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Habitat Diversity, Stability, and Productivity of Malaria Vectors in Irrigated and Nonirrigated Ecosystems in Western Kenya

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Abstract

Several sub-Saharan African countries rely on irrigation for food production. This study examined the impact of environmental modifications resulting from irrigation on the ecology of aquatic stages of malaria vectors in a semi-arid region of western Kenya. Mosquito larvae were collected from irrigated and non-irrigated ecosystems during seasonal cross-sectional and monthly longitudinal studies to assess habitat availability, stability, and productivity of anophelines in temporary, semipermanent, and permanent habitats during the dry and wet seasons. The duration of habitat stability was also compared between selected habitats. Emergence traps were used to determine the daily production of female adult mosquitoes from different habitat types. Malaria vectors were morphologically identified and sibling species subjected to molecular analysis. Data was statistically compared between the two ecosystems. After aggregating the data, the overall malaria vector productivity for habitats in the two ecosystems was estimated. Immatures of the malaria vector (*Anopheles arabiensis*) Patton (Diptera: Culicidae) comprised 98.3% of the *Anopheles* in both the irrigated and non-irrigated habitats. The irrigated ecosystem had the most habitats, higher larval densities, and produced 85.8% of emerged adult females. These results showed that irrigation provided conditions that increased habitat availability, stability, and diversity, consequently increasing the *An. arabiensis* production and potential risk of malaria transmission throughout the year. The irrigated ecosystems increased the number of habitats suitable for *Anopheles* breeding by about 3-fold compared to non-irrigated ecosystems. These results suggest that water management in the irrigation systems of western Kenya would serve as an effective method for malaria vector control.

Key words: environmental modification, irrigation, larval ecology, malaria, *Anopheles*

The Comprehensive Africa Agricultural Development Programme (CAADP), a continent-wide program developed under the African Union, has prioritized improving the reliability of water supplies for agriculture (Woodhouse et al. 2017). In order to boost the food security in arid and semi-arid areas of several sub-Saharan countries, the national policies have steadily incorporated irrigation systems in their agricultural landscapes (Woodhouse et al. 2017, Xie et al. 2018, Gowing et al. 2020). Unfortunately, irrigation can enhance habitat availability, diversity, and stability for anophelines (Ijumba and Lindsay 2001, Mwangangi et al. 2010, Kibret et al. 2017a,

Frake et al. 2020, Hawaria et al. 2020). Such anthropogenic land-use modifications have been reported to increase malaria transmission in Africa (Afrane et al. 2004, Chung 2016, Kyei-Baafour et al. 2020), India (Lee et al. 2016), and Central America (Grieco et al. 2006). In Kenya, where over 80% of the land is classified as arid or semi-arid (Biamah 2005, Maundu et al. 2009), some of these irrigation systems are known to create habitats that are suitable for the breeding of the region's two primary malaria vectors, *Anopheles arabiensis* Patton and (*Anopheles funestus*) s.l. Giles (Mukiama and Mwangi 1989, Afrane et al. 2004, Mathenge et al. 2005, Mwangangi et al. 2006, Muturi et al. 2009, 2013).

Unlike (*An. gambiae*) s.s. Giles, *An.arabiensis* predominates in semi-arid and arid environments of Africa (Lindsay et al. 1998, Gimnig et al. 2001) and is common in irrigated areas (White 1972). This species is mainly zoophilic and exophilic and can sustain malaria transmission in outdoor settings (Killen et al. 2016, Doucoure et al. 2020). In contrast, *An. funestus* is highly anthropophilic and endophilic, making this species an efficient malaria vector in indoor settings (Cohuert et al. 2004, Lwetoijera et al. 2014). In addition, this vectorial system increases malaria transmission stability via vector ecological succession, with *An. arabiensis* being more abundant than *An. funestus* during the planting season while *An. funestus* towards the crop maturation period (Chandler and Highton 1975, Mwangangi et al. 2006, Sogoba et al. 2007).

The most common malaria and vector control method in sub-Saharan Africa, including Kenya, has been long-lasting insecticide-impregnated nets (LLINs) (WHO 2013a, b). However, malaria vectors have developed resistance against pyrethroids (http://www.irmapper.com), the insecticide used to treat the nets (Zaim et al. 2000, Orondo et al. 2021). Indoor residual spraying (IRS) using the micro-encapsulated organophosphate insecticide pirimiphos-methyl (Actellic 300CS) has had a significant impact on the vectors and malaria prevalence where it has been applied (Rowland et al. 2013, Mashauri et al. 2017). However, vectors are known to develop resistance to chemical insecticides, and as such, the implementation of integrated vector management (IVM) programs using environmental management and pesticide rotations (larvicides and adulticides) to control mosquitoes is encouraged (MöRner et al, 2002, WHO 2003, Imbahale et al. 2012).

A prerequisite to applying any biological control of aquatic stages of malaria vectors is a detailed knowledge of their vector and habitat ecology (Dongus et al. 2007, Mereta et al. 2013, WHO 2013a, b). This includes knowledge of habitat availability, stability, and productivity. Such knowledge will allow the informed application of bio-larvicides and larval sources management, such as timely applications of low persistence or long-lasting formulations of the bio-pesticides *Bacillus thuringiensis var. israelensis* Barjac and *Lysinibacillus sphaericus*. It may also guide which vector to target in terms of its malaria transmission capacity and seasonality, thus reducing the densities of emerging adult populations and costs of mosquito control in general (WHO 2013a, b).

This study was undertaken in a semi-arid area of western Kenya where a concrete-lined channel irrigation ecosystem provides water for year-round multiple crop cultivation. Malaria is endemic in this region and vector control using LLINs and IRS with Actellic 300CS has been implemented. The study examined the impact of environmental modifications resulting from irrigation on the ecology of aquatic stages of malaria vectors. Environmental modification caused by irrigation has impacts on human health. Malaria control in irrigated ecosystem requires a collaborated effort between the agriculture and health sector. Policy makers in these sectors require evidence-based policies to manage malaria control. Currently, there is insufficient evidence to demonstrate the impact of environmental modification due to irrigation on vector ecology and malaria transmission. This study intends to fill the gap in knowledge of the effects of environmental modifications on the potential impacts on vector populations.

Materials and Methods

Study Site

This study was conducted in Homa Bay County, western Kenya, a semi-arid malaria-endemic area situated along the southern shores of Winam Gulf, the north-eastern corner of Lake Victoria (34.6°E and 0.5°S; 1,330 m above sea level, Fig. 1). The average annual temperature is approximately 23°C, and rainfall is approximately 1,600 mm, with two distinct rainy seasons between March–May ('long rains') and September–November ('short rains'). The dry season occurs in January–February, and the coolest and wettest season is June–July. Precipitation and minimum/maximum temperatures were recorded monthly during the study period (Supp Fig. S1 [online only]).

Beginning in 2007, the Ministry of Environment, Natural Resources, and Regional Development Authorities of Kenya have undertaken modifications of the local environment by constructing concrete-lined, channel irrigation systems through the Kimira-Oluch Small-holder Farm Improvement Project (KOSFIP). This project was implemented to improve food production at the household level by ensuring a reliable water supply. Gravity-fed irrigation water from the Tende River runs through these canals all year round, and the local community uses the water for crop, animal, and fish farming. Farmers irrigate parcels of lands containing mixed crops, such as rice, vegetables, fruits, or maize. Mosquito breeding has increased as a result of irrigation and the creation of more water sources. The key malaria vectors in this area are *An. arabiensis* and *An. funestus* s.l. The use of insecticide-treated nets has been the primary vector control strategy in this area. In 2018 and 2019, the government implemented IRS using Actellic 300CS that significantly reduced malaria vector populations.

Study Framework

The larval ecology portion of the study was undertaken using the framework as described by Githeko et al. (2012), which enables larval habitat profiling in terms of availability, stability, and productivity. The features allowed for targeted applications of larval source management, larval control and were conducted in the irrigated and non-irrigated ecosystems of Homa Bay to determine the impact of environmental modification on larval ecology. The irrigated ecosystem has either concrete- or earth-lined irrigation canals that distributes water from the main water supply. The non-irrigated ecosystem is an area with no irrigation canals to assist in agriculture.

The two ecosystems were further divided into 10 clusters based on the local villages. Larval sampling was undertaken in 2018 and 2019 from the clusters in the irrigated and non-irrigated ecosystems (Fig. 1). A cluster is an area of 1–2.5 km^2 that consists of 40–50 houses, or 300–500 residents. Within the ecosystems, habitats were classified as either temporary, semipermanent, or permanent. Temporary habitats were habitats that remained aquatic for approximately two weeks, while semipermanent habitats were those that held water for 2–3 months. Permanent habitats were habitats that could sustain their aquatic state for more than 3 months (Mereta et al. 2013). The habitats were within 2 km of nearby households; a distance less than 3.5 km, which is normally covered by starved Anophelines (Kaufmann and Briegel 2004).

