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Phenotypic Divergence in the Reproductive Traits of Marbled Parrotfish *Leptoscarus vaigiensis* (Quoy and Gaimard, 1824) on Variably Protected Reefs in Kenya

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Abstract — Phenotypic divergence in the reproductive traits of marbled parrotfish (*Leptoscarus vaigiensis*) was studied during May 2011-April 2012 at six reef sites exposed to varying levels of fishing pressure in coastal Kenya. Baited fish traps were used to capture fish within two no-take marine parks (Malindi and Watamu) and adjacent reserves in which regulated fishing is allowed. Fish samples were also obtained from fishers operating at two unprotected sites (Kanamai and Vipingo). Reproductive attributes (fecundity, oocyte size and length at first maturity) were determined and revealed significant differences in fecundity between sites ($F=3.742$, $P=0.004$), fish in the parks and reserves having a higher mean fecundity (110 128±75 492 and 145 570±88 873 respectively) than those on unprotected reefs (76 250±55 337). Fish at unprotected sites had higher fecundities at smaller sizes relative to larger fish at protected sites. In terms of length at first maturity (L50), females at unprotected sites matured at lower lengths (11.2 cm, 11.1-11.4 cm, 95% CI) than those in marine parks (16.7 cm, 15.7-17.3 cm, 95% CI) and reserves (16.8 cm, 16.6-17.1 cm, 95% CI). Overall, the results indicated some level of phenotypic divergence of the fish between sites, which is possibly an adaptive strategy to enhance their resilience to fishing pressure, thereby serving to sustain local populations. The real causes of this divergence cannot be partitioned between fishing mortality, genetic variability or habitat-induced variation. The data provide the basis for future research on causes for differences in the life history traits of marbled parrotfish on variably protected reefs.

INTRODUCTION

Parrotfishes (Scaridae) play an important role in enhancing coral reef resilience to perturbation through their grazing activities and sediment removal (Mumby, 2006). Widespread harvesting of these and other fishes may affect local community structure and cascade to declines in ecosystem function and changes in coral reef dynamics. It is likely

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that mechanisms such as phenotypic plasticity (production of different phenotypes by the same genotype under different conditions, sensu Morita & Morita, 2002) causes divergence in the life history attributes of reef fishes, thereby making them resilient to the effects of fishing (Gomes & Monteiro, 2007; Candolin, 2009), hence their ability to sustain populations and coral reef function

Fishing mortality alters inter- and intra-specific competition, which may lead to enhanced availability of food per capita and production of earlier-maturing individuals through phenotypic plasticity (Rijnsdorp, 1993; Taylor & Stefa´nsson, 1999; Law, 2000). Alternatively, fisheries can cause differential selection through gear/size selectivity, favouring genotypes coding for high fecundity and early maturation (Rijnsdorp, 1993; Law & Grey, 1989). Thus, fisheries can trigger changes in the maturation process via two pathways, either by influencing phenotypic plasticity or divergence, 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 divergence in life history traits can occur following an exploitation-mediated reduction in the population density (Hutchings & Baum, 2005) with a resultant decrease in maximum sizes (Jennings & Kaiser, 1998) and the earlier maturation of individuals (Heino & Godo, 2002; Kuparinen & Merila, 2007). Evolutionary change can also occur due to fishing if some of the phenotypic variation within a species is due to genetic differences within the stock (Law & Grey, 1989; Law, 2000).

In this study, we describe changes in the reproductive traits of the commercially important marbled parrotfish (*Leptoscarus vaigiensis*) on Kenyan reefs. Here they are exposed to varying degrees of fishing intensity and protection, and, therefore, provide an opportunity to test the hypothesis of fisheries-induced phenotypic plasticity in the life history traits of fish. *L. vaigiensis* is an ideal candidate for the study as it is a reef fish that is resident in nature (Kaunda-Arara & Rose, 2004).

