

Diet and niche breadth variation in the marbled parrotfish, *Leptoscarus vaigiensis*, among coral reef sites in Kenya

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Abstract

Studies on feeding ecology of fishes are important for understanding ecosystem structure and function. This study tested the hypothesis of diet and niche breadth variation in the marbled parrotfish (*Leptoscarus vaigiensis*) among coral reefs of different protection levels in Kenya. Fish samples were obtained from protected (Malindi and Watamu marine parks), moderately fished (Malindi and Watamu marine reserves) and highly fished (Vipingo and Kanamai) reefs. Total lengths of fish samples were measured and their stomach contents quantified using the point method. Seasonal dietary composition, niche breadths and feeding intensities were compared between the sites using multivariate statistics. Results showed the parrotfish is a predominantly reef macroalgal grazer. Fish from protected sites fed on diverse dietary items compared to those from reserves and highly fished sites. Fish niche breadths differed between sites and seasons. Higher niche breadths occurred in protected sites during the north-east monsoon, while higher values occurred at fished sites during the south-east monsoon season. This study, the first of its kind in Kenya and most of the western Indian Ocean, describes feeding in the marbled parrotfish and spatial variation in niche breadth as influenced by fishing pressure, environmental variability and biological interactions.

Key words: benthic macroalgae, coral reefs, fishing pressure, phenotypic plasticity

Résumé

Les études sur l'écologie alimentaire des poissons sont importantes pour bien comprendre la structure et la fonction de l'écosystème. Cette étude a testé l'hypothèse d'une variation de régime alimentaire et de niche chez le

poisson perroquet *Leptoscarus vaigiensis* dans des récifs coralliens soumis à des niveaux de protection différents au Kenya. Des échantillons de poissons furent prélevés sur des récifs protégés (Parcs Marins de Malindi et de Watamu), pêchés avec modération (Réserves Marines de Malindi et de Watamu) et intensément pêchés (Vipingo et Kanamai). La longueur totale de ces poissons a été mesurée et leur contenu stomacal a été quantifié par la Méthode de point. La composition saisonnière du régime alimentaire, l'étendue des niches et l'intensité trophique furent comparées entre les sites au moyen de statistiques multivariées. Les résultats ont montré que le poisson perroquet est principalement un brouteur de macroalgues de récifs. Les poissons des sites protégés mangeaient des aliments plus variés que les poissons des réserves et des sites fortement pêchés. La taille des niches différait selon les sites et les saisons. Les niches étaient plus grandes dans les sites protégés pendant la mousson du nord-est alors que des valeurs plus élevées étaient relevées dans les sites pêchés pendant la saison de la mousson du sud-est. Cette étude, la première de ce genre au Kenya et dans la plus grande partie de l'ouest de l'océan Indien, décrit l'alimentation du *Leptoscarus vaigiensis* et examine la variation spatiale de la taille des niches, influencée par la pression de la pêche, la variabilité environnementale et les interactions biologiques.

Introduction

In fishes, niche breadths are commonly defined in terms of range of prey organisms found in the guts (Cohen & Lough, 1983) and 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). As proposed

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by the 'niche variation hypothesis' (Van Valen, 1965), population niche breadths are constrained when exposed to strong interspecific competition and broadened when released from such competition and subjected only to intraspecific competition. On the other hand, 'optimal foraging theory' (*sensu* MacArthur & Pianka, 1966) postulates that local biotic conditions such as predation can affect the foraging strategy and therefore diet composition or niche breadths of individuals.

Measures of niche breadth have been used to test several hypotheses including that wide-niched species (generalists) are better adapted to uncertain environments than do those with narrow niche breadths (specialists) (Levins, 1968). Niche expansion can also be associated with an increase in phenotypic variance or

character release (Van Valen, 1965; Bolnick, 2001), polymorphism or adaptive radiation (Bolnick, 2001). Although the relationship between intraspecific competition and species diversification is known from theory (Roughgarden, 1976; Wilson & Turelli, 1986), there is little empirical proof indicating niches diversification in response to intra- or interspecific competition (Blanchard, 2001) as may be mediated by drivers like fishing effort or resource availability.

