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Comparing flow regime, channel hydraulics, and biological communities to infer flow–ecology relationships in the Mara River of Kenya and Tanzania

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Abstract Equatorial rivers of East Africa exhibit unusually complex seasonal and inter-annual flow regimes, and aquatic and adjacent terrestrial organisms have adapted to cope with this flow variability. This study examined the annual flow regime over the past 40 years for three gauging stations on the Mara River in Kenya and Tanzania, which is of international importance because it is the only perennial river traversing the Mara-Serengeti ecoregion. Select environmental flow components were quantified and converted to ecologically relevant hydraulic variables. Vegetation, macroinvertebrates, and fish were collected and identified at target study sites during low and high flows. The results were compared with available knowledge of the life histories and flow sensitivities of the riverine communities to infer flow–ecology relationships. Management implications are discussed, including the need to preserve a dynamic environmental flow regime to protect ecosystems in the region. The results for the Mara may serve as a useful model for river basins of the wider equatorial East Africa region.

Key words environmental flows; East Africa; Mara River; ecological integrity; flow indicators; Kenya; Tanzania

Comparaison du régime d'écoulement, de l'hydraulique en rivière et des communautés biologiques en vue de déduire les relations débit-écologie de la rivière Mara au Kenya et en Tanzanie

Résumé Les rivières équatoriales d'Afrique de l'Est présentent des régimes d'écoulement saisonniers et interannuels inhabituellement complexes et les organismes aquatiques et terrestres vivant à proximité se sont adaptés pour faire face à cette variabilité des écoulements. Cette étude a examiné le régime d'écoulement annuel au cours des 40 dernières années pour trois stations de jaugeage de la rivière Mara au Kenya et en Tanzanie, qui est d'importance internationale car elle est la seule rivière pérenne traversant l'écorégion Mara-Serengeti. Des composantes du débit environnemental ont été quantifiées et converties en variables hydrauliques écologiquement pertinentes. De la végétation, des macro-invertébrés et des poissons ont été prélevés et identifiés sur les sites cibles de l'étude pendant les périodes de basses et hautes eaux. Les résultats ont été comparés aux connaissances disponibles sur les histoires de vie et les sensibilités aux écoulements des communautés riveraines pour déduire les relations débit–écologie. Nous discutons les implications pour la gestion, y compris la nécessité de préserver un régime dynamique des débits environnementaux pour protéger les écosystèmes de la région. Les résultats pour la rivière Mara peuvent servir de modèle pour les bassins hydrographiques de la région équatoriale plus étendue d'Afrique de l'Est.

Mots clefs débits environnementaux ; Afrique de l'Est ; rivière Mara ; intégrité écologique ; indicateurs de débit ; Kenya ; Tanzanie

INTRODUCTION

The science and practice of environmental flows have advanced significantly over the past decade, motivated by a growing understanding of the fundamental role exerted by flow on the ecology of aquatic systems and alarming evidence that the flow regimes of rivers around the world are being severely altered by engineered infrastructure, land-use change, and water withdrawal (Poff *et al*. 1997, Naiman *et al*. 2002, Postel and Richter 2003, Nilsson *et al*. 2005, Arthington *et al*. 2010). Natural flow regimes of rivers are often quite variable over the course of a year and between years. Native plants and animals living in river corridors are adapted to predictable inter-annual and seasonal baseflows, as well as less-predictable extreme events such as floods and droughts. Adaptations are expressed in the life histories of organisms, their behavioural characteristics, and morphology (Lytle and Poff 2004). Life history adaptations, such as the timing of reproduction, are linked to long-term averages in the seasonal occurrence of high and low baseflows (Bonada *et al*. 2007, Naiman *et al*. 2008). This synchronization of life history events and average flow conditions allows organisms to access key habitats and resources when they are most likely to be available. Behavioural adaptations, such as seeking shelter in the event of large floods or delaying spawning when unexpected low flows signal drought, enable organisms to cope with and recover from extreme events. Morphological adaptations, such as animal body form or the relative allocation of above- and below-ground biomass in riparian plants, also impart advantages to organisms in coping with both predictable and unpredictable characteristics of river flow regimes.

