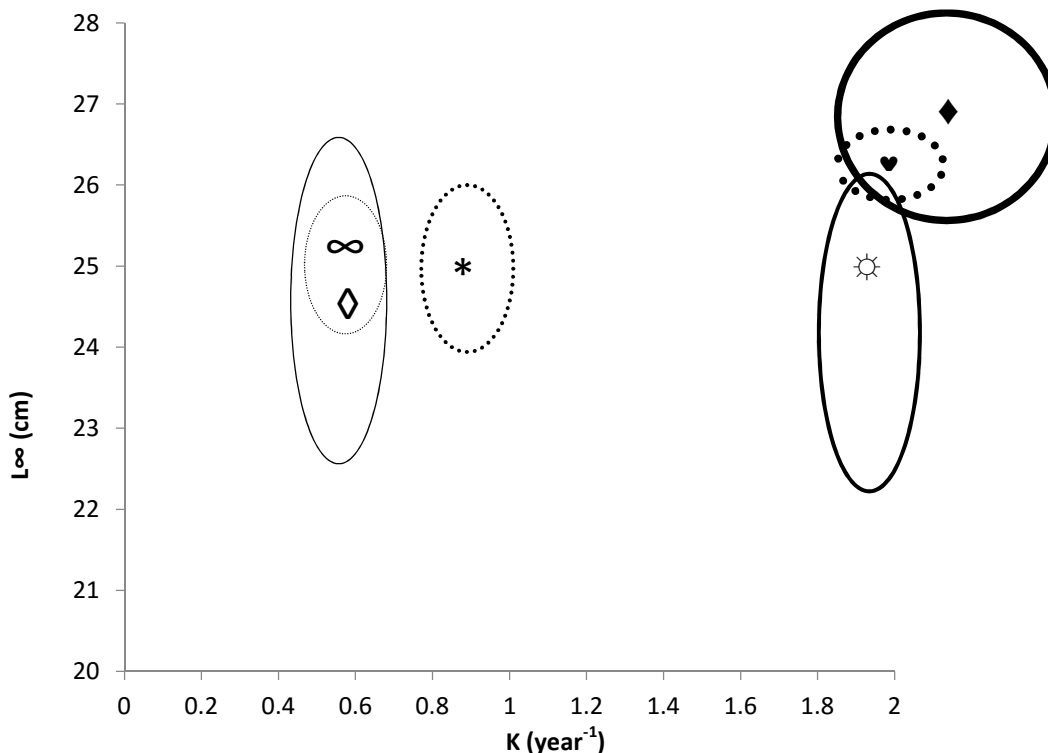


Figure 3: Comparison of VBGF parameters, L_{∞} and K , with 95% confidence regions estimated for *Leptoscarus vaigiensis* at sites of different protection levels in coastal Kenya. Malindi Park (\diamond ,), Watamu Park (∞ , —), Watamu Reserve ($*$,), Kanamai (\odot , —), Vipingo (\heartsuit ,), Malindi Reserve (\blacklozenge , —).

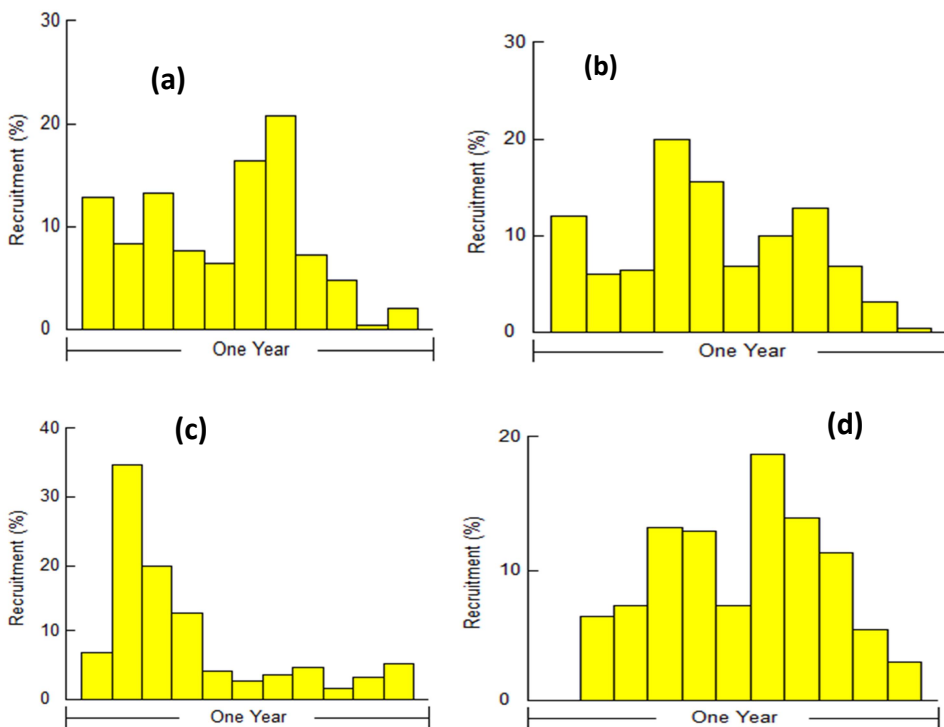
Table 2: Total mortality ($Z \text{ yr}^{-1}$), natural mortality ($M \text{ yr}^{-1}$), fishing mortality ($F \text{ yr}^{-1}$) coefficients and exploitation rate (E) of *Leptoscarus vaigiensis* from six reefs of different protection levels in coastal Kenyan. Dash (-) denote not determined.