METHODS

Study area

Reefs in Kenya can be divided into three conservation categories depending on their level of exposure to fishing pressure, these categories being protected (or marine parks), partially protected (or marine reserves) and unprotected, thereby providing a gradient in protection level. Extractive exploitation of resources is prohibited on protected reefs in Kenya, also designated as marine parks. "Reserves" or partially protected reefs (in the Kenyan context) are buffer areas in which regulated fishing is allowed adjacent to the parks with "traditional" methods that include baited fish traps, fish trapping fences and cast nets; and "unprotected" reefs are open access sites with no formal regulatory framework (McClanahan & Obura, 1995). Samples of *Leptoscarus vaigiensis* were obtained from protected reefs in the Malindi and Watamu Marine Parks, reserves adjacent to these Marine Parks and from unprotected (Vipingo and Kanamai) reefs (Fig. 1). Kenyan reefs are described by Kaunda-Arara and Rose (2004) as predominantly shallow (~10-12 m at high tide), lagoonal fringing reefs that run parallel to the coastline with a mosaic of substrata (seagrass beds, sand, rubble, live coral, etc.) common to all coral reefs. The Kenyan coast experiences seasonal weather caused by both north-easterly and south-easterly monsoon winds described by McClanahan (1988). Briefly, 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.

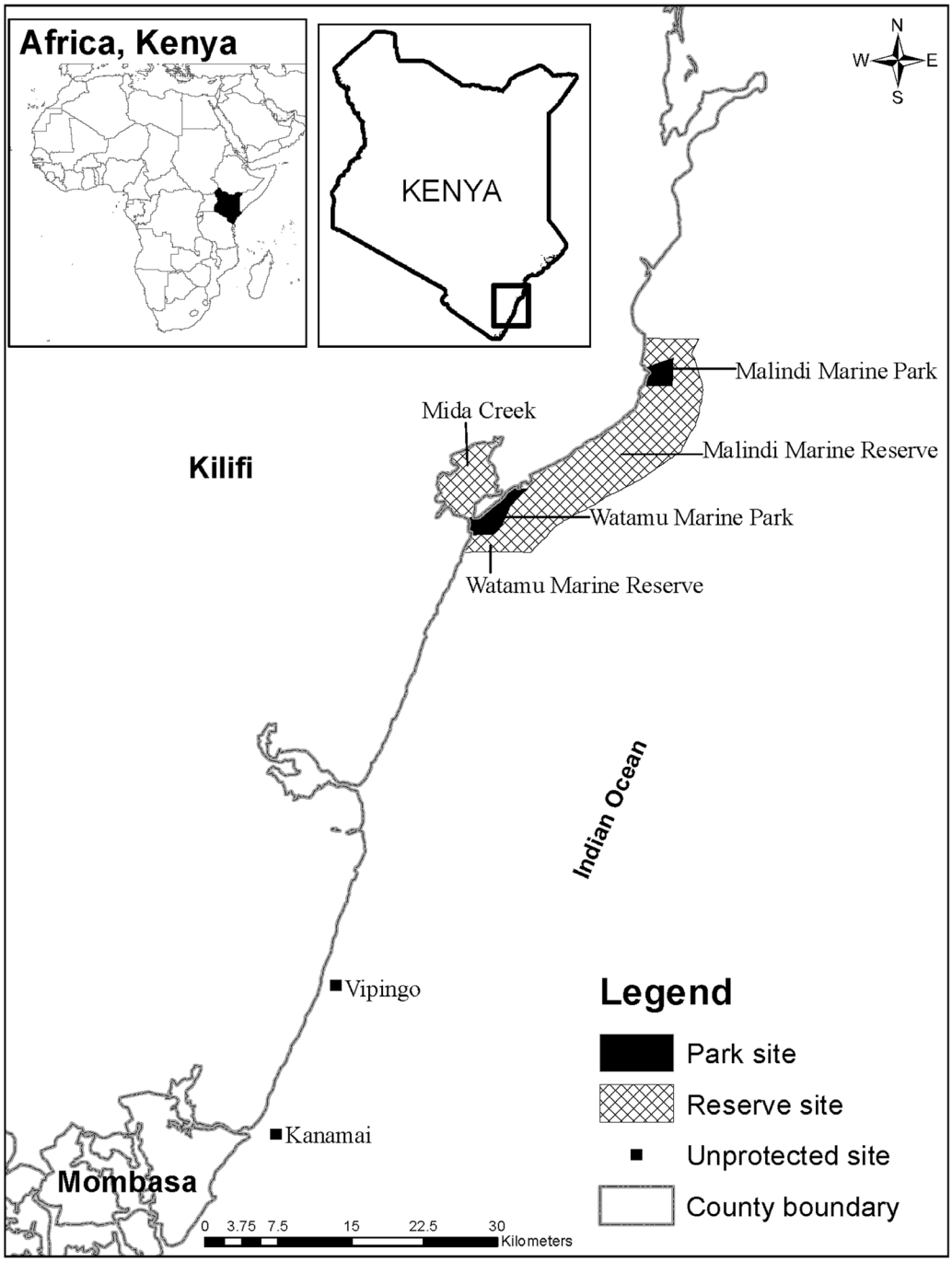

Figure 1. Map of Kenya showing the sites sampled for marbled parrotfish, *Leptoscarus vaigiensis*.

Field and laboratory procedures

Samples of *L. vaigiensis* were caught within protected sites (Malindi and Watamu Parks and their reserves; Fig. 1) on a monthly basis from May 2011 to April 2012 using local traps called *demas*. The baited traps were deployed during low tide and retrieved during the subsequent low tide the following day, having soaked for about 12 hours. Monthly samples were obtained at the unprotected sites (Vipingo and Kanamai; Fig. 1) during the same period, from fishers harvesting *L. vaigiensis* at these sites using cast nets and spear guns. An effort was made to obtain a wide size range of *L. vaigiensis*. All specimens were transported to the laboratory on ice for further processing.