In this study, we aimed at testing the hypothesis of diet and niche breadth variation in the marbled parrotfish, *Leptoscarus vaigiensis* (Quoy & Gaimard, 1824), between coral reefs of different fishing intensity in coastal Kenya. The marbled parrotfish is a less mobile, commercially important coral reef fish and their site fidelity, as is the

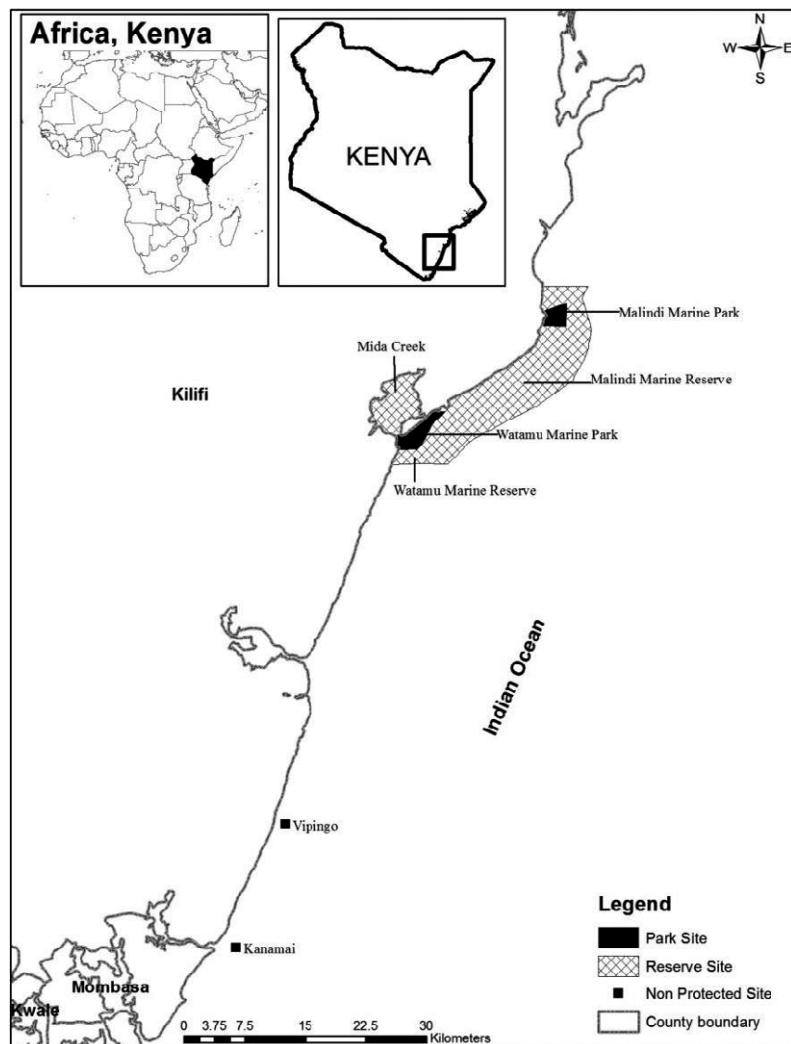


Fig 1 A map of Kenya's coastline showing the sites sampled for the marbled parrotfish, *Leptoscarus vaigiensis*

case for many coral reef fishes (Sale, 2002), is likely to expose them to high fishing mortality at fished sites. We hypothesized that the diversity of its food items (niche breadth) will vary between fished sites (with presumably less interspecific competition) and protected sites such as marine parks (with higher predation rates and competition for food resources due to high fish diversity and biomass).

Materials and methods

The study was carried out on six reef sites of different protection levels in coastal Kenya (Fig. 1). Two of the sites (Malindi and Watamu marine parks) are protected and exclude extractive exploitation of resources and are designated as 'marine parks'. Malindi and Watamu marine reserves are buffer areas adjacent to the parks where regulated fishing by 'traditional' methods is practiced. The other reefs (Kanamai and Vipingo, Fig. 1) are open access sites with no formal regulatory framework. Samples of *L. vaigiensis* were collected from the protected (Malindi and Watamu Parks), reserve (Malindi and Watamu adjacent marine reserves) and nonprotected (Vipingo and Kanamai) reef sites (Fig. 1). Kenyan coral reefs are predominantly shallow (10–12 m at high tide) lagoonal fringing reefs that run parallel to the coastline and have a mosaic of substrate (seagrass beds, benthic algae, sand, coral rubble, live and dead corals) characteristics. These lagoonal reefs have grossly comparable habitat and substrates type along the coast (McClanahan & Shafir, 1990; Kaunda-Arara & Rose, 2004).

The Kenyan coast experiences seasonality caused by both north-easterly and south-easterly monsoon winds described in details in McClanahan (1988). Briefly, the north-east monsoon season (NEM, November–March) is a period of calm seas, elevated sea surface temperatures and higher salinities, while the south-east monsoon season (SEM, April–October) is characterized by rough seas, cool weather, lower salinities and higher primary productivity. Although the influence of this seasonality on the reproductive biology of fishes is known (Nzioka, 1979; Kaunda-Arara & Ntiba, 1998), its effects on feeding ecologies remain largely unstudied but are important in understanding population dynamics of coral reef fishes.