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

3.3 Variation in Recruitment Patterns

Annual relative recruitment patterns of *L. vaigiensis* (Figure 4) shows 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 4c). Recruitment pattern of fish from the non-protected site of Kanamai showed two uneven pulses (Figure 4a), whereas those from Vipingo had three annual recruitment pulses (Figure 4b). Fish from reserve sites had variable recruitment patterns with those from Malindi Reserve showing a single peak (Figure 4c), while those from



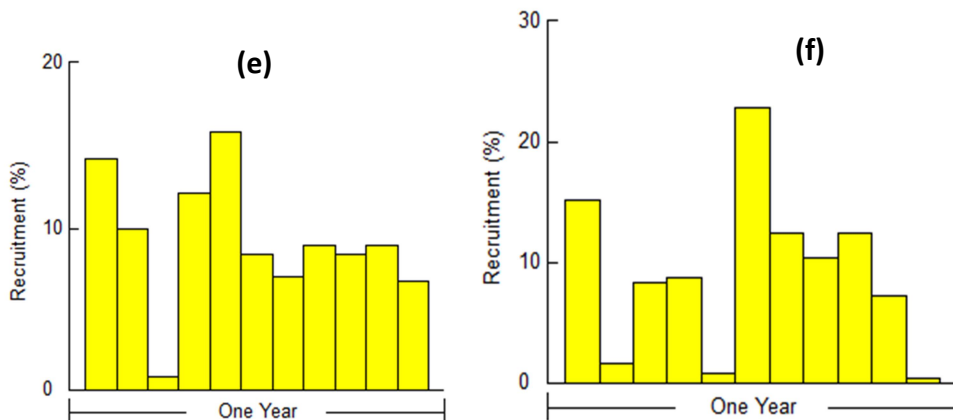


Figure 4: Annual recruitment pattern of *Leptoscarus vaigiensis* at the six sites of different protection levels in coastal Kenya: a) Kanamai, b) Vipingo, c) Malindi Reserve, d) Watamu Reserve, e) Malindi Park, and f) Watamu Park.

Watamu Reserve had two pulses (Figure 4d). Recruitment pattern was similar among fish from park sites with two major annual pulses.

4.0 Discussion

This study estimated in the Western Indian Ocean (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 including nutrient regime, habitat characteristics and degree of predation. 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 and 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 as reported by Locham *et al.*, (2015a). However, the higher asymptotic sizes at fished sites suggest continued growth after maturation (Heino and Godo, 2002). The causes for the continued growth to higher asymptotic lengths at these sites may be mediated by reduced competition for resources. The correlation between L_{∞} and K suggests that asymptotic size is reached faster after maturation (Heino and 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 (Kuparinen and Merila, 2007) 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 and 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 indicate 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 on reproductive output and timing; however, the data generated is inadequate to explain the spatial variability in recruitment as determined.

In conclusion, 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. Additionally, this study has generated the growth and mortality parameters for this commercially important species thereby adding to the scarce database on these parameters (see www.Fishbase.org) within the WIO region. Based on the results of this study, 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.

Acknowledgements

The authors thank PADI Foundation and National Council of Science and Technology (NCST) for funding this study through a fellowship to the first author. We are grateful to the directors of Kenya Wildlife Service (KWS) and Kenya Marine and Fisheries Research Institute (KMFRI) for permitting research in the Marine Protected Areas (Parks) and for providing laboratory facilities, respectively. Field support provided by Mr. Boaz Orembo, Mr. Ben Ogola, Mr. Michael Kazungu and Mr. Sammy Kazungu during data collection was highly appreciated.

