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Shifts in malaria vector species composition and transmission dynamics along the Kenyan coast over the past 20 years

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Abstract

Background: Over the past 20 years, numerous studies have investigated the ecology and behaviour of malaria vectors and *Plasmodium falciparum* malaria transmission on the coast of Kenya. Substantial progress has been made to control vector populations and reduce high malaria prevalence and severe disease. The goal of this paper was to examine trends over the past 20 years in *Anopheles* species composition, density, blood-feeding behaviour, and *P. falciparum* sporozoite transmission along the coast of Kenya.

Methods: Using data collected from 1990 to 2010, vector density, species composition, blood-feeding patterns, and malaria transmission intensity was examined along the Kenyan coast. Mosquitoes were identified to species, based on morphological characteristics and DNA extracted from *Anopheles gambiae* for amplification. Using negative binomial generalized estimating equations, mosquito abundance over the period were modelled while adjusting for season. A multiple logistic regression model was used to analyse the sporozoite rates.

Results: Results show that in some areas along the Kenyan coast, *Anopheles arabiensis* and *Anopheles merus* have replaced *An. gambiae sensu stricto (s.s.)* and *Anopheles funestus* as the major mosquito species. Further, there has been a shift from human to animal feeding for both *An. gambiae* sensu lato (s.l.) (99% to 16%) and *An. funestus* (100% to 3%), and *P. falciparum* sporozoite rates have significantly declined over the last 20 years, with the lowest sporozoite rates being observed in 2007 (0.19%) and 2008 (0.34%). There has been, on average, a significant reduction in the abundance of *An. gambiae* s.l. over the years (IRR = 0.94, 95% CI 0.90–0.98), with the density standing at low levels of an average 0.006 mosquitoes/house in the year 2010.

Conclusion: Reductions in the densities of the major malaria vectors and a shift from human to animal feeding have contributed to the decreased burden of malaria along the Kenyan coast. Vector species composition remains heterogeneous but in many areas *An. arabiensis* has replaced *An. gambiae* as the major malaria vector. This has important implications for malaria epidemiology and control given that this vector predominately rests and feeds on humans outdoors. Strategies for vector control need to continue focusing on tools for protecting residents inside houses but additionally employ outdoor control tools because these are essential for further reducing the levels of malaria transmission.

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Background

Fundamental to the development of sound malaria control programmes is an understanding of how malaria transmission intensity affects malaria prevalence, incidence, severe disease, and mortality [1-3]. To gauge levels of malaria control necessary for achieving meaningful public health improvements, it is necessary to quantitatively define the extent to which site-specific malaria transmission indices must be reduced. Effective vector control strategies that negatively impact the components of vectorial capacity can then be developed [4]. Strategies such as indoor spraying with residual insecticides (IRS), sleeping under long-lasting insecticide-treated bed nets (LLINs), larval habitat management (LHM), and the use of repellents and other vector control measures can then be used selectively to reduce levels of transmission.

Several African countries have already scaled up the delivery of key malaria control measures, notably LLINs [5] and the provision of more effective artemisinin-based combination therapy (ACT) for malaria case management [6]. For example, between 2000 and 2008, globally there was a three to 10-fold increase in ownership and use of ITNs among children under five years of age [7] and a 25-fold increase in global procurement of ACT over the last few years [7]. These changes have contributed to the global decline in malaria morbidity and mortality, and may have motivated many countries to begin thinking through next steps towards malaria elimination [8-10]. Net usage on the coast and throughout Kenya was negligible before 2001. However, LLIN coverage among children five years and below rose from 7% in 2004 to 67% by the end of 2006 [11-13]. This increase in LLIN coverage along with changes in malaria treatment and management, has likely contributed to the steady decline in malaria morbidity and mortality along the Kenyan coast [8-10].