Field and laboratory procedures

Samples of *L. vaigiensis* were caught monthly within protected sites (Malindi and Watamu marine parks and their

reserves, Fig. 1) using local baited traps called *Demas* during 2012. In the nonprotected sites (Vipingo and Kanamai, Fig. 1), samples 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 from the sites were analysed in the laboratory, where total lengths of fish were measured (nearest millimetre) and stomachs removed and preserved in 10% formalin. Contents of the stomachs were observed under a light microscope and the food items identified to the lowest taxon using identification keys (e.g. Morjani & Simpson, 1988; Oliveira, Katrin & Matern, 2005; Bolton, Oyieke & Gwanda, 2007). The point method (Mohamed, 2004) was used to quantify the food items in the 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. The diet item with the highest proportion was given a maximum of sixteen 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.

The monthly frequency of occurrence (F_i) of the food items was computed following Hyslop (1980) as: $F_i = \frac{100n_i}{n}$, where n_i is 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.

Correspondence analysis (CA) was used to examine possible ontogenetic preferences in diet of the fish based on nineteen food items whose numerical abundance was $\geq 0.5\%$. In the analysis, fish of size group 7.0–15.9 cm TL were categorized as juveniles (M1), whereas those of 16.0–21.9 cm TL as maturing (M2) and those of >22.0 cm TL as mature (M3) based on sizes at first maturity from FishBase (www.fishbase.org).

To determine niche breadth (defined as the amount and range of food items used by an individual) of the fish at each site, Levins' measure of niche breadth (B) (Levins, 1968) was derived as:

$$B = 1 / \sum p_i^2,$$

where p_i is the proportion by volume of the i th food category in the diet. 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

Table 1 Percentage frequency of occurrence of food items in the gut of *Leptoscarus vaigiensis* from reef sites in coastal Kenya during north-east monsoon season

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) Marine algae						
Anadyomenaceae						
<i>Anadyomene</i> spp.	–	–	–	–	–	0.9
Areschougiaceae						
<i>Eucheuma</i> spp.	–	–	–	–	–	0.9
Bachelotiaceae						
<i>Bachelotia</i> spp.	13.0	–	–	11.1	–	6.6
Boodleaceae						
<i>Boodlea</i> spp.	–	–	–	–	–	1.9
Champiaceae						
<i>Champia</i> spp.	0.8	–	–	–	–	–
Caulerpaceae						
<i>Caulerpa</i> spp.	0.8	–	3.7	–	1.1	0.9
Ceremiaceae						
<i>Centroceras</i> spp.	32.1	16.7	11.1	36.1	5.4	4.7
<i>Ceramium</i> spp.	32.1	16.7	14.8	25.0	55.4	37.7
Cladophoraceae						
<i>Chaetomorpha</i> spp.	6.9	16.7	7.4	5.6	6.5	10.4
<i>Cladophora</i> spp.	11.5	–	3.7	1.4	19.6	35.8
<i>Rhizoclonium</i> spp.	–	–	7.4	1.4	–	1.9
Corallinaceae						
<i>Amphiroa</i> spp.	0.8	–	–	–	–	–
<i>Cheilosporum</i> spp.	6.9	–	–	1.4	7.6	–
<i>Haliptilon</i> spp.	0.8	–	–	–	5.4	–
<i>Jania</i> spp.	35.9	16.7	18.5	22.2	26.1	15.1
Cystocloniaceae						
<i>Hypnea</i> spp.	–	–	–	1.4	–	–
Dasyaceae						
<i>Dasya</i> spp.	8.4	–	–	8.3	23.9	5.7
<i>Heterosiphonia</i> spp.	–	16.7	–	–	–	–
Dasycladaceae						
<i>Bornetella</i> spp.	–	–	–	–	–	0.9
<i>Neomeris</i> spp.	–	–	–	–	2.2	0.9
Delesseriadeceae						
<i>Vanvoorstia</i> spp.	–	–	–	1.4	–	–
Galaxauraceae						
<i>Actinotrichia</i> spp.	1.5	–	–	2.8	–	–
<i>Galaxaura</i> spp.	0.8	–	–	–	–	–
Rhodomelaceae						
<i>Chondrophycus</i> spp.	32.1	16.7	14.8	48.6	5.4	20.8
<i>Amansia</i> spp.	2.3	–	3.7	2.8	12.0	0.9
<i>Dipterosiphonia</i> spp.	–	–	–	–	2.2	–
<i>Herposiphonia</i> spp.	20.6	16.7	14.8	6.9	20.7	17.9
<i>Laurencia</i> spp.	1.5	–	–	1.4	1.1	–
<i>Leveillea</i> spp.	19.8	16.7	29.6	25.0	15.2	5.7
<i>Lophosiphonia</i> spp.	10.7	–	3.7	2.8	–	0.9
<i>Polysiphonia</i> spp.	2.3	–	–	2.8	3.3	0.9