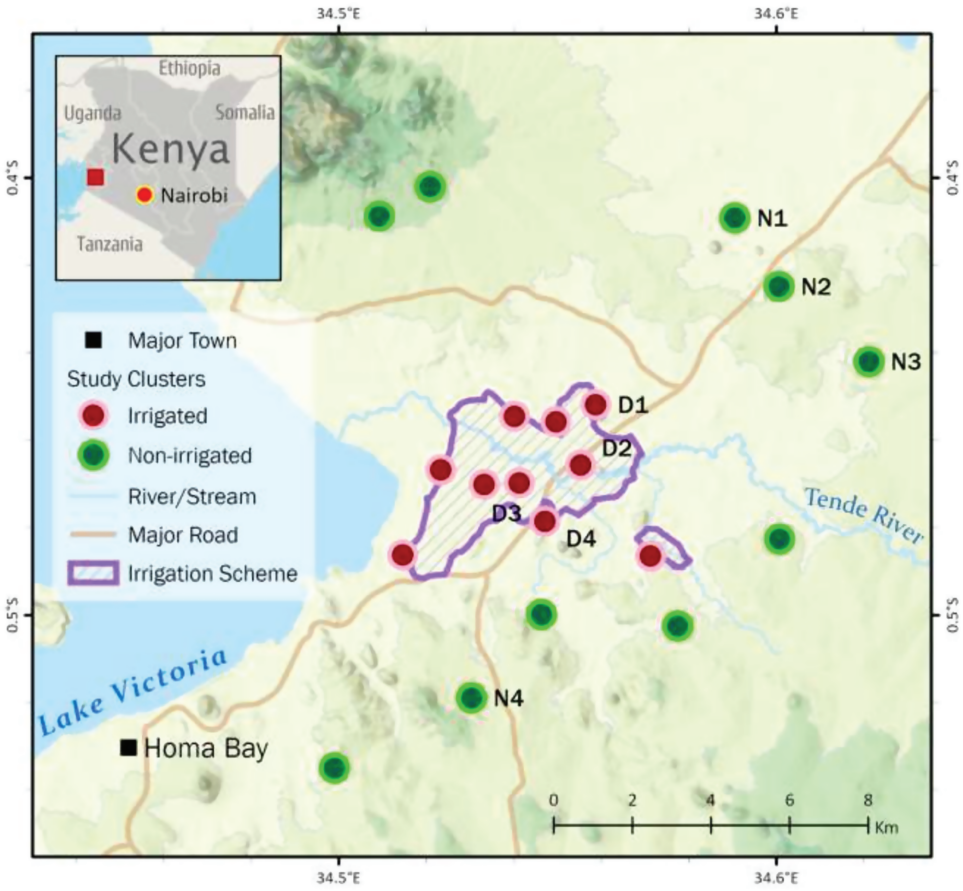

Fig. 1. Map of the study site indicates the sampling clusters in the irrigated and the non-irrigated ecosystems in Homa Bay, Kenya. D1–D4 and N1–N4 indicate clusters where monthly dynamics were conducted in irrigated and non-irrigated ecosystems, respectively.

Larval Habitat Availability and Larval Abundance

Larval habitat availability is defined as the presence of an aquatic habitat capable of harboring immature larval species (Githeko et al. 2012). To determine difference between irrigated and non-irirgated systems in habitat availability and larval abundance, a cross-sectional area-wide samplings were conducted by mapping all available aquatic habitats and examining mosquito larval abundance during the dry season (February–March) and after the rainy season (June–July) in 2018 and 2019 for all 20 clusters. All aquatic habitats within the clusters and 200 m buffer zones from the edge of each cluster were sampled using a standard 350 ml mosquito larvae dipper. Aquatic habitats within 200 m buffer zone from the edge of each cluster were examined because dispersal distance of adult *An. gambiae* mosquitoes is within 200 m (Yao et al. 2022). These habitats were geocoded and documented with metadata, including habitat types, dimensions, and the physical characteristics of the surrounding environment (shade and vegetation cover, distance from the nearest house, land use, habitat substrate, water flow, water clarity). Temporary habitats included animal/human footprints, tire tracks/road paddles, rock pools, rain pools, and water containers, while semipermanent habitats included drainage ditches, irrigated earthen canals, natural ponds, and rice paddies. Permanent habitats included man-made ponds, swamps, concrete-lined irrigation canals, fish ponds, and river edges (Supp Fig. S2 [online only]). Mosquito larvae identification using taxonomic keys (Gillies and De Meillon 1968, Gillies and Coetzee 1987) was done on sampled larvae in the field and enumerated; a subset of the sampled larvae was preserved in absolute ethanol, labeled, and transported to the laboratory for species identification by polymerase chain reaction (PCR). All mosquito larval abundance, including *Anopheles*, (*Culex*), and (*Aedes*) larvae were recorded, and the instar stages of different *Anopheles* larvae were also indicated.

Monthly Habitat and Larval Dynamics

To examine differences in the dynamics of aquatic habitats and larval abundance between irrigated and non-irrigated systems, four clusters in each ecosystem (irrigated and non-irrigated) were randomly selected and examined monthly from February to November in 2019. Sampling was not done in July due to logistical constraint. Sampling was completed in all aquatic habitats within the cluster and 200 m from the edge of each cluster. All sampled habitats were geocoded and documented with metadata as previously described. Larval sampling, morphological identification, and PCR molecular speciation were also completed using the above-mentioned methods. Larval densities of *Anopheles, Culex,* and *Aedes,* and the instar stages of different *Anopheles* larvae species were recorded.

Habitat Stability

Habitat stability is defined as the duration over which a habitat remains aquatic (Githeko et al. 2012). A cohort of 100 aquatic habitats, 50 from irrigated and 50 from non-irrigated ecosystems, was selected in September 2018. The irrigated ecosystem habitats consisted of man-made ponds, swamps, river edges, concrete irrigation lining, drainage ditches, and fish ponds, while the non-irrigated ecosystem habitats were composed of swamps, river edges, natural ponds, drainage ditches, and man-made ponds.

These habitats were followed every 2-weeks between September and November 2018, and then monthly from December 2018 to August 2019. During each visit, the aquatic status of each habitat was recorded. Larval sampling, morphological identification, and PCR molecular speciation were also completed using the above-mentioned methods.

Habitat Adult Vector Productivity Monitoring Using Emergence Traps

Habitat adult vector productivity is defined as a habitat capable of supporting immature stages of larval development until emergence into adults (Githeko et al. 2012). The productivity of malaria vectors in their natural aquatic habitats was determined using floating emergence traps (Service 1973). The emergence traps were constructed from conical metal frames, 1 m in height and 1 m in diameter, and thus each trap covered habitat surface area of 0.785 m^2. The design of the emergence traps prevented oviposition by other gravid mosquitoes. Traps were placed in randomly selected areas within the 2 m area from the habitat edges, and relocated every 2 d within specific habitats. Six replicates were used for each of the 6 habitat types in rice paddies, swamps, man-made ponds, drainage ditches, and fish ponds. This cycle was replicated three times for ten consecutive days. Productivity was determined by the number of emerging female mosquitoes collected using aspiration per habitat type per day. Habitat adult vector productivity was monitored daily for ten consecutive days from September to November 2019. Emerged mosquitoes were identified using taxonomic keys (Gillies and De Meillon 1968, Gillies and Coetzee 1987). In addition, habitats were sampled every morning to determine mosquito larval densities using the standard larval dippers and the sampled larvae returned into the habitats.

Overall Adult Vector Productivity in Each Ecosystem

Based on larval habitat stability and abundance from the field survey and habitat productivity from the emergence traps, the overall daily productivity of adult malaria vectors in the irrigated and non-irrigated ecosystems was modeled as the product of productive aquatic habitats area size and habitat productivity estimation based on emergence traps. In each ecosystem, the total area size of productive aquatic habitats for each cluster was calculated for permanent, semipermanent, and temporary habitats, using the field survey from September 2018 to August, 2019. For large permanent habitats, field observations indicated that mosquito larvae tended to concentrate near the edge of large habitats. Thus, the area within a 2 m distance from the habitat edge was assumed to be the area that permitted mosquito larvae to further develop into pupae and adults. The productivity of temporary habitats was based on an earlier publication in the area (0.2 female adult mosquitoes per m^2 aquatic habitat per day; Himeidan et al. 2009), and productivity of semipermanent and permanent habitats was based on the present study (0.104 and 0.085 adult mosquitoes per m^2 aquatic habitat per day, respectively). Due to the cluster size difference between irrigated and non-irrigated ecosystems, the weekly number of adult female mosquitoes produced from permanent, semipermanent, and temporary larval habitats for the irrigated and non-irrigated ecosystems were calculated and standardized against the study cluster area size.