The total (TL) and standard lengths (SL) of the specimens were recorded to the nearest millimetre and total weights to the nearest 0.1 g. The fish were then dissected and the sex and maturity stages determined visually. The gonads were staged following Bagenal's (1978) maturity stages as I - immature, II - immature, III - maturing, IV - mature, V - active, and VI - spent. The gonads were weighed to the nearest 0.001 g and sections were excised monthly from all mature and active ovaries (stages IV-V) to determine their fecundity. These were weighed to the nearest 0.001 g and stored in Gilson's fluid for at least two months, with frequent shaking to aid the release of oocytes from the ovarian wall (Kaunda-Arara & Ntiba, 1997). Portions of ovaries were taken from either lobe following a preliminary analysis of variance that revealed no significant differences ($P>0.05$) in oocyte size distribution along the antero-posterior axis of either the right or left lobes of the ovary. Fecundity was then determined following the volumetric method described by Bagenal (1978). Briefly, the contents of each bottle containing ovarian portions were poured into a petri dish and the oocytes washed repeatedly in tap water. The clean and separated oocytes were transferred to a one litre beaker containing a known volume of water. A plastic stirrer was used to stir the egg suspension to ensure an even distribution of the oocytes. After 15 strokes of the stirrer, a 5 ml subsample was extracted with a Labsystem finelet pipette. The oocytes in this aliquot were examined, counted and their diameters measured along their horizontal axis using a calibrated eyepiece graticule under a standard dissecting microscope at 40× magnification

Data analysis

The fecundity (F) of each active/mature female fish was estimated from the egg counts in the subsamples according to the formula:

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

Where N is the number of eggs in a subsample, V is the volume of the egg suspension; V_1 is volume of the subsample; W is the weight of the whole ovary; and W_1 the weight of the portion of ovary fixed in Gilson's fluid. Fecundities at sites were log (x + 1) transformed to satisfy ANOVA assumptions of normality and homoscedasticity (Zar, 1999) and then compared using one-way ANOVA. A Student–Newman–Keuls (SNK) multiple comparison test was performed post hoc to establish whether the means were significantly different (Zar, 1999).

Relationships between fecundity (F) and standard length (SL) in specimens from park, reserve and unprotected sites were established using the formula:

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

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. Multidimensional scaling (MDS) ordination was used to test for similarity between sites based on the fecundity estimates.