(continued)

Table 1 (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
Rutaceae						
<i>Murrayella</i> spp.	–	–	–	–	1.1	–
Sargassaceae						
<i>Sargassum</i> spp.	58.0	33.3	51.9	52.8	55.4	55.7
Solieraceae						
<i>Solieria</i> spp.	1.5	–	–	–	–	–
Scytosiphoniaceae						
<i>Rosenvingea</i> spp.	–	–	–	1.4	–	–
Spyridiaceae						
<i>Spyridia</i> spp.	3.8	–	–	1.4	1.1	2.8
Ulvacaeae						
<i>Enteromorpha</i> spp.	55.0	50.00	55.6	61.1	72.8	77.4
<i>Ulva</i> spp.	35.1	33.3	18.5	23.6	32.6	34.9
Valoniaceae						
<i>Valonia</i> spp.	0.8	–	–	–	–	–
<i>Valoniopsis</i> spp.	–	–	–	–	–	0.9
(b) Seagrasses						
Cymodoceaceae						
<i>Cymodocea</i> spp.	1.5	–	–	–	1.1	0.9
<i>Thalassodendron</i> spp.	77.9	33.3	59.3	68.1	91.3	88.7

Dash (–) represents zero occurrence. 'N' denotes number of stomachs examined at sites.

categories, each representing an equal proportion of the diet. The effect of season and site on niche breadths of the species was tested using two-way ANOVA after conversion to Log ($x + 1$) (Zar, 1999). As there is likely to be size-based differences in niche breadths, a skewness index (Sk) was used to compare size-frequency distribution of fishes from the sites. The skewness index was derived from the difference between the median (Md) and mean (μ) of the size frequencies weighted by the median (Zar, 1999).

The feeding intensity (FI) of the fish at sites was derived following Hyslop (1980) as: $FI = \text{weight of food items in stomach} / \text{weight of fish} \times 100$. The monthly mean feeding intensities at sites (y) were then related to niche breadths (x) using the nonlinear second-order polynomial regression of the form: $y = a_0 + a_1x + a_2x^2 + \varepsilon$.

Results

Spatial variation in diet

A total of 42 genera belonging to 22 families of benthic macroalgae and seagrasses formed the diet of *L. vaigiensis* during the NEM season (Table 1). During this season,

diet of the fish at sites consisted mostly of the seagrass, *Thalassodendron ciliatum* (33.3–91.3%), and the algae, *Enteromorpha* spp. (50–77.4%) and *Sargassum* spp. (33.3–58.0%) (Table 1). Eleven genera of algae were common in the diet across all sites during this season, whereas sixteen constituted diet of fish from specific sites (Table 1). 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 1).

During the SEM season (Table 2), 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. Similar to the NEM season, diet of the parrotfish at sites during SEM season consisted mostly of the seagrass, *T. ciliatum* (79.2–88.2%), the algae, *Enteromorpha* spp. (70.0–88.2%) and *Sargassum* spp. (57.3–88.2%) but at higher proportions (Table 2). Thirteen genera of algae were common in the diet across all sites during this season, whereas fourteen

Table 2 Percentage frequency of occurrence of food items in the gut of *Leptoscarus vaigiensis* from reef sites in coastal Kenya during south-east monsoon season