DNA Extraction and Species Identification

All field-collected specimens were morphologically identified as *Anopheles*, *Culex*, and *Aedes* species. DNA was extracted from randomly selected *An. gambiae* s.l. specimens, and identified by PCR following the menhtod of Scott et al. (1993).

Data Analysis

During fieldwork, all information was collected through Open Data Kit (ODK) on tablets and then transferred to the MySQL database server. Larval densities per dip were calculated, and Z-tests were used to determine statistical difference between irrigated and non-irrigated ecosystems, and among different habitat types. Pearson chi-square was used to determine the differences in the occurrence of *Anopheles* larvae among the different habitat types and between the irrigated and non-irrigated ecosystems. The Kaplan–Meier survival analysis was employed to determine the stability of larval habitats in the irrigated and non-irrigated ecosystems. *Anopheles* densities from the emergence traps were analyzed using analysis of variance (ANOVA) to determine difference in the productivity among different habitat types and between the irrigated and non-irrigated ecosystems. Finally, a generalized linear mixed model (GLMM) with Poisson error and log link function was used to analyze the statistical difference in larval densities among temporary, semipermanent, and permanent habitats and the two ecosystems.

Results

Habitat Availability and Productivity

In comparison to clusters in the non-irrigated ecosystem, about 2.9-fold higher number of aquatic habitats were found and 2.6-fold higher number of *Anopheles* larvae were collected in the irrigated ecosystem (Table 1). The area size of clusters from the non-irrigated ecosystem was 28% larger than clusters from the irrigated ecosystem (1.84 vs 1.31 km^2). After adjusting for cluster area size, irrigated ecosystem had about 4-fold higher number of aquatic habitats. The proportion of aquatic habitats that were positive with *Anopheles* larvae was similar. Densities of immature stages decreased significantly with age: among all immature mosquitoes collected, pupae represented a small fraction, and the pupal proportion varied significantly between the irrigated (3.7%) and non-irrigated (1.2%) ecosystems (χ^2 = 69.48, df = 2, P < 0.0001, Table 1). In addition to *Anopheles*, similar number of *Culex* larvae and a few *Aedes* larvae were collected. Within malaria vectors, *An. gambiae* s.l. accounted for 94.7–95.4% of all *Anopheles* collected (Table 1).

Seasonality showed significant impact on larval habitat availability and larval densities (Fig. 2). Habitat availability fluctuated more dramatically in the non-irrigated ecosystem than in the irrigated ecosystem. Significant difference in the number of available habitats was detected between the two ecosystems only during the dry season (P < 0.05, Fig. 2A). In terms of larval densities, overall the rainy season exhibited significantly higher *Anopheles* density than the dry season (F = 15.09, df = 1,1311, P < 0.0001). Differences in *Anopheles* densities between irrigated and non-irrigated ecosystems was pronounced during the dry season in the temporary (Fig. 2B) and semipermanent habitats (Fig. 2C). Additionally, larval densities in permanent habitats were significantly higher in irrigated ecosystems than in non-irrigated ecosystems during the rainy season (Fig. 2D).

Monthly Habitat and Larval Density Dynamics

To determine whether irrigated and non-irrigated ecosystems differed in aquatic habitat abundance and larval density in months between dry and rainy seasons, the availability of aquatic habitats and larval density in 8 randomly selected clusters from the irrigated and non-irrigated ecosystems were monitored. The average area size of the cluster study area in the irrigated and non-irrigated ecosystems was similar (2.63 ± 0.06 km^2 and 2.78 ± 0.24 km^2, respectively). Compared to the non-irrigated ecosystem, there were significantly

Table 1. Habitat availability and immature mosquito counts during the dry and wet season in 2018 and 2019

Parameters	Irrigated	Non-irrigated	Test[a]	*P*-value
Number of clusters surveyed	10	10		
Mean cluster area size (±SD), km^2	1.31 ± 0.68	1.84 ± 0.93	t = 1.45, df = 16	0.083
Total number of habitats	985	331		
Total immature mosquito counts	19,485	7,849		
Anopheles total counts and habitat infestation				
Total counts	8,661	3,316		
Habitat infestation (%)	542 (55)	202 (61)	χ^2 = 3.63, df = 1	0.057
Anopheles immature counts by stage				
1st–2nd instar (%)	5,518 (64.9)	2,330 (70.3)		
3rd–4th instar (%)	2,687 (31.5)	945 (28.5)		
Pupa (%)	317 (3.7)	39 (1.2)	χ^2 = 69.48, df = 2	<0.0001
Mosquito counts by species				
Anopheles counts by species	8,661	3,316		
An. gambiae s.l.	8,260 (95.4)	3,140 (94.7)		
An. funestus s.l.	148 (1.7)	125 (3.8)		
An. coustani	86 (1.0)	46 (1.4)		
An. pharoensis	28 (0.3)	3 (0.1)		
Unidentified *Anopheles*	139 (1.6)	2 (0.1)	χ^2 = 101.79, df = 4	<0.0001
Culex counts	10,824	4,533		
Aedes counts	88	0		

[a]df: degrees of freedom; t: t-test; χ^2: chi-square test.

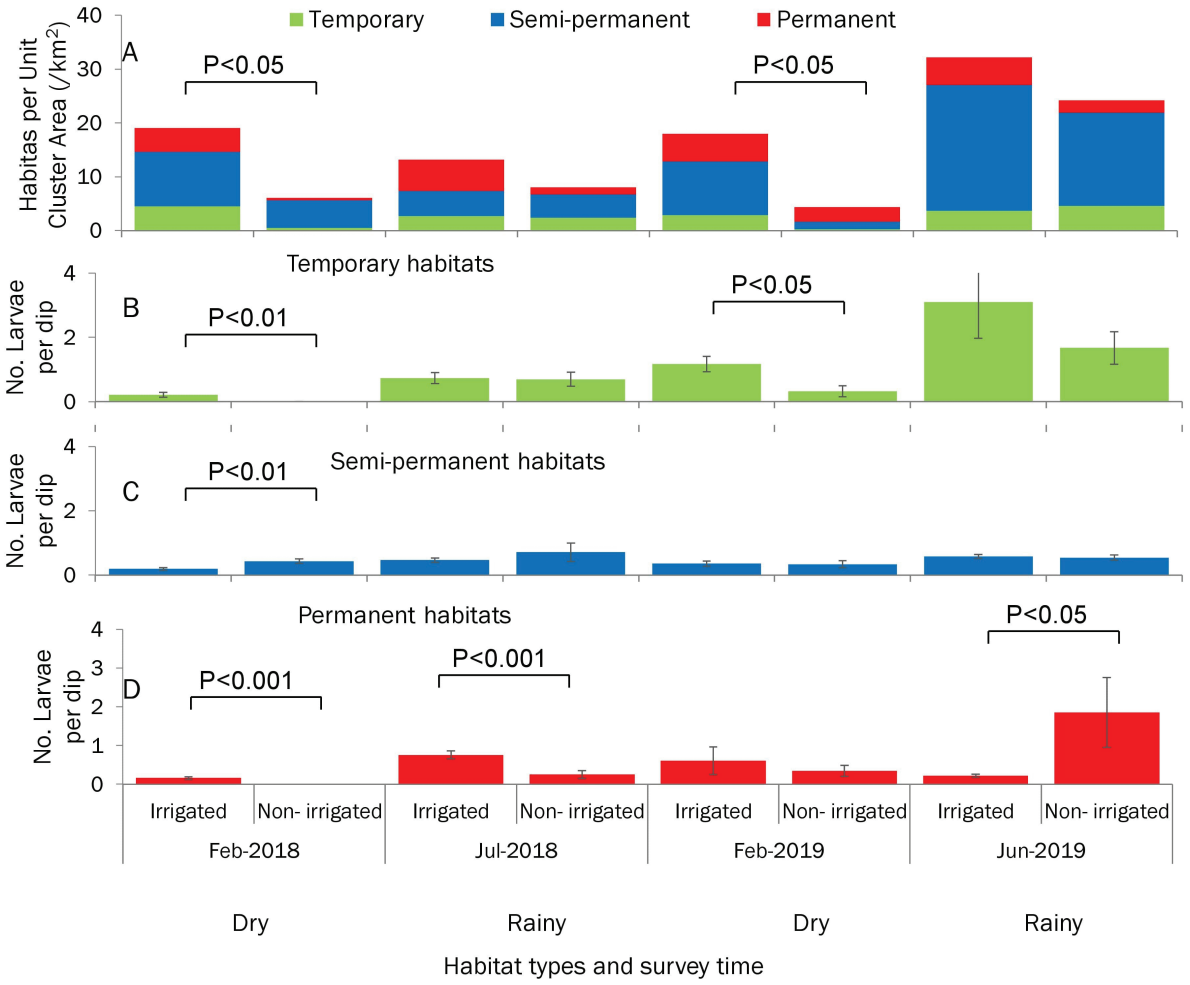

Fig. 2. The total number of habitats in a unit cluster area (A) and mean larval densities per dip in temporary (B), semipermanent (C), and permanent (D) in irrigated and non-irrigated ecosystems during the seasonal sampling in 2018 and 2019.