The most ecologically relevant components of flow regimes are the magnitude, frequency, duration, timing, and rates of change of different flow levels. These basic flow components have been subdivided into more than 150 quantifiable indices, which capture the fine details of the regime, but a subset of 33 indices is more commonly applied (Richter *et al*. 1996, Olden and Poff 2003). Common indices include magnitude of mean or median flows for each month of the year, and of maximum and minimum flows extending over select periods from 1 to 90 days, the timing of maximum and minimum flows during the year, the frequency and duration of high and low pulses, and the rates and number of reversals of rising and falling water levels. Analysis of these indices helps identify and quantify environmental flow recommendations (Mathews and Richter 2007).

As river flow regimes are being modified across the globe, special research emphasis is now being devoted to measuring and quantifying ecological responses to flow alterations. Although relatively few quantitative relationships have been described thus far, there is clear evidence that altering flow regimes leads to ecological changes in rivers, and the majority of these changes result in declining ecological status, as expressed by reductions in the abundance and diversity of fish, macroinvertebrates, and native riparian plant species (Mantel *et al*. 2010, Poff and Zimmerman 2010, Greet *et al*. 2011, Mimms and Olden 2012). New research activities are needed to investigate changing ecological characteristics across gradients of flow alteration and during pre- and post-alteration periods (Poff and Zimmerman 2010).

This paper reports the findings of an investigation into the flow regime characteristics and ecological status of the Mara River, which drains the Mara-Serengeti ecoregion of Kenya and Tanzania. The hydraulic regulation of East African rivers lags behind that of rivers in other regions of Africa and the world; however, ambitious plans for dam building and water development are under way. The Mara River is largely free-flowing at this time, but three dams are proposed—two on the river's principal headwater tributaries and one on its main channel just downstream of Serengeti National Park. As part of an initial environmental flow assessment to protect the river's ecological status, we analysed the river's flow regime using discharge data covering the past 40 years, examined hydraulic cross-sections at points along the river corridor, and sampled fish, macroinvertebrates, and riparian vegetation in the same locations during both low and high flows. Our research objectives were to characterize the river's flow regime, identify biological communities inhabiting the river corridor, and consider the potential linkages between the past and present flow regime and ecological condition. Based on these results we discuss potential ramifications of flow alterations in the river.

STUDY AREA

The Mara River basin

The Mara River rises from the Mau Escarpment on the western margin of the Rift Valley, Kenya, at approximately 3000 m a.s.l., and discharges into Lake Victoria at Musoma Bay, Tanzania, at approximately 1130 m a.s.l. Prior to the population growth and agricultural expansion of the past century, the 13 500-km^2 river basin was covered by montane forest in its headwater regions and a mixture of shrublands and grasslands throughout its middle and lower sections. Two perennial tributaries, the Nyangores and Amala rivers, drain the forested headwaters and join to form the Mara mainstem, which is also perennial throughout its length (Fig. 1). In the middle and lower reaches, five ephemeral tributaries drain shrublands and grasslands. These are the Talek, Sand, Tabora, Somonche, and Tigite rivers. Pastoralists of the Kalenjin ethnic group are believed to have inhabited the highlands of this region for more than 1000 years, and the Maasai people, who inhabit the middle and lower portions of the basin, most likely migrated into the region during the 17th and 18th centuries (Ogot 1992). In 1973, forests still covered roughly 1000 km^2 of the headwater regions, and shrublands and grasslands covered a combined 11 000 km^2 (Mati *et al*. 2008). Cultivated land accounted for approximately 1500 km^2, or 11%, of the basin in 1973, composed mainly of small-scale farms below 2000 m a.s.l. and tea plantations at higher elevations (Mati *et al*. 2008). By the year 2000, the area of farms and tea plantations had expanded to nearly 4500 km^2, with corresponding decreases in natural land cover (Mati *et al*. 2008). Basin-scale land cover has not been assessed since 2000, but agricultural expansion has certainly continued.