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) Marine algae						
Acinetosporaceae						
<i>Hincksia</i> spp.	–	–	1.0	–	–	–
Bachelotiaceae						
<i>Bachelotia</i> spp.	6.3	–	5.0	4.0	2.1	4.7
Bonnemaisoniales						
<i>Asparagopsis</i> spp.	0.7	–	–	–	–	–
Boodleaceae						
<i>Boodlea</i> spp.	0.7	–	–	–	1.0	1.6
<i>Cladophoropsis</i> spp.	–	–	1.0	–	–	3.1
Champiaceae						
<i>Champia</i> spp.	0.7	–	–	–	–	–
Caulerpaceae						
<i>Caulerpa</i> spp.	9.9	17.6	11.0	11.2	16.7	6.3
Ceremiaceae						
<i>Centroceras</i> spp.	19.0	–	–	7.2	–	4.7
<i>Ceramium</i> spp.	40.8	41.2	42.0	22.4	44.8	48.4
Cladophoraceae						
<i>Chaetomorpha</i> spp.	4.2	–	5.0	2.4	1.0	1.6
<i>Cladophora</i> spp.	19.7	11.8	16.0	20.8	17.7	15.6
Corallinaceae						
<i>Amphiroa</i> spp.	–	–	1.0	–	–	–
<i>Cheilosporum</i> spp.	14.8	17.6	14.0	14.4	7.3	1.6
<i>Haliptilon</i> spp.	–	–	2.0	–	–	–
<i>Jania</i> spp.	66.2	64.7	26.0	14.4	17.7	25.0
Cystocloniaceae						
<i>Hypnea</i> spp.	–	–	–	–	–	–
Dasyaceae						
<i>Dasya</i> spp.	17.6	–	14.0	20.0	16.7	32.8
<i>Dictyurus</i> spp.	–	–	–	–	1.0	–
<i>Heterosiphonia</i> spp.	0.7	–	2.0	–	–	–
Dasycladaceae						
<i>Bornetella</i> spp.	–	–	1.0	–	2.1	–
Delesseriadeceae						
<i>Vanvoorstia</i> spp.	–	–	–	–	1.0	1.6
Galaxauraceae						
<i>Galaxaura</i> spp.	–	–	1.0	–	–	–
Gracilariaceae						
<i>Gracilaria</i> spp.	2.1	–	–	1.6	–	1.6
Lomentariaceae						
<i>Gelidiopsis</i> spp.	–	–	–	0.8	–	1.6
Rhodomelaceae						
<i>Chondrophyucus</i> spp.	12.0	11.8	5.0	11.2	3.1	7.8
<i>Amansia</i> spp.	2.1	–	–	–	1.0	–
<i>Dipterosiphonia</i> spp.	0.7	–	–	0.8	–	–
<i>Chondria</i> spp.	–	5.9	1.0	–	–	1.6
<i>Herposiphonia</i> spp.	9.9	11.8	19.0	11.2	22.9	14.1

(continued)

Table 2 (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
<i>Laurencia</i> spp.	3.5	5.9	1.0	0.8	–	6.3
<i>Leveillea</i> spp.	23.9	23.5	24.0	6.4	8.3	12.5
<i>Lophosiphonia</i> spp.	8.5	5.9	–	4.8	1.0	3.1
<i>Polysiphonia</i> spp.	4.2	5.9	5.0	1.6	1.0	6.3
Rhodymeniaceae						
<i>Botryocladia</i> spp.	0.7	–	–	–	–	–
Rutaceae						
<i>Murrayella</i> spp.	1.4	–	–	–	–	–
Sargassaceae						
<i>Hormophysa</i> spp.	0.7	–	–	2.4	–	–
<i>Sargassum</i> spp.	78.9	88.2	75.0	60.0	57.3	78.1
Siphonocladaceae						
<i>Chamaedoris</i> spp.	0.7	–	–	–	–	–
Sphacelariaceae						
<i>Sphacelaria</i> spp.	0.7	–	–	–	1.0	–
Spyridiaceae						
<i>Spyridia</i> spp.	2.1	–	–	2.4	8.3	6.3
Ulvaceae						
<i>Enteromorpha</i> spp.	83.8	88.2	70.0	74.4	84.4	87.5
<i>Ulva</i> spp.	34.5	35.3	31.0	29.6	22.9	40.6
Valoniaceae						
<i>Valonia</i> spp.	0.7	–	–	–	–	–
<i>Valoniopsis</i> spp.	0.7	–	–	–	–	–
Wrangeliaceae						
<i>Griffithsia</i> spp.	–	5.9	1.0	–	–	–
<i>Tiffaniella</i> spp.	–	–	–	0.8	–	–
(b) Seagrasses						
Cymodoceaceae						
<i>Cymodocea</i> spp.	0.7	5.9	1.0	–	–	–
<i>Thalassodredon</i> spp.	88.0	88.2	80.0	79.2	86.5	87.5

Dash (–) represents zero occurrence. 'N' denotes number of stomach examined at sites.

constituted diets of fish from specific sites (Table 2). 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 2).

Correspondence analysis was performed to analyse spatial variation of feeding (Fig. 2). The results indicated the red algae, *Actinotrichia* spp., associated with diets of all size categories of *L. vaigiensis*, while the filamentous green algae, *Cladophora* spp., associated exclusively with diets of immature size groups (Fig. 2). The genera *Caulerpa* (green algae), *Cheilosporum* (red algae), *Laurencia* (red algae) and *Leveillea* (red algae) exclusively associated with diets of

maturing size 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 (Fig. 2). The groups, *T. 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 (Fig. 2).