Mean oocyte diameters at the active stage V were compared between sites using one-way ANOVA after log (x + 1) transformation of the data, and the size-frequency distribution of the oocytes was examined using graphical plots.

The length at first maturity (L50) of the specimens was determined per site by calculating the proportion of mature (stages

IV-V) individuals for each length class (King, 1995). The results of these analyses were fitted to a logistic function using least-squares regression with the SOLVER routine in Microsoft™ Excel:

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

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 (stages IV-V) was regarded as the size at first maturity. A non-parametric bootstrapping technique (Efron & Tibshirani, 1993) was used to resample the data to form three site-specific subsets of the length data. The L50 was estimated separately for females for each of these subsets using the above procedure. It was not computed for males, largely due to the small sample size of mature male gonads at unprotected sites and inherent difficulties in estimating their maturity stages.

RESULTS and DISCUSSION

Sample structure

A total of 1 281 Leptoscarus vaigiensis were caught during the study period, of which 860 (67.14%) were caught during the SEM and 421 (32.86%) during the NEM (Table 1). There were more males than females at all sites but the overall sex ratio (M:F) of 1.29:1 was not significantly different from unity (χ^2 = 12.723, P = 0.364; Table 1).

Fecundity

Fecundity estimates from 117 active/mature female *L. vaigiensis* differed significantly between sites (F = 3.742, df = 2, P = 0.004; Table 2), being significantly higher in Malindi Reserve (156 456 ± 99 233) and Watamu Marine Park (137 669 ± 88 048) than at the unprotected sites of Vipingo (92 299 ± 53 647) and Kanamai (77 459 ± 62 275; Table 2). SNK *post hoc* tests confirmed these differences but revealed no significant differences between the fecundity at sites with the same level of protection viz. the Malindi and Watamu Marine Parks, associated reserves, and the unprotected sites of Kanamai and Vipingo (Table 2). Values of 'a' and 'b' (equation 2) varied between sites, with higher values for 'a' in reserves and unprotected sites relative to those in the marine parks, suggesting that fish at the fished sites had higher fecundities than those at protected sites at equivalent sizes (Fig. 2). Also, the 'b' exponents for fish in the marine parks were higher (b ≈ 3) than those in reserves and at unprotected sites (b <3), indicating that they grew isometrically relative to those at the other sites (Fig. 2). However, ANCOVA of the b values indicated

Table 1. Numbers of *Leptoscarus vaigiensis* caught during the north-east (NEM) and south-east monsoons (SEM) at reef sites with different levels of protection in coastal Kenya.

Sites	NEM			SEM			Total
	M	F	Immature	M	F	Immature	
Malindi Marine Park	39	27	0	87	28	0	181
Watamu Marine Park	34	12	1	48	29	2	126
Watamu Reserve	3	5	0	7	6	0	21
Malindi Reserve	58	56	0	134	90	0	338
Kanamai	28	28	2	99	112	16	285
Vipingo	67	53	8	80	106	16	330
Overall sex ratio (M:F)	1.28:1						
χ^2	12.723						
P	0.364						

Table 2. Mean fecundity (±SD) estimates of sexually active/mature *Leptoscarus vaigiensis* caught at protected (marine parks), partially protected (reserves) and unprotected sites in coastal Kenya.

Sites	Mean fecundity (oocytes)	N
Watamu MarinePark	137 669 ± 88 048	9
Malindi Marine Park	108 655 ± 64 314	14
Watamu Reserve	106 610 ± 67 289	3
Malindi Reserve	156 456 ± 99 233*	46
Vipingo (unprotected)	92 299 ± 53 647	27
Kanamai (unprotected)	77 459 ± 62 275	18
ANOVA F	3.742	
p	0.004	
df	5	

*Difference in fecundity between Malindi Reserve and other sites (except Watamu Park) significant ($p < 0.05$).