Although the Mara basin is typical of the situation across many river basins of East Africa, it is also special because of its international profile and biodiversity conservation importance. The Mara River is the only perennial source of inflowing surface water for the Mara-Serengeti ecoregion, and it is the focus of the annual migration of close to two million wildebeest (*Connochaetus taurinus*), plains zebra (*Equus quagga*), and other ungulates and their predators (Gereta *et al*. 2002, 2009). Masai Mara National Reserve and Serengeti National Park are the most renowned and well-visited conservation areas in the region, and they are an important input to the economies of both Kenya and Tanzania. However,

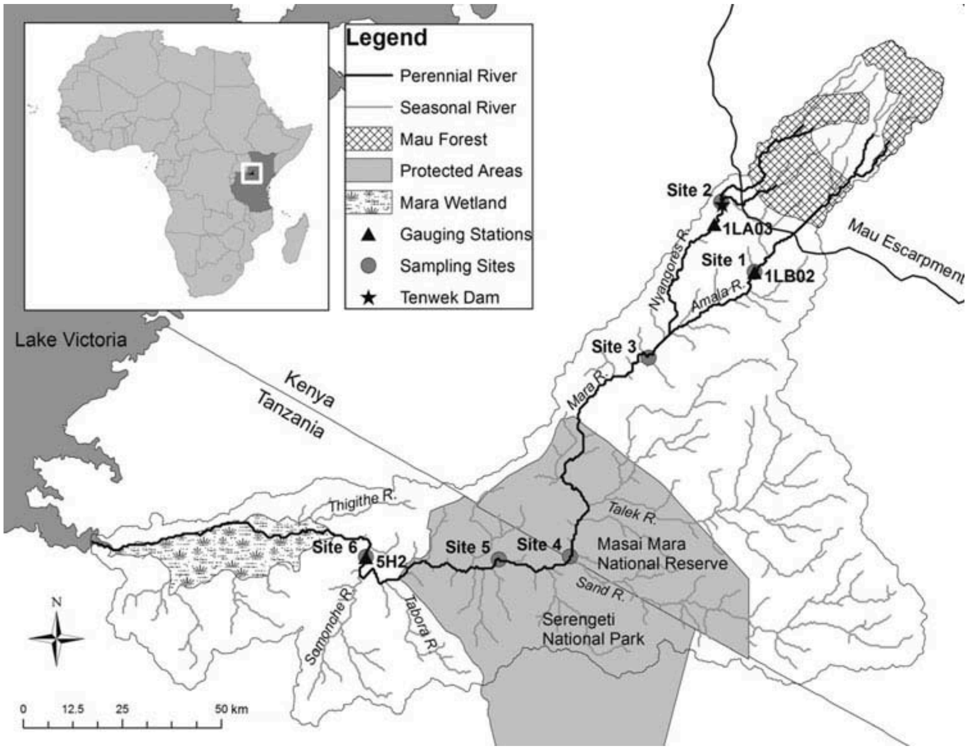


Fig. 1 Map of the Mara River basin showing the location of gauging stations, sampling points, and other features referred to in the text.

pressures on the conservation areas are high, and surveys indicate an alarming decrease in wildlife numbers over the past 30 years (Ogutu *et al*. 2011). Preservation of the conservation areas requires concerted action on several fronts (e.g. reducing poaching and habitat fragmentation), but continued river flows and healthy riparian corridors are understood to be crucial to the survival of the ecoregion.