Size and niche breadth variation between sites

Niche breaths of the fishes from nonprotected sites of Kanamai and Vipingo showed a general decline during the

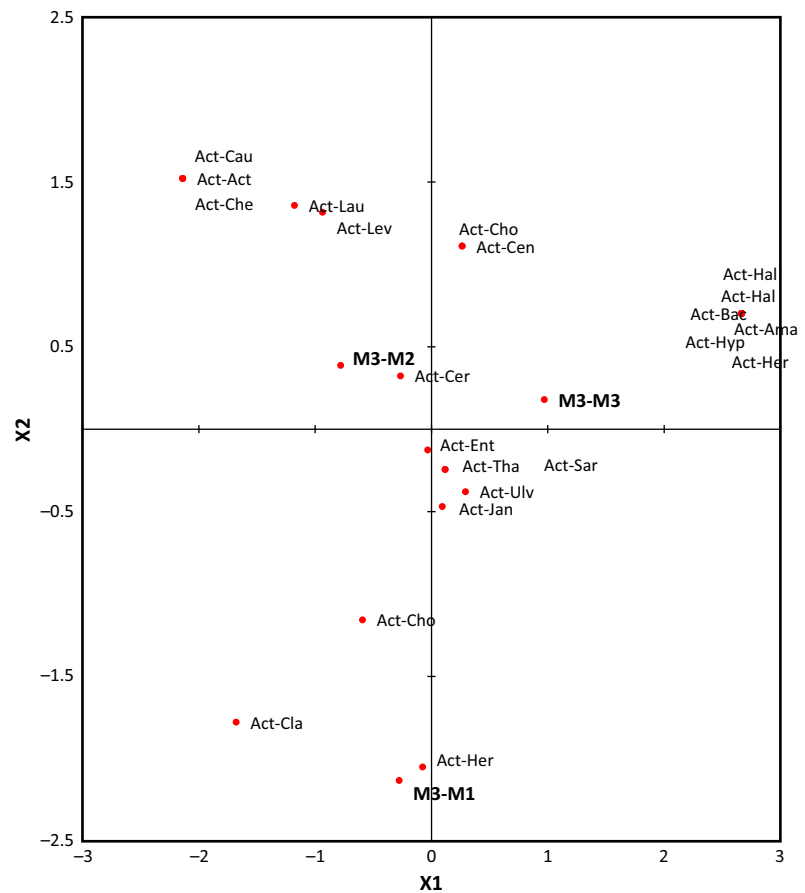


Fig 2 Correspondence analysis of the association of food items with maturity categories of *Leptoscarus vaigiensis* in coastal Kenya. M1, M2 and M3 stand for immature, maturing and mature size groups, respectively. Names of algal genera are abbreviated as contained in Tables 1 and 2. Only food items with $\geq 0.1\%$ numerical abundance were used in the analysis

calm NEM months (January–March) following a rise during November–December months of the season (Fig. 3). The niche breadths (mean \pm SE) 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–October months of this season (Fig. 3). The long-term average of the niche breadth for the fish from nonprotected sites of Vipingo (1.9 ± 0.7) and Kanamai (1.7 ± 0.6) was comparable during the NEM season as was the case during the SEM season (Vipingo = 2.2 ± 0.5 ; Kanamai = 1.9 ± 0.5).

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, Fig. 3), followed by a decline in the NEM months of November–December (Fig. 3), thereby showing a similar pattern as the nonprotected sites (Kanamai and Vipingo). The long-

term average of the niche breadth (mean \pm 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 nonprotected 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 (Fig. 3). Temporal patterns of niche breadth variation were therefore seasonally different for the park sites when compared to the nonprotected sites and the moderately fished reserve sites. Results of two-way ANOVA indicated that both site and season as well as their interaction significantly influenced niche breadths of the parrotfish (sites, $F = 4.985$, $P < 0.001$; seasons, $F = 9.859$, $P < 0.002$; sites \times season, $F = 6.879$, $P < 0.001$).

Skewness index (Sk) of the length frequencies of fish from the sites showed no substantial difference in size distribution of fish from Vipingo (Sk = 0.13), Watamu