more semipermanent (χ^2 = 56.41, df = 1, P < 0.0001) and permanent (χ^2 =35.26, df = 1, P < 0.0001) habitats in the irrigated ecosystem, but similar number of temporary habitats (χ^2 = 3.12, df = 1, P > 0.05) (Fig. 3A and B). The irrigated ecosystem exhibited higher number of aquatic habitats and a significantly larger average area size of the aquatic habitats was than the non-irirgated ecosystem (Fig. 3C and D). Significantly higher *Anopheles* larval density was found in permanent habitats in non-irrigated ecosystem than in irrigated ecosystem (F = 6.25, df = 2,15, P < 0.01), but not in temporary (F = 0.17, df = 2,15, P > 0.05) and semipermanent (F = 0.89, df = 2,15, P > 0.05) habitats (Fig. 3E and F).

Habitat Stability

Among a cohort of 100 aquatic habitats enrolled in September 2018, 17 habitats were classified as semipermanent (man-made ponds, irrigation lining, and drainage ditches) and 33 were permanent habitats (swamps, river edges, and fish ponds) in the irrigated ecosystem. In the non-irrigated ecosystem, there were 28 semipermanent (man-made ponds and drainage ditches) and 22 permanent (swamps, river edges, and natural ponds) habitats. One-year monitoring of these habitats found that habitats in the irrigated ecosystem remained aquatic longer than the habitats in the non-irrigated ecosystem. On average, 89.4% and 92.3% of the permanent and semipermanent habitats remained aquatic on the inspection days in the irrigated ecosystem, respectively (Fig. 4A), significantly higher than those in the non-irrigated ecosystem (79.1% for permanent habitats, Z = 12.23, P < 0.0001; and 69.2% for semipermanent habitats; Z = 10.69, P < 0.0001; Fig. 4B). The largest difference in habitat stability between the irrigated and non-irrigated ecosystems occurred during the dry season.

In terms of larval density, permanent and semipermanent habitats exhibited no significant difference within the irrigated (F = 0.21, df = 1,23, P > 0.05; Fig. 4C) and non-irrigated ecosystems (F = 0.06, df = 1,23, P > 0.05; Fig. 4D). However, average *Anopheles* larval densities in the non-irrigated ecosystem were significantly higher than in the irrigated ecosystem for both permanent habitats (F = 5.62, df = 1, 23, P < 0.05) and semipermanent habitats (F = 5.46, df = 1, 23, P < 0.05). The period when the density differed the largest between the irrigated and non-irrigated ecosystems was in the dry period.

Habitat Productivity Surveillance Using Mosquito Emergence Traps

Overall, (*An. Coustani*) were the predominant adults collected from the five habitat types, followed by (*An. Pharoensi*)s and *An. gambiae s.l.*, while *An. funestus* were collected only from the rice paddies (Fig. 5A). The number of emerged *Anopheles* female mosquitoes varied significantly from 0.08 to 0.23 per trap-night among the 5 habitat types (F = 2.54, df = 4,85, P < 0.05; Fig. 5A), with drainage ditches having the highest productivity and the fish ponds the lowest productivity. The larval habitat types used for adult mosquito productivity surveillance did not differ significantly in larval densities (Fig. 5B). Habitat productivity of adult mosquitoes varied significantly from 1.1% to 4.4% (P < 0.01), with the highest in swamps and the lowest in man-made ponds and fish ponds (Fig. 5C).

Overall Adult Malaria Vector Productivity in Each Ecosystem

After assessing for habitat availability, dynamics, and stability, the overall malaria vector productivity for all the habitats in irrigated and non-irrigated ecosystems in the study clusters was estimated. For both irrigated and non-irrigated ecosystems, semipermanent habitats produced the largest number of adult vectors as they were most abundant and most productive (Fig. 6). The daily productivity of adult vectors from permanent and semipermanent habitats in the irrigated ecosystem was 1.4–3.2 fold higher than those in the non-irrigated ecosystem, and similar for the temporary habitats (Table 2). The overall adult malaria vector productivity of clusters from the irrigated ecosystem was estimated to be 137.0 female malaria mosquitoes per km^2 cluster area per day,1.9 fold higher than clusters from the non-irrigated ecosystem (72.1 female malaria mosquitoes per km^2 cluster area per day) (Table 2).

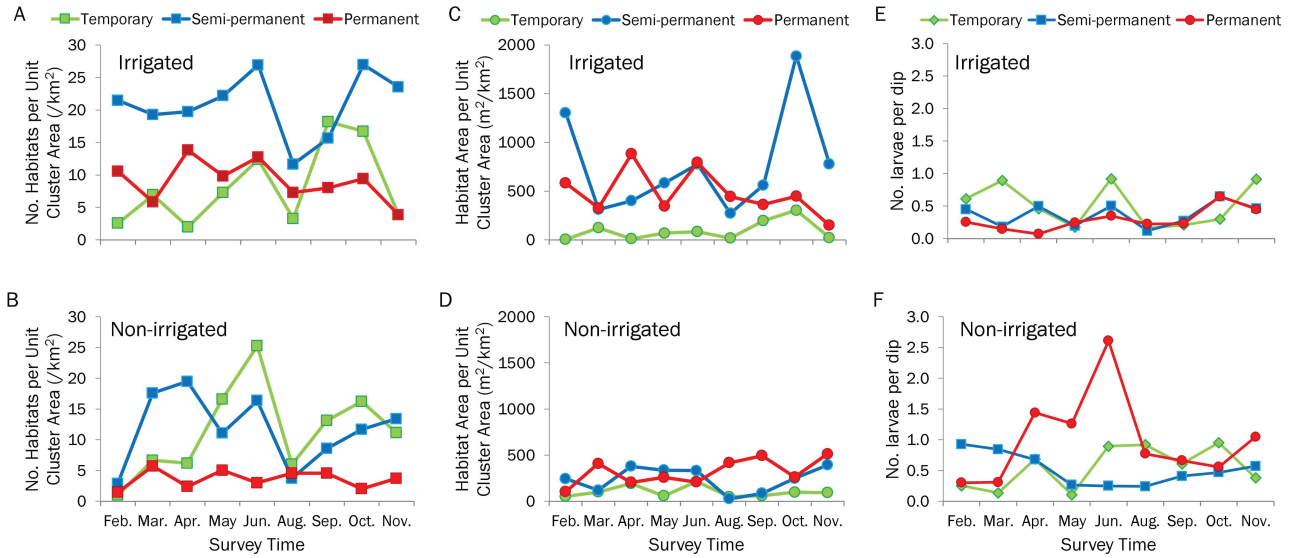

Fig. 3. Number of habitat per unit cluster area (/km^2) in the irrigated (A) and non-irrigated (B) ecosystem; habitat area per unit cluster area (m^2/km^2) in irrigated (C) and non-irrigated (D) ecosystem; larval density in the irrigated (E) and non-irrigated (F) ecosystem during monthly larval dynamics in 2019 in temporary, semipermanent, and permanent habitats.