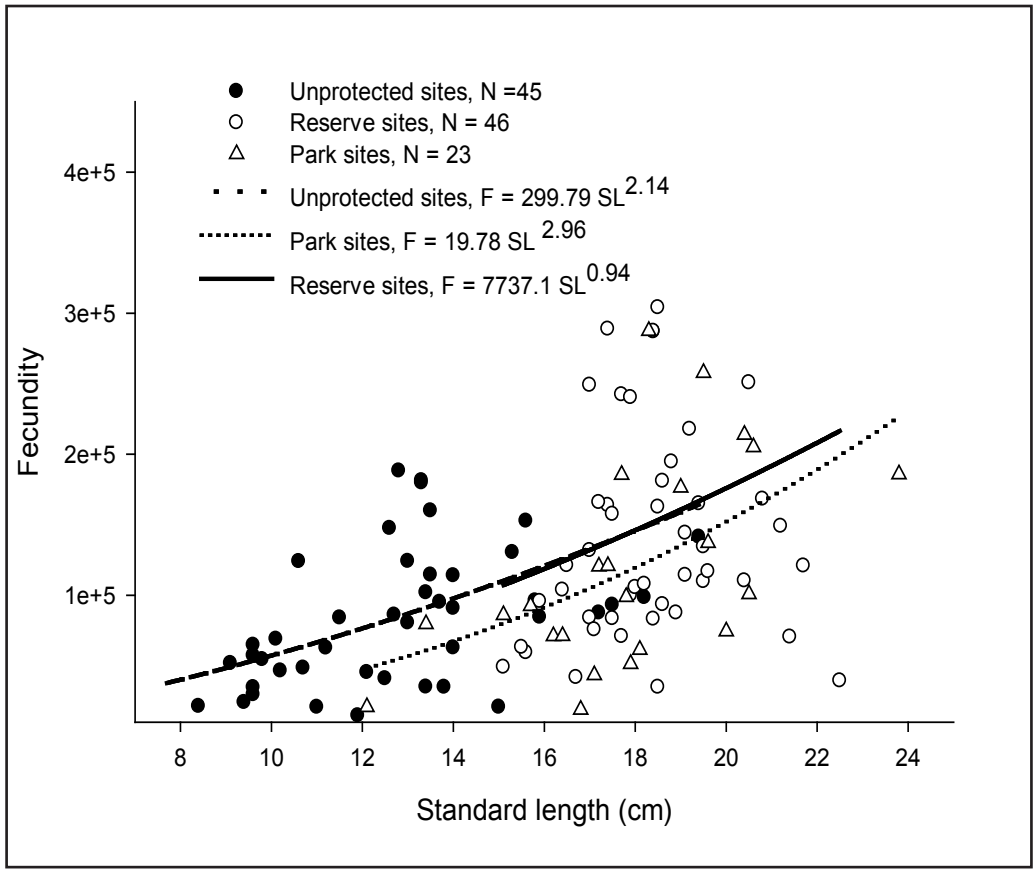

Figure 2. Relationships between fecundity (F) and standard length (SL) in *Leptoscarus vaigiensis* at reef sites with different levels of protection in coastal Kenya. N denotes number of ovaries examined at sites.

Table 3. ANCOVA output for the comparison of slopes of log fecundity and log standard length relationships in *Leptoscarus vaigiensis* caught on different reefs in coastal Kenya.

Source	*SS*	*df*	*MS*	*F*	*P*
Corrected model	2.519E11	11	2.290E10	4.173	0.000
Sites	1.388E10	5	2.776E9	0.506	0.771
SL	4.048E10	1	4.048E10	7.376	0.008
Sites×SL	1.174E10	5	2.347E9	0.428	0.828
Error	5.763E11	105	5.488E9		

a non-significant interaction between length (covariate) and sampling site (independent variables), suggesting that the effect of length on fecundity was independent of sites; this may be an artefact of small sample sizes from the marine parks (Table 3). The sites were uniformly distributed in the MDS analysis (data not shown).