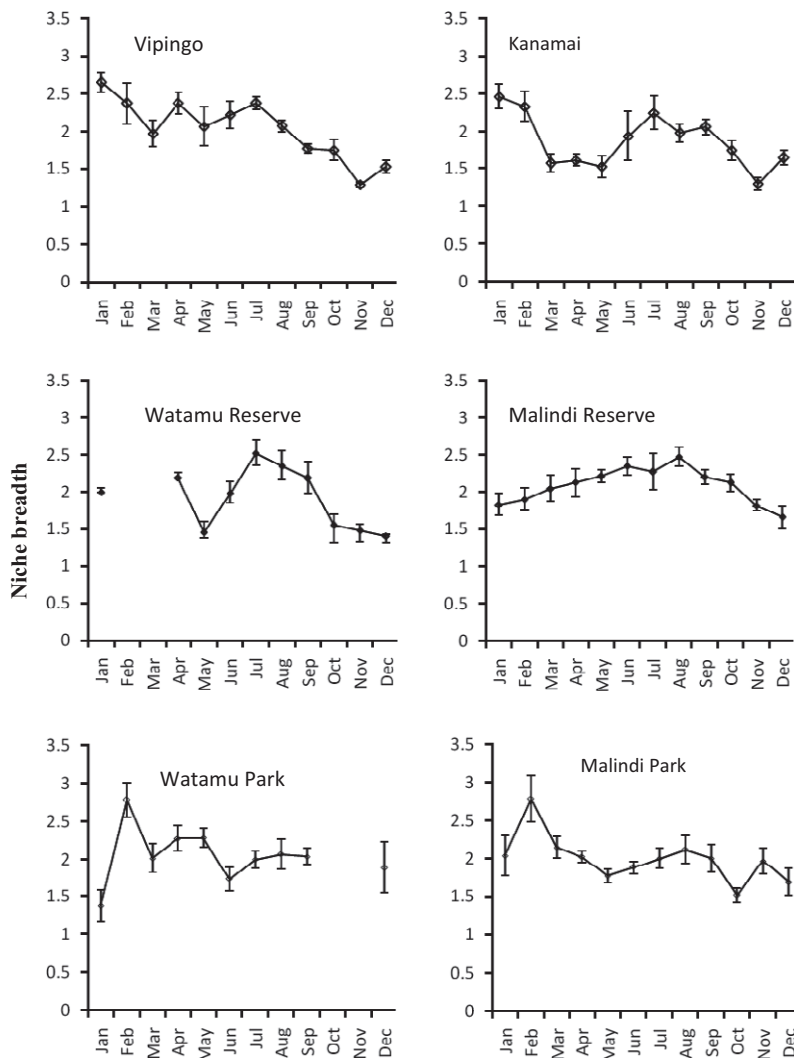


Fig 3 Temporal variation in niche breadth of marbled parrotfish, *Leptoscarus vaigiensis*, at reef sites of different protection levels in coastal Kenya. Vertical bars represent standard error of the mean

Reserve ($Sk = 0.11$), Malindi Reserve ($Sk = 0.07$), Watamu Park ($Sk = 0.14$) and Kanamai ($Sk = 0.24$). However, size distribution of fish from Malindi Park ($Sk = -0.02$) had a marginal negative skewness.

The relationship between feeding intensity and niche breadth of fishes at the different reef sites showed site-specific patterns (Fig. 4). Fish from the marine park sites had a pattern of variation of niche breadth with feeding intensity that appears to be inverse of the other (Fig. 4a). 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 (Fig. 4a). Parrotfishes at the 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 (Fig. 4b). The pattern of variation at the nonprotected sites showed fishes at Kanamai reef to have higher niche breadths than those in Vipingo at a feeding intensity range of 1.35–2.25 beyond which the fishes at Kanamai are predicted to have higher niche breadths (Fig. 4c).

Discussion

The marbled parrotfish exploits a variety of marine flora on Kenyan reefs with the most important being the seagrass,