Despite a total human population approaching one million, extractive water use in the Mara River basin for irrigation (approximately 300 ha of mostly green beans and maize), domestic use, and consumption by domestic and wild animals was estimated to be only 24×10^6 m^3 $year^{-1}$ in 2005, which is less than 2% of the average total annual runoff, which exceeds 1×10^9 m^3 $year^{-1}$ (Hoffman 2007). However, because use of water from the river is spatially variable and increases during dry seasons and droughts, there is a risk that water demand could soon, or may already, exceed available flows during dry periods in portions of the basin. Water storage structures are currently limited in the Mara River basin and mainly off channel; no significant storage dams are located on the river. One small dam was built at the site of a natural waterfall at Tenwek in 1986 and is producing run-of-river mini hydropower (320 KW; Fig. 1). Other small weirs divert water for local irrigation projects, but little quantitative information is available about these and some are unpermitted. Plans for new water development projects are also plentiful. In the 2008–2012 Development Plan under Kenya Vision 2030, districts in the Kenyan portion of the Mara River basin planned to rehabilitate and expand water supplies from six community water projects. In Tanzania, there are plans to rehabilitate and expand 12 water supply projects and 12 pipe schemes, and to construct two new supply schemes (NELSAP 2008). Further details about the projects, as well as their current status, are unknown. Most notably, the World Bank is financing feasibility studies for three dams and multipurpose reservoirs, two of which will include hydropower and are to be located on the Mau Escarpment, and one of which is to be located downstream of Serengeti National Park. These projects are intended to increase water security in the basin and support economic development. They also have the potential to significantly modify the natural flow regime of the river.

Meteorology and climatic boundary conditions

The Mara River basin lies in Africa's most complex region of seasonal rainfall patterns (Herrman and Moor 2011) and exhibits two wet seasons linked to annual oscillations of the inter-tropical convergence zone (ITCZ). The ITCZ passes over the region between October and December (OND) as it moves into the Southern Hemisphere and between March and May (MAM) as it returns to the Northern Hemisphere, and each passage coincides with a wet season. The "short rains," as they are called locally, come in OND and mark the beginning of the hydrological year. The "long rains" come during MAM. Intra- and inter-annual variability in these rains, and the dry periods in between, are high due to other controlling factors, especially variable sea-surface temperatures in the adjacent Indian Ocean, which strongly influence the OND short rains (Webster *et al*. 1999, Black 2005). Spatially, rainfall in the river basin varies more consistently as a function of elevation, with higher rains on the Mau Escarpment; however, significant differences in rainfall also occur between catchments on the escarpment due to topographic effects and the regional influence of Lake Victoria (Camberlin *et al*. 2009). Future climate projections for East Africa call for increasing rainfall during wet seasons and reduced incidence of droughts (Shongwe *et al*. 2011). These projections have a physical basis also linked to influences of the Indian Ocean, and confidence in the projections is higher than in other areas of Africa owing to coherence between multiple models applied (Shongwe *et al*. 2011).

The historical record of rainfall in the Mara River basin dates back to the early 1920s and includes data from more than 40 different stations; however, as is common in much of the region, many of these stations operated for limited periods of time. A recent analysis examined data from 37 stations, each covering at least 20 years and together covering the period from approximately 1960 to the present (Valimba 2012). Long-term annual precipitation averages ranged from nearly 1500 mm on the Mau Escarpment to just over 600 mm per year in the headwaters of the ephemeral Sand tributary, but little detail is available on spatial variability. At the river's mouth long-term annual average precipitation is approximately 800 mm (Valimba 2012). Years of basin-wide drought appear to occur slightly more often in the record than years of excessive rainfall, although conditions can vary greatly among seasons. For example, it is uncommon for both the short rains and long rains to fail in the same year. Long-term trends in rainfall have not been explicitly investigated in the Mara.

METHODS

Study sites

Field activities were conducted at six sites along the perennial course of the Mara River extending from the Mau Escarpment to just above the Mara wetland (Fig. 1). Sites 1 and 2 were located near gauging stations 1LB02 and 1LA03, respectively, of the Kenyan Water Resource Management Authority on the Amala and Nyangores headwater tributaries; Site 3 was located downstream of the Amala and Nyangores confluence but upstream of the boundary of Masai Mara National Reserve; Site 4 was located at the Kenya–Tanzania border roughly 300 m upstream of the confluence with the ephemeral Sand River; Site 5 was located at Kogatende Ranger Station in Serengeti National Park (SNP); and Site 6 was located downstream of the SNP boundary near the Mara Mines gauging station operated by the Mara sub-basin office of the Tanzanian Ministry of Water. Sites were visited by members of the research team prior to final selection to confirm whether each included a mixture of habitats judged to be representative. Sites 1–4 were sampled during medium and high flows in March and July 2007, respectively, and during low flows in February 2009. Sites 5–6 were visited during low flows and high flows in February and May 2012, respectively. Coordinates, sampling dates, and discharge at the time of each sampling event are presented in Table 1.