Differences in the fecundity of *L. vaigiensis* at the various sites may be attributable to variability in fishing intensity between them, which, in turn, would be attributable to differences in their level of protection. *L. vaigiensis* is largely a resident reef fish (Kaunda-Arara & Rose, 2004), thereby precluding the likelihood of movement between sites. Fishing selectively removes large and highly fecund individuals from sites (Jennings & Kaiser, 1998), leaving small individuals with the reduced fecundity reported here and in other studies (e.g. Jennings & Phillips, 1992; Wilson *et al*., 2010). However, even if harvesting is 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 fish at the intensely fished, unprotected sites in this study relative to the reserves and marine parks. However, there could be other causes for spatial changes in fecundity, including genotypic variation (Dieckmann & Heino, 2007) and differences in inter- and intra-species interactions at the sampling sites (Law, 2000). We found that levels of fecundity of small-sized fish at heavily-fished sites were higher than those of equivalent-sized fish at less fished and unfished sites. It is likely that this is caused by the early maturation observed at fished sites,

Table 4. Oocyte diameters (±SD) in active gonads (stage V) in *Leptoscarus vaigiensis* caught on different reefs in coastal Kenya.

Sites		Mean size (mm)	Modal size (mm)	Size range (mm)	N
Kanamai		0.17 ± 0.07	0.20	0.06-0.28	1 209
Vipingo		0.19 ± 0.06	0.20	0.10-0.28	632
Malindi Marine Park		0.23 ± 0.08	0.20	0.10-0.36	3 363
Malindi Reserve		0.19 ± 0.07	0.20	0.08-0.30	14 714
Watamu Marine Park		0.18 ± 0.07	0.20	0.08-0.28	2 295
Watamu Reserve		0.18 ± 0.07	0.20	0.08-0.28	537
ANOVA	F	1.147			
	p	0.345			
	df	5			