Over the past 20 years, studies on malaria vectors have been conducted along the Kenyan coast. Initially studies focused on malaria transmission dynamics and high incidence of severe malaria [14-17], but surprisingly found lower transmission than in western Kenya – providing evidence that high incidence of severe malaria can occur even at relatively low intensities of transmission [16,17]. These studies were proceeded by investigations of mosquito blood-feeding behaviour [15,18], vector distribution patterns [19,20], spatial-temporal variations in malaria prevalence and intensity of transmission [20], vector population genetics [21], community-based vector control [22,23], malaria vector control [24-26] and larval ecology of malaria vectors [27-29].

In the light of on-going malaria control interventions and the recent downward trend of malaria prevalence along the Kenyan coast, accurate knowledge of how these interventions have altered the ecology of major vectors and the risk of malaria transmission will facilitate allocation of vector control efforts where they are most needed. The aim of this paper is to examine trends in *Anopheles* species composition, densities, and blood-feeding behaviour over a 20-year period, between 1990 and 2010. The results are discussed in terms of malaria transmission dynamics and vector control to explore what more is needed to further interrupt transmission on the coast of Kenya.

Methods

Study area

Studies from 1990 to 2010 were conducted in 49 villages located in Malindi and Kilifi Districts on the Kenyan coast (Figure 1). The data collected during these periods was standardized to show mean indoor-resting mosquito densities over different periods. The study areas have been described in detail elsewhere [15,19-22,24-27,29-34]. Briefly, the coastal plain is made up of dense forest, savannah type vegetation, seasonal swamps, dry thorn bush, and a number of plantations interspersed with uncultivated land. Altitudes range from 0 to 400 m above sea level. Sisal, coconut, and cashew nut plantations are extensive along the coast, although subsistence farming is practiced throughout the coastal area. The houses in rural areas of coastal Kenya mainly consist of framed poles and branches from top to bottom covered with grass. Mud is often used to support the upper structure, while palm leaves often replace grass as roofing material. Many households keep goats, chickens, and cattle as domestic animals.

Coastal Kenya has two rainy seasons: the long rains occur between April and July and the short rains occur between October and November. Mean annual precipitation ranges from 750 to 1,200 mm [34]. Over the past 20 years, people living in near proximity to the Sabaki and Jaribuni rivers have started small-scale irrigated agriculture. The Kenyan Government, through the Economic Stimulus Programme and Vision 2030 Strategies has also continued to develop the Lango Baya Irrigation Scheme in Malindi. Horticultural crops grown under these irrigation activities include kale, hot pepper, okra, green maize, brinjals (aubergine) and tomatoes. The agronomic practices in the irrigation system use pesticides, mainly of the class organophosphates.

Mosquito sampling

Several methods were used for entomological sampling, including Centers for Disease Control and prevention (CDC) light traps, pyrethrum spray collection (PSC), human landing catches, and manual aspiration for collecting day resting mosquitoes indoors (DRI) [15,18,20,21,25,32]. The mosquitoes were expressed in densities (mean mosquitoes per house or trap) for the analyses. To overcome some of the limitation in data collections in which the relative use of each method was not the same during each year; the