References

- Benno, B.L. (1992). *Some features of beach seine fishery along the Dar es Salaam coast, Tanzania*. M. Sc. thesis, University of Kuopio. Finland. pp 68.
- Candolin, U. (2009). Population responses to anthropogenic disturbance: Lessons from three-spined sticklebacks *Gasterosteus aculeatus* in eutrophic habitats. *Journal of Fisheries Biology*, 75, 2108-2121.
- Cardinale, M. and 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.
- Dalzell, P. (1996). Catch rates, selectivity and yields of reef fishing. In N.V.C. Polunin and C.M. Roberts (Eds.), *Reef fisheries* (pp. 161-192). London: Chapman and Hall.
- Dieckmann, U. and Heino, M. (2007). Probabilistic maturation reaction norms: their history, strengths, and limitations. *Marine Ecological Progress Series*, 225, 253-269.
- Dumas, J. and Prouzet, P. (2003). Variability of demographic parameters and population dynamics of Atlantic salmon, *Salmon salar* L. in south-west French river. *ICES Journal of Marine Science*, 60, 356-370.
- Efron, B. and Tibshirani, R. (1993). *An introduction to the bootstrap*. New York: Chapman and Hall. pp 436.
- Enberg, K., Jørgensen, C., Dunlop, E., Heino, M. and Dieckmann, U. (2009). Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evolutionary Applications* 2, 394-414.
- Gayanilo, Jr., Sparre, F., and Pauly, P.D. (1996). *FAO-ICLARM Stock Assessment Tools* (FISAT). Rome: Food and Agriculture Organisation of the United Nations. pp 168.
- Gulland, J.A. (1971). *The fish resources of the ocean*. London: Fishing News Books. pp 255.
- Haug, R. and 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.
- Heino, M. and 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, 562-75.
- Hicks, C. C. and 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.
- Hutchings, J. and 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.

- Jennings, S. and Kaiser, M. J. (1998). The effects of fishing on marine ecosystems. *Advances in Marine Biology*, 68, 201-352.
- Kaunda-Arara, B., Rose, G.A., Muchiri, S. M. and Kaka, R. (2005). 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(2), 105-116.
- Kaunda-Arara, B. and Rose, G. A. (2004). Outmigration of tagged fishes from marine reef National Parks to fisheries in coastal Kenya. *Environmental Biology of Fishes*, 70, 363-372.
- Kelly, J. E., Frank, K. T. and Leggett, W.C. (2009). Degraded recruitment synchrony in Northwest Atlantic cod stocks. *Marine Ecology Progress Series*, 393, 131-146.
- Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin*, 77, 765-774.
- Kuparinen, A. and Merila, J. (2007) Detecting and managing fisheries-induced evolution. *Trends in Ecology and Evolution*, 22, 652-659.
- Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, 57, 659-668.
- Locham, A.L., Kaunda-Arara, B., Wakibia, J. and Muya, S. (2015). Phenotypic divergence in reproductive traits of the marbled parrotfish, *Leptoscarus vaigiensis* (Quoy and Gaimard 1824), among reef of varying protection levels in Kenya. *Western Indian Ocean Journal of Marine Science*, 1, 69-80.
- McClanahan, T. R. (1988). Seasonality in East Africa's coastal waters. *Marine Ecological Progress Series* 44, 191-199.
- McClanahan, T. R. and Obura, D. (1995). Status of Kenyan Coral reefs. *Coastal Management*, 23, 57-76.
- Morita, K. and 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.
- 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, University of Nairobi, Kenya. pp 94.
- Otieno, A. N. (2002). *Catch assessment on the artisanal fisheries of Mpunguti Marine Reserve, Shimoni and Funzi Bay, southcoast Kenya*. Unpublished M. Sc. Thesis, University of Nairobi, Kenya. pp 118.
- 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. (1983). Length-converted catch curves: a powerful tool for fisheries research in the tropics - Pt. 1. *Fishbyte*, 1, 9-13.
- Pauly, D. (1982). Studying single-species dynamics in a tropical multispecies context. *ICLARM Conference Proceedings*, 9, 33-70.

- Pauly, D. (1980). On the interrelationship between natural mortality, growth parameters, mean environmental temperature in 175 fish stock. *International Council for the Exploration of the Sea (ICES)*, 39(3), 175-192.
- Pauly, D. and Munro, J. L. (1984). Once more on growth comparison in fish and invertebrates. *Fishbyte, ICLARM*, 2(1), 1-21
- Pauly, D., Ingles, J. and 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 and B. J. Rothschilds (Eds.), *Panaeid shrimps- their ecology and management* (pp. 220-234). London: Fishing News Books.
- Quoy, J.R. and Gaimard, P. (1824). Zoologie. Poissons. In : L. de Frechet. Voyage autour de monde, entrepris par ordre du Roi, exécuté sur les corvettes de S M l'URANIE et la PHYSICIENNE, pendant les années 1817-1820. Paris.
- Russ, G. (2003). Grazer biomass correlates more strongly with production than biomass of algal turfs on a coral reef. *Coral Reef*, 22, 63 - 67.
- Sparre, P. and Venema, S. C. (1998). *Introduction to tropical fish stock assessment. Part 1 manual*. Fisheries Technical Paper 306. Rome: Food and Agriculture Organization of the United Nations.
- Trippel, E. A. (1995). Age at maturity as a stress indicator in fisheries. *BioScience*, 45, 759-771.