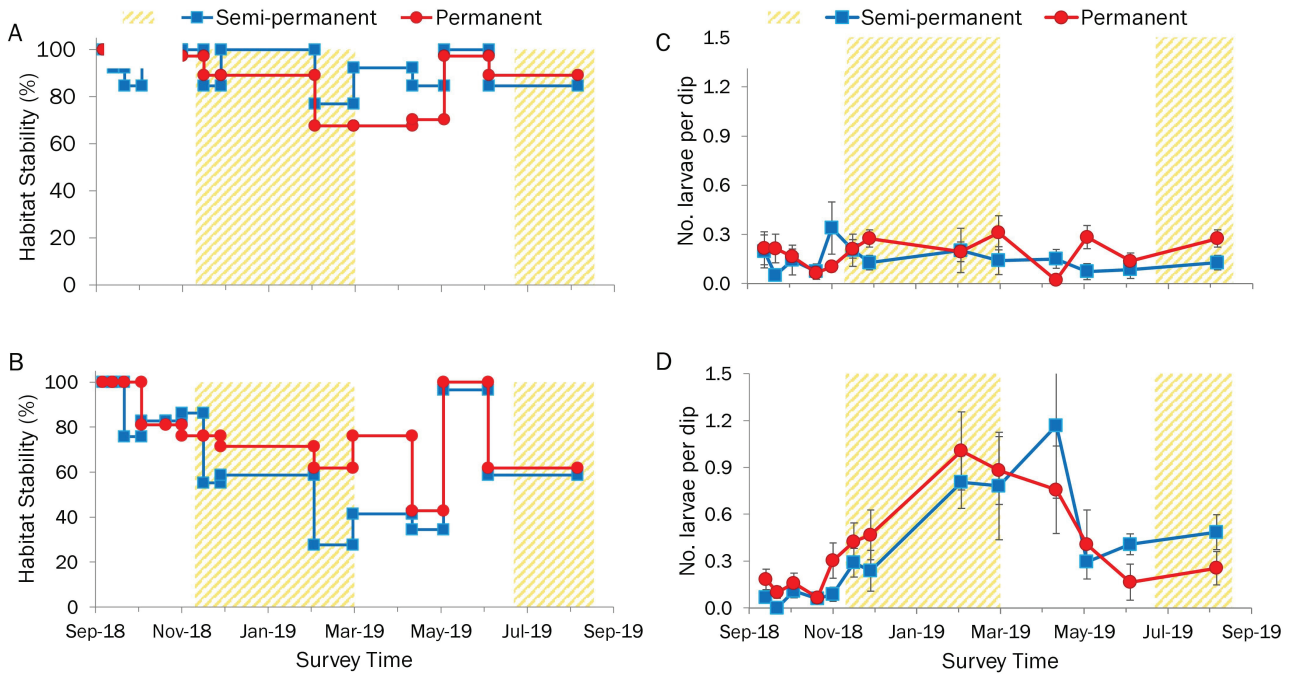

Fig. 4. Habitat stability in the irrigated (A) and non-irrigated (B) ecosystems, and *Anopheles* densities per dip in the irrigated (C) and non-irrigated (D) ecosystems from September 2018 to August 2019.

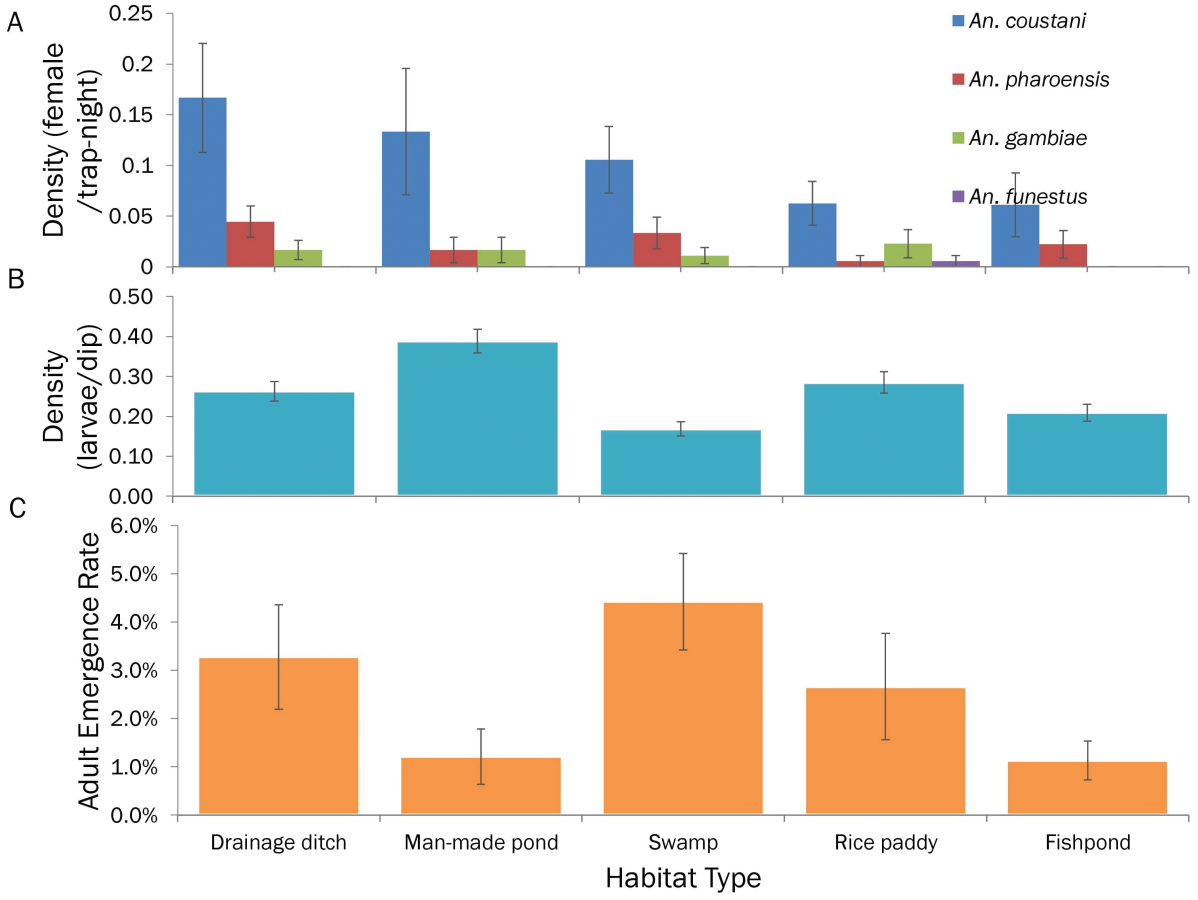

Fig.5. Densities of female adult *Anopheles* per trap-night (A) collected from the emergence traps, densities of larval *Anopheles* per dip (B) collected from the habitats, and adult emergence rate (C) from the different types of habitats where emergence traps were conducted.

Molecular Species Identification

In the seasonal larval surveillance and dynamics, molecular species identification was made on a subset (1,399 samples) of the *An. gambiae* s.l. sampled during this study. *Anopheles arabiensis* comprised 98.3% of the specimens analyzed, with the remainder being *An. gambiae*. For the adult mosquito productivity surveillance through the emergency traps, all female *An. gambiae* s.l. samples (12) were analyzed for species identification. *An. arabiensis* was the only species identified within *An. gambiae* s.l. in the adult mosquito productivity experiment. *An. funestus* s.s was the only sibling species identified by PCR from the seasonal surveillance (73) and the emergence traps (1).

Discussion

This study was conducted in Homa Bay, an area with high ITN coverage (>80%) (National Malaria Control Programme 2015), and IRS was conducted in February/March 2018 and 2019 using the organophosphate insecticide Actellic 300CS. IRS activities in this region have resulted in a significant decrease in the proportion of primary malaria vectors (Abong'o et al. 2020). Despite the establishment of the KOSFIP irrigation system in Homa Bay County, its impact on malaria vector dynamics and transmission remains unknown. Through aquatic habitat characterization, this study aimed to understand the effect of irrigation on malaria vector larval ecology, which provides insight for larval source management. This study found that the irrigated ecosystem had more habitats and higher larval productivity than the non-irrigated ecosystem. Furthermore, more stable habitats were observed in the irrigated ecosystem. Seasonality had a significant effect in the non-irrigated ecosystem but had no effect in the irrigated ecosystem, with 3–5 times more stable aquatic habitats in the irrigated ecosystem than in the non-irrigated during the dry season. Larval productivity was found to be higher in more stable habitats, with semipermanent habitats having higher densities than permanent habitats. *An. arabiensis* accounted for the greatest proportion of anophelines larvae (>95%), while other *Anopheles* species accounted for only 2% each.