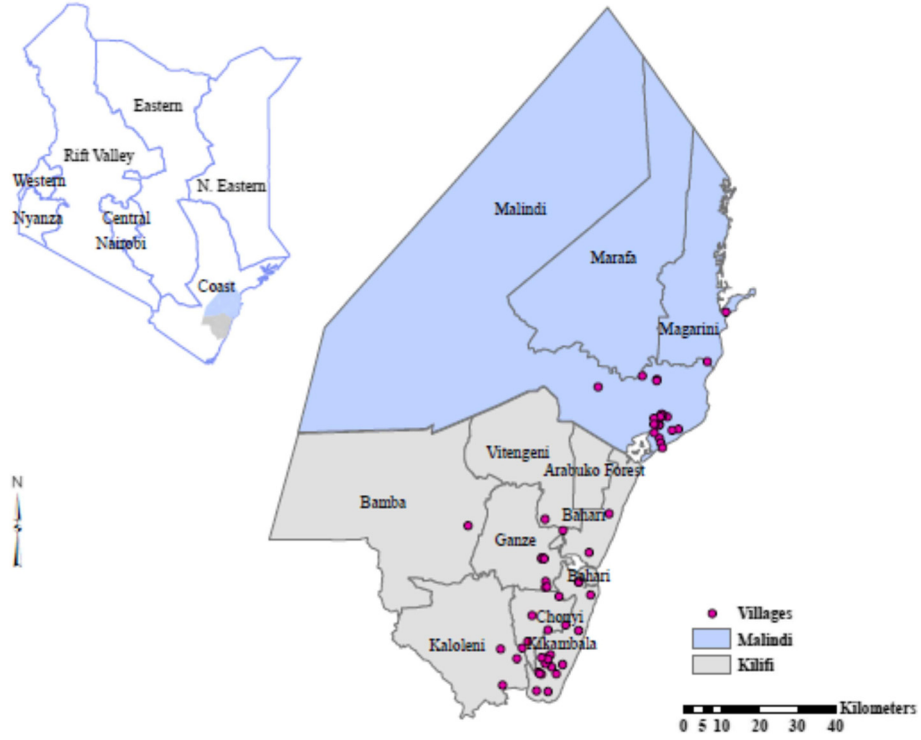

Figure 1 Map showing the locations of villages sampled in Kilifi and Malindi Districts.

sampling was categorized according to the rainfall pattern along the Kenyan coast. This grouped each year in 4 categories namely long wet season (April to July), short wet season (October and November), long dry season (December to March) and short dry season (August and September).

Mosquito identification

Mosquitoes were identified to species based on morphological characteristics [35]. Females were further classified as unfed, blood-fed, semi-gravid or gravid [36]. Genomic DNA was extracted from the legs and wings of a proportion of females in the *Anopheles gambiae* complex using the methods of Collins *et al* [37,38] and amplified using specific diagnostic primers for *An. gambiae s.s., Anopheles arabiensis, Anopheles quadriannulatus* and *Anopheles merus* according to previously described methods [39,40]. *Anopheles funestus*, which is a complex of nine sibling species [41,42], was not identified to sibling species level.

Circumsporozoite protein and blood meal ELISA

The mosquitoes were cut transversely between the thorax and abdomen. The heads and thoraces of anopheline mosquitoes were tested using a *Plasmodium falciparum* sporozoite enzyme linked immunosorbent assay (ELISA) [43-45]. The fully blood-fed abdomens were tested for host sources of blood by ELISA [46]. Test samples were visually assessed for positivity [47].

Statistical analysis

The analyses were performed using STATA v10.1 (StataCorp, College Station, TX, USA). Both descriptive and inferential analyses were considered. To study the mosquito abundance over the 20-year period while adjusting for season and pre-post LLIN coverage scale-up, a negative binomial generalized estimating equations (GEE) model, assuming exchangeable working correlation, taking calendar year, pre-post scale-up (coded 1 if year is after 2003, and 0 otherwise) and season (wet or dry) as the covariates with household as the cluster was used [48,49]. In this case, wet season comprised the months April, May, June, October, and November. Because of limiting software capability, a standard negative binomial model was used to initially obtain a maximum likelihood value for the ancillary parameter. The same model was fitted separately for *An. gambiae* and *An. funestus*. Mosquito collections were presented as densities in each sampling village. To study the sporozoite rate over the period while controlling for season, a multiple logistic regression model was fitted, but with season redefined into four categories: long wet season, short wet season, long dry season and short dry season. This is because field sampling was done in different months over the year. Odds ratios (OR) were computed for each season in comparison to the long wet season (April to July), which had the highest number of *P. falciparum* sporozoite positive mosquitoes.