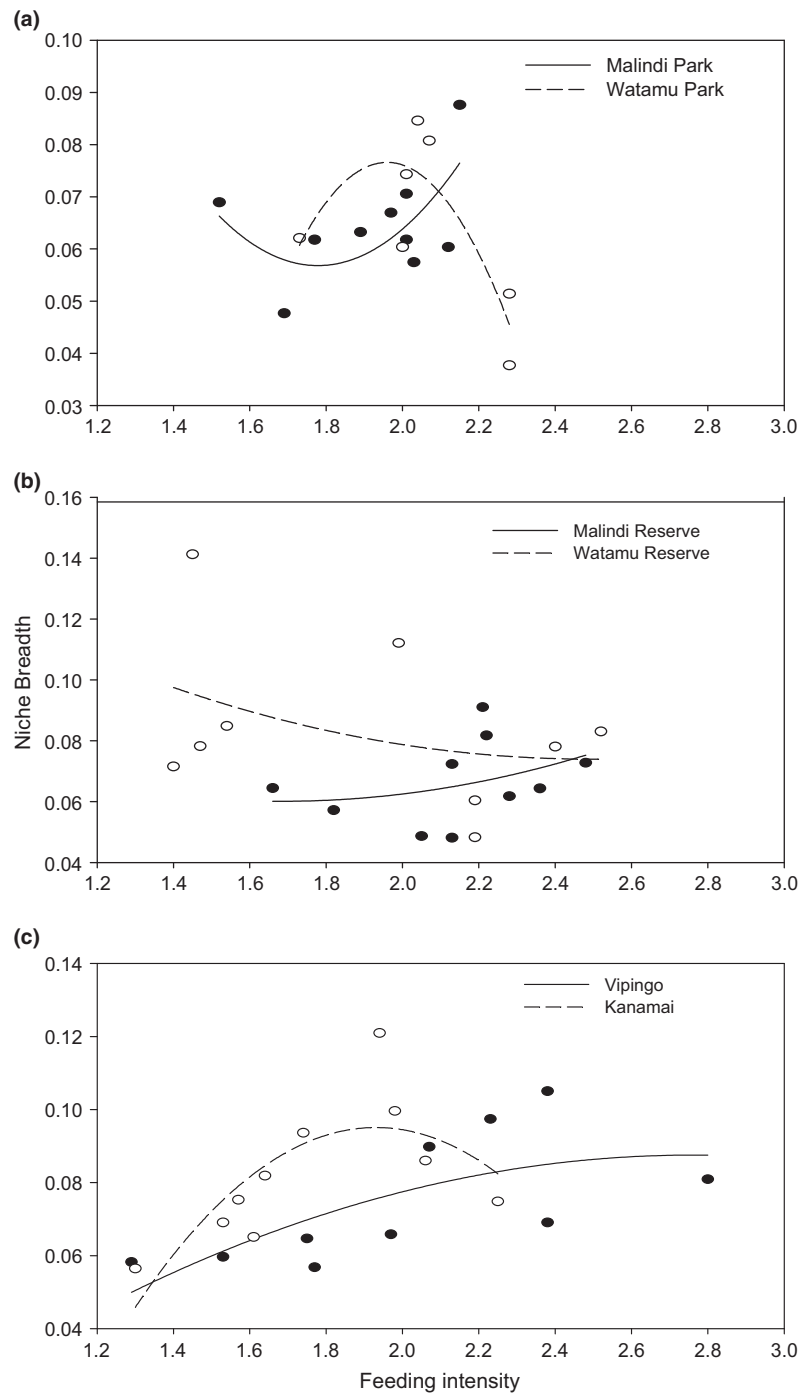


Fig 4 Second-order polynomial regression of niche breadth on feeding intensity of marbled parrotfish, *Leptoscarus vaigiensis*, from reefs of different protection levels in coastal Kenya

T. 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, Marques & Saldanha, 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 of the effect of protection level on the diet of the parrotfish. However, in general, there was higher diet diversity at sites during the hydrodynamically rough SEM season than during the calm NEM season. 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 is less intensive. Increased fishing activities on Kenyan reefs during the calm NEM season (Kaunda-Arara & Rose, 2004) together with increased predation during this season (McClanahan & Shafir, 1990) may cause fish in fished sites (reserves and nonprotected areas) to forego foraging opportunities for relative safety as a trade-off between predation and survival. This notion is further supported by the general similarity in the relationship between niche breadths and feeding intensity at the reserve and nonprotected 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 interspecific competitions, can be modified by environmental variability (such as monsoon seasonality) and fish behaviour. There was significant influence of site and season on niche breadth of the parrotfish with synchronized timing of peak niche breadths at sites of same protection regime. This synchronized timing likely indicates the 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 to broader niche breadths during the calm NEM season.

The results of CA indicated association of certain food items with the different maturity categories of fish. Certain food items associated more with immature or mature individuals suggesting 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 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 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 (McClanahan & Shafir, 1990; Kaunda-Arara & Rose, 2004).

In conclusion, the present study has shown that the marbled parrotfish consumes a variety of plant food resources. Increased fishing activities during the calm NEM season likely cause fish in fished sites (reserves and nonprotected areas) to forego foraging opportunities as a trade-off between mortality and survival. This trade-off is reflected by the low diet diversity (narrow niche breadths) during the NEM season for fish in the fished sites. Broader niche breadths for fish from park sites during NEM season relative to fished sites is likely a function of greater interspecific competition (there is higher diversity and biomass of fish in parks) as predicted by the niche variation hypothesis. Unstable environmental conditions during the rough SEM season appear to promote wider niche breadths at fished sites; however, the influence of environmental stability on niche breadth variation will need further testing. Nonetheless, the present study provides, for the first time in Kenya and most of the western India Ocean, baseline data on diet composition and niche breadth variation of the commercially important *L. vaigiensis* and the likely influence of fishing pressure on feeding dynamics of coral reef fishes.

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