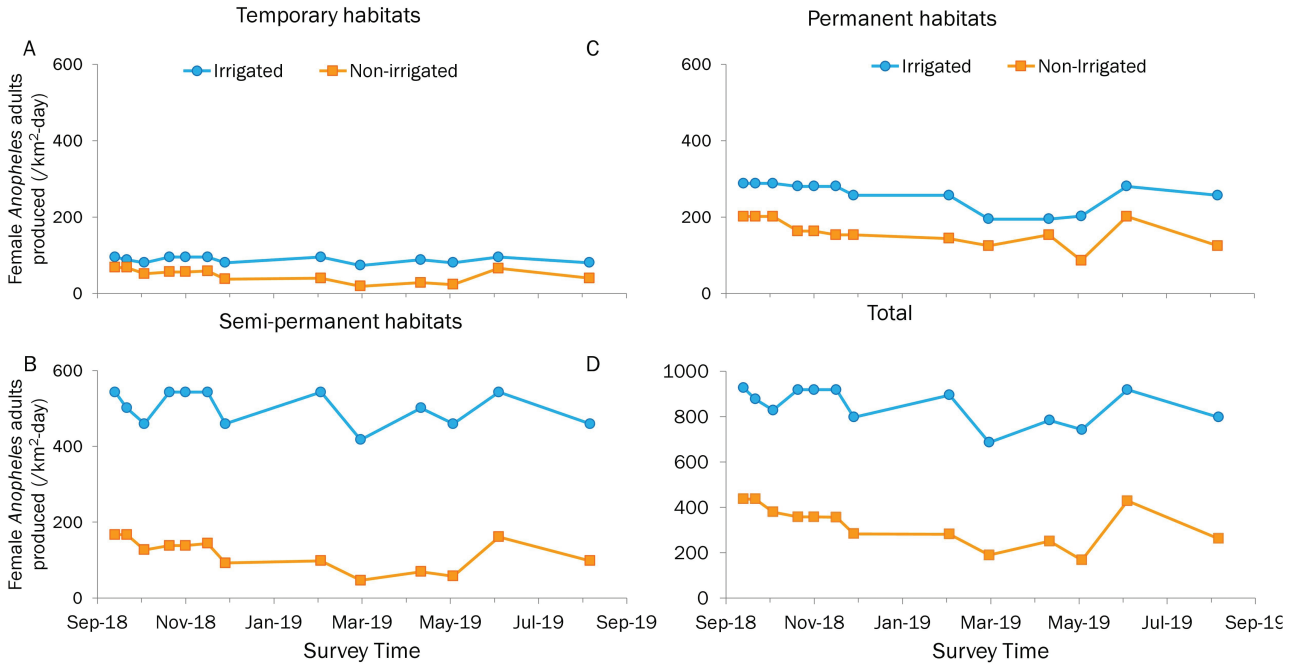

Fig. 6. Predicted number of emerged female *Anopheles* adults produced in unit cluster area per day (/km²-day) in Temporary (A), Semipermanent (B), Permanent (C) habitats, and all/combined (D) habitat types.

Table 2. Estimated adult malaria vector productivity for larval habitats in the study clusters in the irrigated and non-irrigated ecosystems

	Irrigated				Non-irrigated			
Habitat type	Permanent	Semipermanent	Temporary	Total	Permanent	Semiper-manent	Temporary	Total
Habitat counts (/km²-cluster area) (95% CI)	9.0 (6.6, 11.5)	20.8 (17, 24.7)	8.1 (3.4, 12.9)	37.9	3.6 (2.5, 4.7)	11.6 (7.1, 16.1)	11.3 (5.7, 17.0)	26.5
Habitat area (m²/km²-cluster area) (95% CI)	951 (579, 1316)	2,029 (236, 3996)	175 (0, 359)	3,155	1,551 (486, 2252)	309 (155, 493)	116 (69, 177)	1,976
Habitat effective area (m²/km²-cluster area) (95% CI)	485 (302, 662)	748 (361, 1168)	91 (15, 170)	1,324	339 (208, 429)	230 (136, 343)	97 (54, 147)	666
Female vector emerge rate (/m², from emergence trap)	0.085	0.104	0.200	–	0.085	0.104	0.200	–
Daily female vector productivity (number of female adults per km² cluster area)	41.2	77.6	18.2	137.0	28.8	23.9	19.4	72.1

The current study found no significant difference in *An. gambiae* s. l. populations in either of the ecosystem. In non-irrigated areas, rainfall had a significant influence on the number of larval habitats since more habitats were sampled during the wet season as opposed to the dry season. The findings supported previous research that found a significant increase in larval habitats, including temporary pools that were highly productive for *Anopheles* breeding (Nsereko et al. 2020). In contrast to the non-irrigated ecosystem, where larval abundance peaked after seasonal rain, larval abundance in the irrigated ecosystem was associated with irrigation, while rainfall had little effect.

Temporary habitats significantly contributed to the larval vector abundance in both ecosystems during the rainy seasons, and such has also been reported elsewhere as having high larval survivorship for *An. gambiae* s.l. (Gilles and Warrell 1996, Mwangangi et al. 2010, Nsereko et al. 2020). These habitats have been observed to be the preferred *Anopheles* oviposition sites due to fewer predators (Service 1977, Sunahara et al. 2002, Munga et al. 2007, Silberbush and Blaustein 2008, Munga et al. 2013). The habitat type influenced *Anopheles* densities in irrigated and non-irrigated ecosystems. Both habitat type and seasonality affected *Anopheles* densities in both ecosystems. Seasonality had a strong influence on habitat availability in the non-irrigated as compared to irrigated ecosystem with more stable larval habitats. This could be due to the constant availability of water in the irrigated ecosystem, which was not significantly affected by seasonal weather changes. The monthly larval sampling revealed higher *Anopheles* larval densities in the non-irrigated compared to irrigated ecosystem. The study attributes the observed difference to limited breeding sites in the non-irrigated ecosystem with concentrated breeding in temporary water pools (animal and human footprints) that serve as communal water collection points.

The overall adult vector productivity, which integrated the effects of habitat diversity, stability, and availability, shows that permanent and semipermanent habitats were more productive than temporary habitats in both ecosystems. The daily productivity of adult female vectors from the habitats was higher in the irrigated ecosystems. With semipermanent habitats dominating the current study site, the overall adult vector productivity was calculated based on some assumptions; more field surveys and data collections are needed to validate this idea. However, because *An. arabiensis* was found in various habitats, all aquatic habitats should be treated as potential vector breeding sites (Sattler et al. 2005).

Malaria vector control strategies are determined by several factors, such as vector species availability, vector abundance, vector feeding, resting behavior, and the endemic nature of the disease in the targeted area. Vector abundance and *Anopheles* breeding sites are essential to reduce malaria transmission and should be targeted to guide interventions (Craig et al. 1999, Coetzee et al. 2000, Eisele et al. 2003). The relationship between larval densities and adult vectors in irrigated and non-irrigated ecosystems remains contentious with regards to malaria cases (Ijumba and Lindsay 2001), with some studies correlating larval densities with increase in malaria cases in irrigated areas (Kibret et al. 2010, Kibret et al. 2017b), while others showing no correlation (Hunter et al. 1993, Ijumba et al., 1997). Previous studies have shown that the rate of adult vector emergence from their aquatic habitats is very low (approximately 1–4% of the immature stages) (Service 1971, 1973; Mukiama and Mwangi 1989, Munga et al. 2006, Munga et al. 2007) thus affirming the none correlation between larval densities and malaria cases. In addition, the current study has shown that the number of female *Anopheles* vectors emerging from the breeding sites is low as collected from the emergence traps.

Conclusion

Environmental modification through the construction of an irrigation system increases the availability and stability of vector breeding habitats as observed in the study site. Seasonality had no influence on larval densities in the irrigated ecosystem since more habitats were stable. This poses a constant threat to malaria transmission due to a higher number of potential breeding sites. Environmental modifications that result in more malaria vectors could offset gains achieved by using LLINs and IRS, making controlling mosquito production in irrigated ecosystems crucial in preventing malaria transmission in the region.

Conflict of Interest

All authors have no conflict of interest to declare

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Authors' Contributions

GY, JWK, and AKG conceived and designed the research. PWO, HA, BMO, KO, CJO, and WOO participated in the fieldwork and data collection. PWO and DZ participated in laboratory analysis. PWO, AKG, DZ, MCL, XW and GZ did the data analysis. MCL determined the study site demarcations. PWO and AKG drafted the manuscript. XW, MCL and GY edited the manuscript. All authors read and approved the final version of the manuscript.

Supplementary Data

Supplementary data are available at *Journal of Medical Entomology* online.

Figure S1. Monthly weather 2018-2019 in the study site in Homa Bay, Kenya.