Table 1 Observed percent distribution of *Anopheles gambiae* s.l. and *Anopheles funestus* s.l. by year and season

Variables	# Observed	% *An. gambiae* s.l.	% *An. funestus* s.l.
All	33,529	54.3	45.7
Covariates			
Year			
1990	22	95.5	4.5
1991	673	91.8	8.2
1994	1,236	86.6	13.4
1995	530	9.1	90.9
1997	4,970	83.2	16.8
1998	549	57.9	42.1
1999	3,325	78.0	22.0
2000	5,646	70.6	29.4
2001	5,193	27.9	72.1
2002	901	15.3	84.7
2003	367	80.4	19.6
2006	330	16.1	83.9
2007	4,773	24.3	75.7
2008	4,700	44.6	55.4
2010	314	67.5	32.5
Pre-post scale-up			
pre	23,412	62.7	37.3
post	10,117	34.8	65.2
Season			
Wet	16,658	63.6	36.4
Dry	16,871	45.1	54.9

The *P. falciparum* sporozoite rates were calculated as the number of mosquitoes that tested positive by ELISA divided by the total number of mosquitoes tested. The proportions of mosquitoes feeding on a given host were compared using Chi- square and/or Fisher's exact test. These analyses did not assume spatial dependence among the villages. All tests were performed at the 5% level.

Results

Vector abundance

Of 33,529 mosquitoes collected, 18,194 (54.3%: 96% CI 53.7–56.8) were *An. gambiae* and the rest *An. funestus*. This proportion was significantly greater in the wet season (63.6%) than in dry season (45.1%; $X^2 = 1{,}158.3$, df = 1, $p < 0.001$). Table 1 shows the distribution of the two species by year and season. Apart from recently in 2010, the densities of *An. funestus s.l.* only exceeded *An. gambiae s.l.* in 2001 and 2002 (Figure 2). Figure 2 and Table 1 show that the densities of both mosquito species increased between 1990 and 2001, thereafter the densities of both *An. gambiae* s.l. and *An. funestus* declined. After controlling for the other two factors, there was, on average, a significant 6% reduction the chance of observing an *An. gambiae s.l.* (IRR = 0.94, 95% CI 0.90–0.98), but a significant 32% increase in the chance of observing an *An. funestus s.l.* (IRR = 1.32, 95% CI 1.25–1.39) for a unit increase in time/year. Season was also significantly associated with the abundance of both *An. gambiae* and *An. funestus s.l.* The abundance of *An. gambiae s.l.* was significantly lower in dry season as compared to wet season (IRR = 0.51, 95% CI 0.49–0.53) after adjusting for year and LLIN scale-up. *Anopheles funestus* were, however, more abundant in dry season than wet season (IRR = 1.08, 95% CI 0.90–1.30), although not significantly so. A significant