Hydrology

Historical daily flow discharge data ($m^3\ s^{-1}$) were obtained from the Ministry of Water in Tanzania and the Ministry of Water and Irrigation in Kenya. A total of 11 discharge gauging stations have been operating in the Mara River basin (eight in Kenya and three in Tanzania) since 1953, but long-term records are available for only three (Table 2, Fig. 1). Stations 1LB02 and 1LA03 are on the Amala and Nyangores tributaries (near Sites 1 and 2) and provide fragmented flow records dating back to 1955 and 1964, respectively. These stations drain similar catchment areas, including the forested headwaters of the basin. Station 5H2 is on the mainstem Mara River, 10 km upstream of the North Mara Mine (near Site 6), an open-pit gold mine located roughly 20 km south of the Kenya–Tanzania border. The 10 580-km^2 catchment area above this station represents approximately 78% of the entire

Table 1 Information about sampling stations, including location, dates sampled, and flow conditions.

Site	Site coordinates		Macroinvertebrate sampling				Fish sampling			
	Latitude	Longitude	Low flow		High flow		Low flow		High flow	
			Date	Q	Date	Q	Date	Q	Date	Q
Site 1	0°53′53.39″ South	35°26′15.67″ East	21 February 2009	0.2	5 September 2008	4.2	21 February 2009	0.2	16–17 July 2007	7.9
Site 2	0°59′21.84″ South	35°15′37.83″ East	22 February 2009	0.6	6 September 2008	13.1	22 February 2009	0.6	–	–
Site 3	1°5′33.11″ South	35°11′48.35″ East	23 February 2009	1.0	9 September 2008	18.8	23 February 2009	1.0	18–19 July 2007	16.9
Site 4	1°33′3.56″ South	35°1′1.25″ East	24 February 2009	1.1	11 September 2008	19.7	24 February 2009	1.1	20–21 July 2007	15.9
Site 5	1°33′13.83″ South	34°51′24.63″ East	9–10 February 2012	2.6	10–12 May 2012	118	9–10 February 2012	2.6	10–12 May 2012	118
Site 6	1°32′47.45″ South	34°33′14.73″ East	7–8 February 2012	2.5	8–9 May 2012	255	7–8 February 2012	2.5	8–9 May 2012	255

Table 2 Information about gauging station used in this study, including length and completeness of data sets used.

Country	River	Station ID	Catchment area (km^2)	Coordinates		Length of record	% Complete
Kenya	Amala at Kapkimolwa Bridge	1LB02	693	0°53′56.23″ S	35°26′14.62″ E	Oct. 1955–Dec. 2008	68
	Ny angores at Bomet Bridge	1LA03	697	0°47′23.50″ S	35°20′47.45″ E	Oct. 1963–Dec. 2006	86
Tanzania	Mara at Mara Mine	5H2	10 580	1°32′52.80″ S	34°33′14.40″ E	Aug. 1969–Jun. 2012	53

basin. Discharge data from this site begin in 1969 and are 83% complete until 1990; however, the record between 1990 and 2004 is largely missing.

Data obtained from water authorities were visually screened to check for irregularities and errors. A number of observations were noted, including extended periods of unchanging flow conditions, some repetition in seasonal data, apparent transcription errors such as misplaced decimal points, and use of incorrect units. It was also common for data to be missing in monthly blocks, probably because daily stage observations were recorded manually on monthly datasheets that might have been lost or never entered into the digital database. The resulting data sets include periods of continuous records that, when summed, exceed 15 years for the Mara mainstem, 12 years for the Amala River, and 32 years for the Nyangores River. The extent of flow records and periods of overlap and gaps are presented in Fig. 2. We have assumed that these records are sufficient to characterize the components of the flow regime used in this study. Because the Mara River has no major dams regulating its flow, and land-use change and extractive water use has progressed gradually, we chose to analyse the flow record as a single period. This approach is supported by a recent detailed assessment of 44 years of Nyangores discharge data, which identified only subtle changes to the flow regime (Juston *et al*. 2013).