Figure S2. The diversity of habitat types surveyed in the study area, Homa Bay, Kenya.

References Cited

Abong'o, B., J. E. Gimnig, S. J. Torr, B. Longman, D. Omoke, M. Muchoki, F. Ter Kuile, E. Ochomo, S. Munga, and A. M. Samuels. 2020. Impact of indoor residual spraying with pirimiphos-methyl (Actellic 300CS) on entomological indicators of transmission and malaria case burden in Migori County, western Kenya. *Sci. Reports.* 10: 1–14.

Afrane, Y. A., E. Klinkenberg, P. Drechsel, K. Owusu-Daaku, R. Garms, and T. Kruppa. 2004. Does irrigated urban agriculture influence the transmission of malaria in the city of Kumasi, Ghana? *Acta Trop.* 89: 125–134.

Biamah, E. K. 2005. *Coping with drought: options for soil and water management in semi-arid Kenya*. Wageningen Univ. Res. Centre, Wageningen.

Chandler, J., and R. Highton. 1975. The succession of mosquito species (Diptera, Culicidae) in rice fields in the Kisumu area of Kenya, and their possible control. *Bull. Entomol. Res.* 65: 295–302.

Chung, B. 2016. Impact of irrigation extension on malaria transmission in Simret, Tigray, Ethiopia. *Korean J. Parasitol.* 54: 399–405.

Coetzee, M., M. Craig, and D. Le Sueur. 2000. Distribution of African malaria mosquitoes belonging to the Anopheles gambiae complex. *Parasit. Today.* 16: 74–77.

Cohuet, A., F. Simard, C. S. Wondji, C. Antonio-Nkondjio, P. Awono-Ambene, and D. Fontenille. 2004. High malaria transmission intensity due to *Anopheles funestus* (Diptera: Culicidae) in a village of savannah–forest transition area in Cameroon. *J. Med. Entomol.* 41: 901–905.

Craig, M. H., R. Snow, and D. Le Sueur. 1999. A climate-based distribution model of malaria transmission in sub-Saharan Africa. *Parasit. Today.* 15: 105–111.

Dongus, S., D. Nyika, K. Kannady, D. Mtasiwa, H. Mshinda, U. Fillinger, A. W. Drescher, M. Tanner, M. C. Castro, and G. F. Killeen. 2007. Participatory mapping of target areas to enable operational larval source management to suppress malaria vector mosquitoes in Dar es Salaam, Tanzania. *Int. J. Health Geogr.* 6: 37.

Doucoure, S., O. Thiaw, A. Wotodjo, C. Bouganali, N. Diagne, P. Parola, and C. Sokhna. 2020. *Anopheles arabiensis* and *Anopheles funestus* biting pattern in Dielmo, an area of low level exposure to malaria vectors. *Malar. J.* 19: 230.

Eisele, T. P., J. Keating, C. Swalm, C. M. Mbogo, A. K. Githeko, J. L. Regens, J. I. Githure, L. Andrew, and J. C. Beier. 2003. Linking field-based ecological data with remotely sensed data using a geographic information system in two malaria endemic urban areas of Kenya. *Malar. J.* 2: 44.

Frake, A. N., W. Namaona, E. D. Walker, and J. P. Messina. 2020. Estimating spatio-temporal distributions of mosquito breeding pools in irrigated agricultural schemes: a case study at the Bwanje Valley Irrigation Scheme. *Malar. J.* 19: 1–21.

Gillies, M. T., and B. De Meillon. 1968. The anophelinae of Africa south of the Sahara (Ethiopian zoogeographical region). *Publ. S. Afr. Inst. Med. Res.* 54: 1–343.

Gillies, M., and M. Coetzee. 1987. A supplement to the anophelinae of Africa south of the Sahara. *Publ. S. Afr. Inst. Med. Res.* 55: 1–143.

Gilles, H. M., **and** D. A. Warrell (eds.). **1996**. *Bruce-Chwatt's essential malariology*, 3rd ed. Edward Arnold (Publisher) Ltd., Boston, USA.

Gimnig, J. E., M. Ombok, L. Kamau, and W. A. Hawley. 2001. Characteristics of larval anopheline (Diptera: Culicidae) habitats in Western Kenya. *J. Med. Entomol.* 38: 282–288.

Githeko, A. K., E. N. Ototo, and Y. Guiyun. 2012. Progress towards understanding the ecology and epidemiology of malaria in the western Kenya highlands: opportunities and challenges for control under climate change risk. *Acta Trop.* 121: 19–25.

Gowing, J., D. Walker, G. Parkin, N. Forsythe, A. T. Haile, and D. A. Ayenew. 2020. Can shallow groundwater sustain small-scale irrigated agriculture in sub-Saharan Africa? Evidence from NW Ethiopia. *Groundw. Sustain. Dev.* 10: 100290.

Grieco, J. P., S. Johnson, N. L. Achee, P. Masuoka, K. Pope, E. Rejmankova, E. Vanzie, R. Andre, and D. Roberts. 2006. Distribution of *Anopheles albimanus*, *Anopheles vestitipennis*, and *Anopheles crucians* associated with land use in northern Belize. *J. Med. Entomol.* 43: 614–622.

Hawaria, D., A. Demissew, S. Kibret, M. -C. Lee, D. Yewhalaw, and G. Yan. 2020. Effects of environmental modification on the diversity and positivity of anopheline mosquito aquatic habitats at Arjo-Dedessa irrigation development site, southwest Ethiopia. *Infect. Dis. Poverty.* 9: 9.

Himeidan, Y. E., G. Zhou, L. Yakob, Y. Afrane, S. Munga, H. Atieli, A. El-Rayahel, A. K. Githeko, and G. Yan. 2009. Habitat stability and occurrences of malaria vector larvae in western Kenya highlands. *Malar. J.* 8: 234.

Hunter, J. M., L. Rey, K. Chu, E. Adekolu-John, and K. E. Mott. 1993. *Parasitic diseases in water resources development: the need for intersectoral negotiation*. World Health Organization, Geneva. https://apps.who.int/iris/bitstream/handle/10665/38322/9241561556.pdf?sequence=1&isAllowed=y.

Ijumba, J. 1997. *The impact of rice and sugarcane irrigation on malaria transmission in the lower Moshi area of northern Tanzania*. PhD thesis, Zoo. Inst., Copenhagen, Denmark

Ijumba, J., and S. Lindsay. 2001. Impact of irrigation on malaria in Africa: paddies paradox. *Med. Vet. Entomol.* 15: 1–11.

Imbahale, S. S., A. Githeko, W. R. Mukabana, and W. Takken. 2012. Integrated mosquito larval source management reduces larval numbers in two highland villages in western Kenya. *BMC Public Health*. 12: 362.

Kaufmann, C., and H. Briegel. 2004. Flight performance of the malaria vectors *Anopheles gambiae* and *Anopheles atroparvus*. *J. Vector Ecol.* 29: 140–153.

Kibret, S., Y. Alemu, E. Boelee, H. Tekie, D. Alemu, and B. Petros. 2010. The impact of a small-scale irrigation scheme on malaria transmission in Ziway area, Central Ethiopia. *Trop. Med. Int. Health*. 15: 41–50.

Kibret, S., G. G. Wilson, D. Ryder, H. Tekie, and B. Petros. 2017a. The influence of dams on malaria transmission in sub-Saharan Africa. *EcoHealth*. 14: 408–419.

Kibret, S., G. G. Wilson, D. Ryder, H. Tekie, and B. Petros. 2017b. Malaria impact of large dams at different eco-epidemiological settings in Ethiopia. *Trop. Med. Health*. 45: 4.

Killeen, G. F., N. J. Govella, D. W. Lwetoijera, and F. O. Okumu. 2016. Most outdoor malaria transmission by behaviourally-resistant Anopheles arabiensis is mediated by mosquitoes that have previously been inside houses. *Malar. J.* 15: 225.

Kyei-Baafour, E., B. Tornyigah, B. Buade, L. Bimi, A. R. Oduro, K. A. Koram, B. A., Gyan, K. A. Kusi. 2020. Impact of an irrigation dam on the transmission and diversity of *Plasmodium falciparum* in a seasonal malaria transmission area of northern Ghana. *Journal of Tropical Medicine*. **2020**.

Lee, E., J. Burkhart, S. Olson, A. A. Billings, J. A., Patz, E. J. Harner. 2016. Relationships of climate and irrigation factors with malaria parasite incidences in two climatically dissimilar regions in India. *Journal of Arid Environments*. 124:214-224.