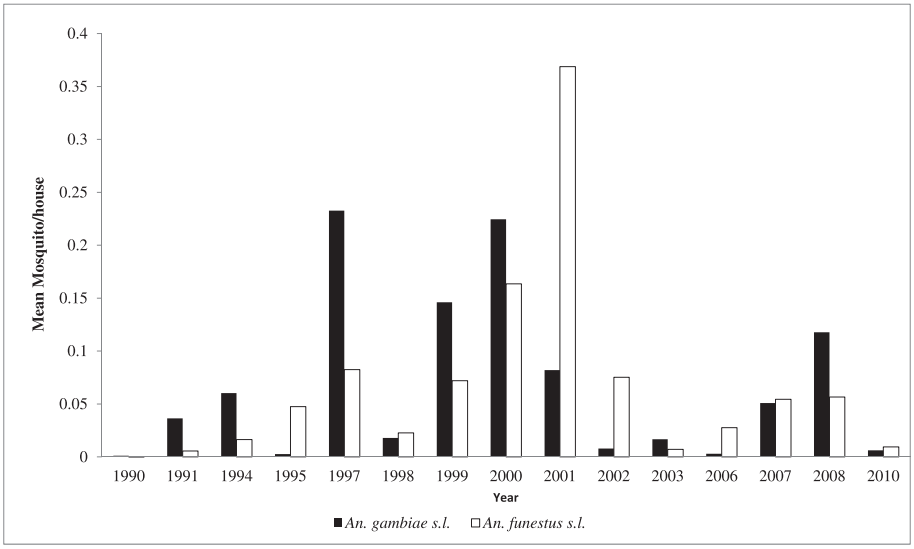

Figure 2 The *Anopheles gambiae* s.l. and *An. funestus* s.l. mean densities from 1990 to 2010.

Table 2 Changes in proportion of *Anopheles gambiae* s.l. sibling composition over the years

Period	Number tested	% An. gambiae ss	% An. arabiensis	% An. merus	% An. quadriannulatus
1990 - 1995*	-	-	-	-	-
1997 - 1998	1,388	78.89	14.84	6.27	0.00
2002 - 2003	803	45.70	5.48	48.82	0.00
2007 - 2008	595	0.00	93.02	5.00	1.97

***An. gambiae* s.l. mosquitoes not tested for sibling species.**

reduction of both species in the post LLIN distribution scale-up period was observed (*An. gambiae s.l.*: IRR = 0.08, 95% CI 0.04–0.17; *An. funestus s.l.*: IRR = 0.10, 95% CI 0.04–0.24). The ancillary parameter was 8.74 and 14.58 for *An. gambiae* and *An. funestus* models, respectively.

Shift in *Anopheles gambiae* s.l. sibling species composition over time

Of the four *An. gambiae* complex sibling species identified, *An. gambiae* s.s., which was the dominant indoor-resting mosquito species between 1997 and 1998 accounting for 78.89%, has been declining over the years significantly to very low levels and sometimes undetectable levels in the study sites, especially between 2007 and 2008. On the other hand, *An. arabiensis* has seen an upward trend from 14.84% between 1997 and 1998 to being the dominant *An. gambiae* complex sibling species in late 2000 (Table 2). *Anopheles merus* increased between 2002 and 2003 but declined after 2007. *Anopheles quadriannulatus*, a member of the *An. gambiae* complex, that was not known to occur along the Kenyan coast, was found in 2007, accounting for nearly 2% of the sample (Table 2).

Plasmodium falciparum sporozoite rates

A total of 33,383 mosquitoes (*An. gambiae* s.l. and *An. funestus*) were tested for *P. falciparum* sporozoites. Data for the years 1997 to 2008 was used. The overall sporozoite rate was 4.6%. High sporozoite rates were observed in 1997 (5.94%), 2000 (7.96%), 2001 (6.83%), and 2003 (8.65%), which had the highest rate. There was a significant association between *P. falciparum* sporozoite positivity and year. Compared to 1997 and after controlling for season, there was significantly lower sporozoite rate in 2002 (OR = 0.68, 95%CI 0.51–0.91), 2007 (OR = 0.03, 95% CI 0.01–0.10), and 2008 (OR = 0.06, 95%CI 0.03–0.11). The odds of a mosquito being positive were also lower in 1998, but not significantly so (OR = 0.65, 95% CI 0.35–1.19). After controlling for year, season was also found to be significantly associated with sporozoite positivity. Compared to long wet season, the odds of being positive were significantly high during the long dry (OR = 1.23, 95% CI 1.02–1.49) and short dry seasons (OR = 1.14, 95% CI 1.00–1.29) (Table 3).

Further analyses indicated that although *P. falciparum* infectiousness by *Anopheles* mosquitoes as indicated by positive sporozoite rates was found to be taking place throughout the four seasons, there was seasonal variability in sporozoite rates during each year (Table 4). The highest sporozoite rate observed during this period was 23.81% during the short dry season in 1998.