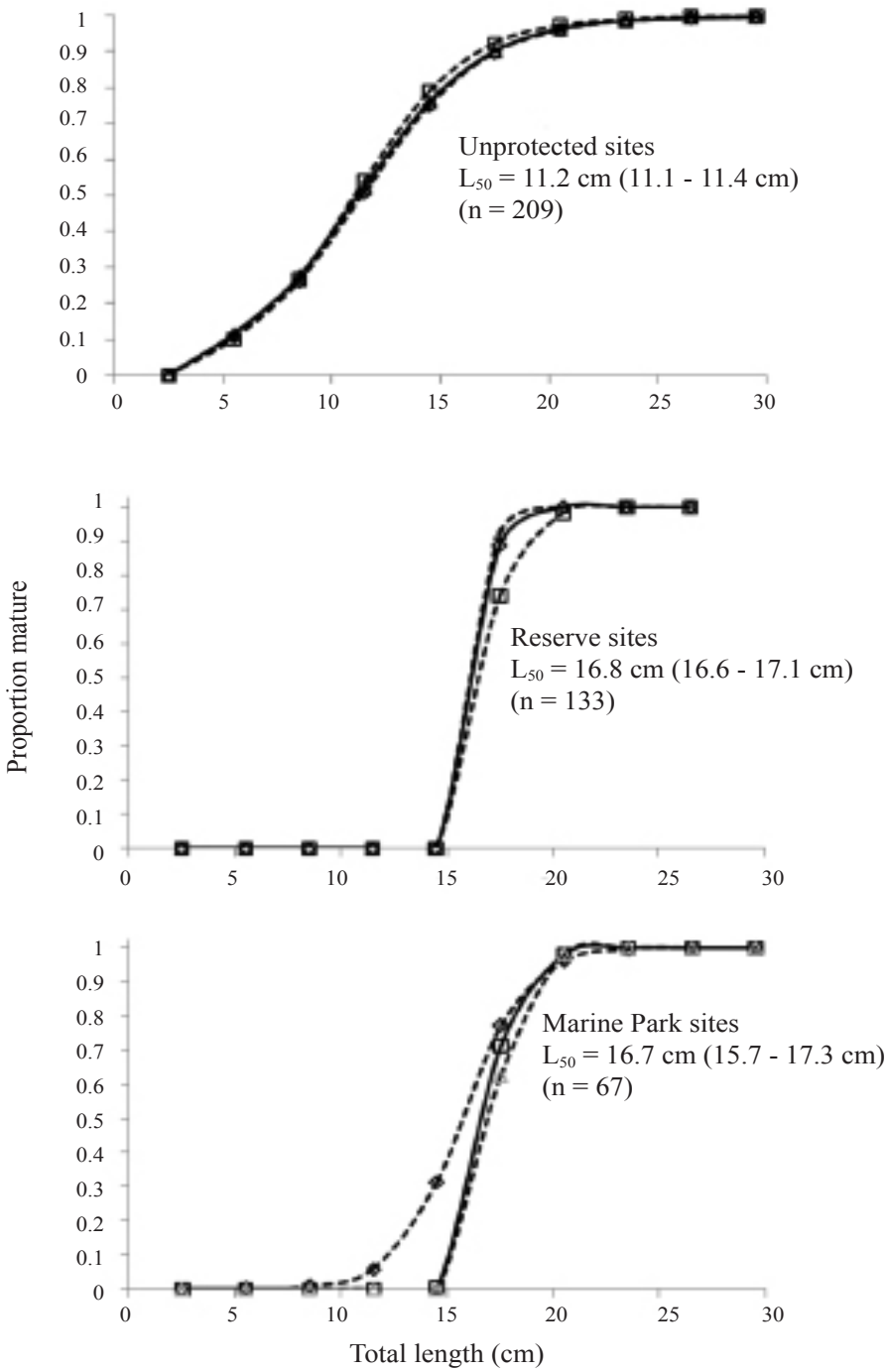

Figure 3. Length at first maturity ogives (solid lines) of female *Leptoscarus vaigiensis* caught at sites with different levels of protection in coastal Kenya; confidence intervals of the estimates are given in parentheses. The dashed lines represent the 95% confidence intervals for lengths at first sexual maturity (L_{50}).

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 on the south coast and the unfished and reserve sites in the north (Fig. 1), together with the resident 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.

Oocyte diameters

Oocyte diameters were estimated from 22 740 oocytes at maturity stage V (Table 4). The diameters ranged from 0.18 mm in Vipingo to 0.26 mm in Malindi (Table 4), with a modal value of 0.2 mm at all sites. Mean oocyte diameters were not significantly different between sites ($F = 1.147$; $P = 0.345$; Table 4).

Higher survival is expected amongst juveniles emanating from large larvae (Tomkiewicz *et al*., 2003; Raventos & Macpherson, 2005) 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 & Flemings, 2000; Heath *et al*., 2003) as a phenotypic response to stress. However, in this study we found a higher proportion of small eggs in *L. vaigiensis* at fished sites, although the mean egg diameter was not significantly different between sites. It is possible that *L. vaigiensis* at unprotected 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 & Phillip, 1992). Clearly, studies on predator-prey manipulations would be required to test this hypothesis.

Length at first maturity (L_{50})

A comparison of the estimates of length at first maturity (L_{50}) indicated that the lowest L50 for female *L. vaigiensis* occurred at unprotected sites (mean 11.2 cm, range 11.1-11.4 cm, 95% CI), whereas the highest L_{50} occurred at reserve sites (mean 16.8 cm, range 16.6-17.1 cm, 95% CI; Fig. 3). The L_{50} of female *L. vaigiensis* in the marine parks was 16.7 cm (range 15.7-17.3 cm, 95% CI; Fig. 3).

The earlier maturity of female fish at unprotected sites relative to those in marine parks and reserves is possibly a compensatory response to ensure that fish at the former 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; Olsen *et al*., 2004; Kuparinen & Merila, 2007). 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. Differences in growth rate and maturation may thus be a phenotypic response to changes in food availability. However, it may also develop over time in response to selective mortality (Law, 2000).

This study has thus shown divergence in the reproductive attributes of *L. vaigiensis* which is probably induced by fishing pressure. Fish at unprotected sites have equivalent or higher fecundities at smaller sizes relative to larger fish at protected sites. They mature earlier, possibly as an adaptive strategy which enhances their resilience to fishing pressure and helps to sustain local populations. Although the results suggest some level of phenotypic divergence or plasticity, the real causes of this plasticity cannot be apportioned between fishing mortality, genetic variability or habitat-induced variations. The results, however, provide a basis for future research aimed at partitioning the observed divergence in the reproductive traits of *L. vaigiensis* to its actual causes.

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