Lindsay, S., L. Parson, C. Thomas. 1998. Mapping the range and relative abundance of the two principal African malaria vectors, *Anopheles gambiae* sensu stricto and *An. arabiensis*, using climate data. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265, 847-854.

Lwetoijera, D. W., C. Harris, S. S. Kiware, S. Dongus, G. J. Devine, P. J. Mccall, S. Majambere. 2014. Increasing role of Anopheles funestus and *Anopheles arabiensis* in malaria transmission in the Kilombero Valley, Tanzania. *Malaria Journal*. 13:1-10.

Mashauri, F. M., A. Manjurano, S. Kinung'hi, J. Martine, E. Lyimo, C. Kishamawe, C. Ndege, M. M. Ramsan, A. Chan, C. D. Mwalimu. 2017. Indoor residual spraying with micro-encapsulated pirimiphos-methyl (Actellic® 300CS) against malaria vectors in the Lake Victoria basin, Tanzania. *PloS one*. 12:e0176982.

Mathenge, E. M., G. O. Misiani, D. O. Oulo, L. W. Irungu, P. N. Ndegwa, T. A. Smith, G. F. Killeen, B. G. Knols. 2005. Comparative performance of the Mbita trap, CDC light trap and the human landing catch in the sampling of *Anopheles arabiensis*, *An. funestus* and culicine species in a rice irrigation in western Kenya. *Malar J.* 4:7.

Maundu, P., S. Kibet, Y. Morimoto, M. Imbumi, R. Adeka. 2009. Impact of Prosopis juliflora on Kenya's semi-arid and arid ecosystems and local livelihoods. *Biodiversity*. 10:33-50.

Mereta, S. T., D. Yewhalaw, P. Boets, A. Ahmed, L. Duchateau, N. Speybroeck, S. O. Vanwambeke, W. Legesse, L. De Meester, P. L. Goethals. 2013. Physico-chemical and biological characterization of anopheline mosquito larval habitats (Diptera: Culicidae): implications for malaria control. *Parasites & vectors*. 6:1-16.

MöRner, J., R. Bos, M. Fredrix, W. H. Organization. **2002**. Reducing and eliminating the use of persistent organic pesticides: guidance on alternative strategies for sustainable pest and vector management.

Mukiama, T. K., R. W. Mwangi. 1989. Field studies of larval *Anopheles arabiensis* Patton of Mwea irrigation scheme, Kenya. *International Journal of Tropical Insect Science*. 10:55-62.

Munga, S., N. Minakawa, G. Zhou, A. K. Githeko, G. Yan. 2007. Survivorship of immature stages of *Anopheles gambiae* sl (Diptera: Culicidae) in natural habitats in western Kenya highlands. *Journal of Medical Entomology*. 44:758-764.

Munga, S., J. Vulule, E. J. Kweka. 2013. Response of *Anopheles gambiae* sl (Diptera: Culicidae) to larval habitat age in western Kenya highlands. *Parasites & vectors*. 6:1-6.

Muturi, E. J., L. Kamau, B. G. Jacob, S. Muriu, C. M. Mbogo, J. Shililu, J. Githure, R. J. Novak. 2009. Spatial distribution, blood feeding pattern,

and role of *Anopheles funestus* complex in malaria transmission in central Kenya. *Parasitology research*. 105:1041-1046.

Muturi, E. J., J. M. Mwangangi, J. C. Beier, M. Blackshear, J. Wauna, R. Sang, W. R. Mukabana. 2013. Ecology and behavior of *Anopheles arabiensis* in relation to agricultural practices in central Kenya. *Journal of the American Mosquito Control Association*. 29:222-230.

Mwangangi, J. M., E. J. Muturi, J. Shililu, S. M. Muriu, B. Jacob, E. W. Kabiru, C. M. Mbogo, J. Githure, R. Novak. 2006. Survival of immature *Anopheles arabiensis* (Diptera: Culicidae) in aquatic habitats in Mwea rice irrigation scheme, central Kenya. *Malaria journal*. 5:1-8.

Mwangangi, J. M., J. Shililu, E. J. Muturi, S. Muriu, B. Jacob, E. W. Kabiru, C. M. Mbogo, J. Githure, R. J. Novak. 2010. *Anopheles* larval abundance and diversity in three rice agro-village complexes Mwea irrigation scheme, central Kenya. *Malaria journa.*, 9:1-10.

Nsereko, G., Kadobera, D., Okethwangu, D., Nguna, J., Rutazaana, D., Kyabayinze, D. J., Opigo, J. & Ario, A. R. 2020. Malaria outbreak facilitated by appearance of vector-breeding sites after heavy rainfall and inadequate preventive measures: Nwoya District, Northern Uganda, February–May 2018. *Journal of environmental and public health*.

Orondo, P. W., S. G. Nyanjom, H. Atieli, J. Githure, B. M. Ondeto, K. O. Ochwedo, C. J. Omondi, J. W. Kazura, M. C. Lee, G. Zhou. *et al*. **2021**. Insecticide resistance status of Anopheles arabiensis in irrigated and non-irrigated areas in western Kenya. *Parasit. Vectors*. 14: 335. doi:10.1186/s13071-021-04833-z

Rowland, M., P. Boko, A. Odjo, A. Asidi, M. Akogbeto, R. N'guessan. 2013. A new long-lasting indoor residual formulation of the organophosphate insecticide pirimiphos methyl for prolonged control of pyrethroid-resistant mosquitoes: an experimental hut trial in Benin. *PloS one*. 8:e69516.

Sattler, M. A., D. Mtasiwa, M. Kiama, Z. Premji, M. Tanner, G. F. Killeen, C. Lengeler. 2005. Habitat characterization and spatial distribution of *Anopheles* sp. mosquito larvae in Dar es Salaam (Tanzania) during an extended dry period. *Malaria journal*. 4: 1-15.

Scott, J. A., W. G. Brogdon, F. H. Collins. 1993. Identification of single specimens of the *Anopheles gambiae* complex by the polymerase chain reaction. *Am J Trop Med Hyg*, 49.

Service, M. 1971. The daytime distribution of mosquitoes resting in vegetation. *Journal of Medical Entomology*. 8:271-278.

Service, M. 1973. Mortalities of larvae of *Anopheles-gambiae* giles complex and detection of predators by precipitin test. *Bulletin of Entomological Research*. 62:359-369.

Silberbush, A., L. Blaustein. 2008. Oviposition habitat selection by a mosquito in response to a predator: are predator-released kairomones air-borne cues? *Journal of Vector Ecology*. 33:208-211.

Sogoba, N., S. Doumbia, P. Vounatsou, I. Baber, M. Keita, M. Maiga, S. F. Traoré, A. Touré, G. Dolo, T. Smith. 2007. Monitoring of larval habitats and mosquito densities in the Sudan savanna of Mali: implications for malaria vector control. *The American Journal of Tropical Medicine and Hygiene*. 77:82-88.

Sunahara, T., K. Ishizaka, M. Mogi. 2002. Habitat size: a factor determining the opportunity for encounters between mosquito larvae and aquatic predators. *Journal of Vector Ecology*. 27:8-20.

White, G. 1972. The *Anopheles gambiae* complex and malaria transmission around Kisumu, Kenya. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 66, 572-581.

WHO (World Health Organization). **2003**. *Guidelines for dengue surveillance and mosquito control*.

WHO (World Health Organization). **2013a**. Larval source management: a supplementary malaria vector control measure: an operational manual. 116 pp.

WHO (World Health Organization). **2013b**. *Methods for maintaining coverage with long-lasting insecticidal nets (LLIN): Vector Control Technical Expert Group Report to MPAC*.

Woodhouse, P., G. L. Veldwisch, J. -P. Venot, D. Brockington, H. Komakech, and A. Manjichi. 2017. African farmer-led irrigation development: re-framing agricultural policy and investment? *J. Peasant Stud*. 44: 213–233.

Xie, H., N. Perez, W. Anderson, C. Ringler, and L. You. 2018. Can sub-Saharan Africa feed itself? The role of irrigation development in the region's drylands for food security. *Water Int*. 43: 796–814.

Yao, F. A., A. -A. Millogo, P. S. Epopa, A. North, F. Noulin, K. Dao, M. Drabo, C. Guissou, S. Kekele, M. Namountougou, *et al*. **2022**. Mark-release-recapture experiment in Burkina Faso demonstrates reduced fitness and dispersal of genetically-modified sterile malaria mosquitoes. *Nat. Commun*. 13: 1–11.

Zaim, M., A. Aitio, and N. Nakashima. 2000. Safety of pyrethroid-treated mosquito nets. *Med. Vet. Entomol*. 14: 1–5.