Anopheles host feeding patterns over time

Table 5 presents a summary of the feeding patterns over time. There has been a significant reduction in human blood index (HBI) from 99% and 100% to 16% and 3% for *An. gambiae* s.l. and *An. funestus,* respectively, between 1997 and 2008. These mosquitoes have switched to primarily feeding on bovines. Other meal sources included, bovine, goat, donkey, human-bovine, and chicken – although only *An. gambiae* was noted to feed on chicken but, again, this was only in 1997.

Conclusion

The present study illustrates marked changes in densities of *An. gambiae* s.l. and *An. funestus*. *Anopheles*

Table 3 *Plasmodium falciparum* sporozoite rates and logistic regression model results*

Variables	# Tested	% Positive	OR	95% CI	P value
All	33,383	4.60			
Explanatory					
Year					
1997	1,027	5.94	1		
1998	335	3.88	0.65	(0.35-1.19)	0.162
2000	5,555	7.96	**1.50**	**(1.12-2.01)**	0.006
2001	4,521	6.83	1.24	(0.92-1.67)	0.154
2002	17,210	3.83	**0.68**	**(0.51-0.91)**	0.010
2003	451	8.65	1.38	(0.90-2.12)	0.141
2007	1,601	0.19	**0.03**	**(0.01-0.10)**	<0.001
2008	2,683	0.34	**0.06**	**(0.03-0.11)**	<0.001
Season					
Long Wet	18,214	4.62	1		
Short Wet	3,206	4.09	1.00	(0.81-1.22)	0.968
Long Dry	4,095	4.71	**1.23**	**(1.02-1.49)**	0.034
Short Dry	7,868	4.70	**1.14**	**(1.00-1.29)**	0.044

* Bold = significant at 5% level; OR = odds ratio; CI = confidence interval.

Table 4 The number of mosquitoes tested in each season and sporozoite rates (in parentheses)

	Total *Anopheles* mosquitoes tested			
Year	**Long Wet**	**Short Wet**	**Long Dry**	**Short Dry**
1997	47 (2.13)	315 (2.86)	511(5.68)	154 (14.29)
1998	7 (0.00)	139 (3.60)	168 (1.79)	21 (23.81)
2000	3,150 (6.29)	1,157 (9.16)	207 (5.80)	1,041 (12.10)
2001	2,629 (8.18)	273 (3.30)	604 (6.62)	1,015 (4.43)
2002	11,573 (3.66)	a*	982 (6.62)	4,655 (3.65)
2003	a*	a*	451 (8.65)	a*
2007	37 (0.00)	709 (0.14)	515 (0.39)	340 (0.00)
2008	771 (0.39)	613 (0.16)	659 (0.46)	642 (0.31)

Legend: a* No *Anopheles* mosquitoes tested for sporozoites.

gambiae s.l. decreased markedly between 1990 and 2008 while *An. funestus* increased between 1990 and 2002 before decreasing thereafter. Similar trends have been reported in western Kenya [50] and in Tanzania [51,52], even in areas where LLINs are not widely used [51]. It appears that multiple factors, including ongoing vector control interventions (e g, widespread use of LLINs, indoor residual spraying), improvements in house constructions [53,54], and human-mediated ecological disturbances [55] may have contributed to the observed decline in mosquito density. The Kenya coast in areas along the Sabaki River, such as Lango Baya, Chakama and Burangi, has seen an increase in irrigated agricultural activities that have a direct influence in vector densities and behaviour.

The primary vectors of malaria on the Kenyan coast have shifted from human to animal feeding; this has also coincided with significant reductions in sporozoite rates. Along the Kenyan coast there was mass distribution of LLINs in 2006 and in 2012 there was a mass LLIN distribution to achieve universal coverage. Reductions in mosquito density may be attributed to ongoing mass distribution of LLINs in the study area [5,11]. Long-term use of LLINs impacts malaria vectors by killing/repelling host-seeking mosquitoes, diverting host-seeking mosquitoes to non-human hosts and/or inducing shifts from indoor to outdoor feeding. The observed reduction in vector density and shifts from human to animal feeding suggest that all these mechanisms have contributed to the declining malaria prevalence. Animals are dead-end hosts for human malaria parasites and may have contributed to low sporozoite rates by reducing the probability of human-vector contact.