Flow discharge data were analysed in a spreadsheet and using the Indicators of Hydrologic Alteration (IHA) software, which is now widely applied in the analysis of river flow regimes (Version 7.1; TNC 2009). Because many gaps in the data corresponded to missing months, we analysed monthly data for mean and median using only complete months; data gaps within months were filled by linear interpretation when fewer than 7 days were missing. Months with larger gaps were excluded from the analysis. This approach resulted in 12–34 years of complete monthly data for station 1LB02, 35–38 years for 1LA03, and 18–28 years for 5H2. IHA was applied to calculate select inter-annual flow indices. Missing data were filled by the program using a linear interpolation approach, and years of missing data were excluded from the statistical analyses. This resulted in 4 years being excluded for station 1LB02, 1 year for 1LA03, and 10 years for 5H2.

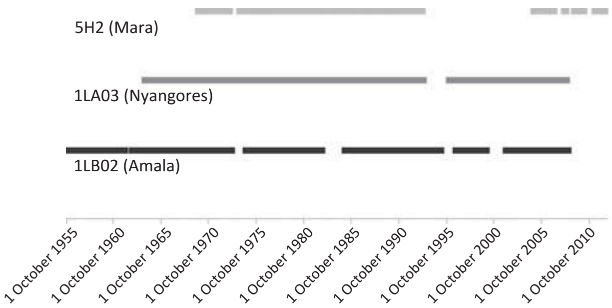


Fig. 2 Schematic representation of the discharge records used, illustrating the extent of the records, their alignment, and data gaps. Station details are presented in Table 2.

Given the gaps in the available Mara records, only a subset of possible statistics was used (as described below) and caution was taken in evaluating the resulting statistics and interpreting their ecological significance. Median values were calculated for indices, including peak values for extremely low flows, small floods, and large floods. Moving averages for maximum and minimum flows extending over 1, 7, 30, and 90 days were also calculated as means. The threshold for high flows was set at the 75th percentile of daily flows for the period. Small floods were defined as high flows with a peak flow greater than a 2-year return internal event, whereas large floods were defined as high flows with a peak flow greater than a 10-year return internal event. Annual flow duration curves were generated from daily data. Please refer to the IHA Manual (TNC 2009) for detailed information on quantification procedures for all flow indices.

Hydraulic cross-sections and modelling

Hydraulic cross-sections were established at intervals of 65–200 m along reaches at each site in order to capture variability in hydraulic regimes. Each site included 4–6 transects through sections of riffles, pools, and runs. A geometric survey was undertaken at each site to determine the distance between transects, water surface elevation (relative to a fixed benchmark), water surface slope (based on the thalweg), bed elevation profiles, stage of zero flow elevation, and water depth. Bed material size was determined for both pools and riffles at each site. Velocity was measured at 0.6 of the depth at shallow depths, or as the average of the velocities at 0.2 and 0.8 of the depth at greater depths at each interval using a Flow-Tracker Handheld Acoustic Doppler Velocimeter (ADV) and/or current meter (Son-Tek, San Diego, CA, USA). Discharge was determined using the velocity–area method (ISO 1997).

Hydraulic models were developed to relate discharge to other measured flow parameters for the purpose of interpolating or extrapolating hydraulic parameters to discharge levels other than those measured. The Physical Habitat Simulation Model (PHABSIM) was used to calculate hydraulic parameters for sites 1–4 (Milhous and Waddle 2012) and the HEC-RAS model was used for sites 5–6 (USACE 2010). Habitat suitability curves were not developed because of a lack of sufficient calibration data in the Mara. The hydraulic models were calibrated using data collected during low-flow sampling and model performance was validated with data collected during medium- or high-flow sampling. Once calibration was satisfactory, simulated parameters were used to produce rating relationships between streamflow and wetted perimeter, depth, width, velocity, and cross-sectional area.