The observed decrease in *An. gambiae s.s* populations and the coinciding increase in *An. arabiensis* populations may be attributed to differences in their ecology. *Anopheles gambiae s.s.* is anthropophilic, endophagic and endophilic and its frequent contact with LLINs may have contributed to its downward trend. Conversely, *An. arabiensis* exhibits a combination of exophilic and partial zoophilic tendencies, which may have reduced its contact with LLINs promoting its upward trend [50,56-58]. Some studies along the Kenya coast indicate that *An. gambiae s.s.* may be found occurring in some focal areas which have been characterized as malaria hotspots in Kilifi District [59]. Understanding the ecology of *An. gambiae* and other malaria vectors in these hotspots will be a step closer towards the achievement of malaria-specific Millennium Development Goals [60-63].

In the current study, members of the *An. funestus* complex were not identified to species due to logistic difficulties. However, given the observed shift from human to animal feeding, it is likely that *Anopheles parensis,* a predominantly zoophilic member of *An. funestus* complex, has replaced the highly anthropophilic *An. funestus s.s.* as the most dominant species of this complex [41,42,64]. Currently molecular capability for analysis of sibling species of *An. funestus* [41,64] is well developed; consequently further studies are needed to assess the distribution and abundance of sibling species of the *An. funestus* complex along the Kenyan coast.

In conclusion, the results seen on the Kenyan coast show a downward trend in key entomological indices, which may

Table 5 Host-feeding patterns of *Anopheles funestus* and *Anopheles gambiae* s.l. between 1997 and 2008 (parenthesis shows proportion)

Species	**Year**	**Human**	**Bovine**	**Goat**	**Donkey**	**Human-Bovine**	**Chicken**
An. funestus	1997	148 (1.00)	0	0	0	0	0
	1998	35 (0.97)	0	1 (0.03)	0	0	0
	2002	1,458 (0.85)	249 (0.15)	0	0	0	0
	2007	7 (0.05)	113 (0.80)	20 (0.14)	1 (0.01)	1 (0.01)	0
	2008	2 (0.03)	47 (0.80)	8 (0.14)	0	2 (0.03)	0
An. gambiae s.l.	1997	826 (0.99)	0	3 (0.004)	0	1 (0.001)	2 (0.002)
	1998	283 (0.99)	0	3 (0.01)	0	1 (0.003)	0
	2002	245 (0.80)	62 (0.20)	0	0	0	0
	2007	38 (0.14)	202 (0.75)	27 (0.10)	0	2 (0.01)	0
	2008	41 (0.16)	187 (0.72)	28 (0.11)	0	4 (0.02)	0

help explain the reduction seen in malaria prevalence and incidence. The changes in the composition of *An. gambiae* complex have undoubtedly important implications for the epidemiology and strategies for control of malaria in the study area. With increase of *An. arabiensis* populations along the Kenya coast, mosquito control strategies should incorporate both indoor and outdoor control tools, which will help in significantly reducing the levels of malaria transmission. Scale up of LLINs to universal coverage, coupled with larval habitat management strategies, stakeholder involvement and community engagement packaged in integrated vector management (IVM) strategy, would be ideal to significantly reduce indoor and outdoor resting vectors [65-67].

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

JMM, BOO, JTM, JN, and HG conducted all data mining, extraction and preparations and further provided scientific guidance in data cleaning, analysis and manuscript preparation. CMM, EJM, JG and CB, offered scientific guidance in data analysis and manuscript preparation. JK and JCB provided overall supervision of the study and preparation of manuscript. All authors actively contributed to the interpretation of the findings and development of the final manuscript and approved the final manuscript.

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