Biology

Vegetation surveys were conducted at all sites except at Site 2 in sample plots placed along transects running perpendicular to the river bed from the active channel to the edge of the riverine forest. In and within 10 m of the active channel, plots encompassed full areas of distinct vegetation types. Further along the transects, plots were located at 10-m intervals. In each sample plot, information was recorded on species composition and size classes, and vegetation zones were classified according to dominant plant species. The distribution of species was analysed in relation to channel cross-sectional profile.

Macroinvertebrates were sampled at sites 1–4 by kick-netting with a 500-µm kick net (Wildco, Yulee, FL, USA) in pools, riffles, runs, and emergent vegetation for a total of 16 sub-samples per site. Sites 5 and 6 were surveyed for macroinvertebrates using a 500-µm Surber sampler (limited to shallow reaches during low flows) (Wildco, Yulee, FL, USA) and a standard scoop net. Samples were collected in riffles, pools, and marginal vegetation for three sub-samples per site. During all sampling efforts, macroinvertebrates were collected in the field and preserved using 70% ethanol until they could be sorted and identified in the laboratory to the lowest possible taxonomic level (Day *et al.* 2003). Macroinvertebrates at each site were analysed according to the number of taxa and the number of individuals. Taxa and sites were also characterized using the South African Sensitivity Score (SASS) and average score per taxon (ASPT), a scale from 1 to 15. Higher ASPT scores indicate an increasing abundance of species susceptible to pollution or other perturbations (Dickens and Graham 2002), which may vary in response to changing flow regime. Although this scoring system was developed for South Africa, it is based on macroinvertebrate classifications at the family level, which facilitates its application to neighbouring regions of Africa. It has recently been applied successfully in another study within the Mara River basin (Minaya *et al.* 2013). Each site was also analysed for macroinvertebrate species diversity using the Shannon-Weiner diversity index (H').

Fish were surveyed at all sites using gillnets placed in riffles, runs, and pools and a backpack electroshocker in shallower sections for standardized periods of time. Fish were identified to species in the field using regional field guides (Bernacsek 1980, Eccles 1992, Skelton 1993). Length and weight were measured, and gonad state was assessed using a five-point scale (Bagenal 1978). Catch per unit effort (CPUE, number of fish captured/hour) and relative abundance and distribution of each taxa were determined, and the Shannon-Wiener diversity index (H') was calculated for each site. Fish species were also characterized according to their environmental guild, a classification system that groups species that respond similarly to changing hydrology and geomorphology (Welcomme *et al.* 2006). Neither fish nor macroinvertebrate samplings were conducted at Site 5 during the wet season because of the presence of an aggressive hippopotamus.

RESULTS

The river flow regime

Flow discharge data from the three long-term gauging stations in the Mara River basin describe the perennial flow regime of the river, which is confined to the Amala and Nyangores tributaries in the headwaters of the river basin and the mainstem Mara River extending to Lake Victoria. The effect of seasonal flows in ephemeral tributaries is also evident in the mainstem flow regime described by the record from the Mara Mines station. Mean monthly flows in the Amala and Nyangores rivers follow a bimodal pattern, with the highest mean flows in May and August/September (Table 3). Mean monthly flows remain relatively high during June–August, whereas the lowest values occur in the period from October to April. There is no peak in mean monthly discharge of the headwater catchments during the short rains period of October–December and, despite having similar catchment areas, mean monthly discharge of the Nyangores

Table 3 Mean monthly discharge ($m^3 s^{-1}$) and coefficient of variation (CV) at gauging stations. (CV is calculated as standard deviation of all the daily flow values divided by the mean flow).

	Amala		Nyangores		Mara	
	Mean	CV	Mean	CV	Mean	CV
Annual	4.01	1.47	8.44	0.82	47.2	1.74
October	4.38	1.16	9.02	0.66	19.8	0.94
November	2.37	1.05	6.79	0.77	30.4	1.87
December	3.17	2.08	6.53	1.03	60.6	2.08
January	4.10	1.99	4.44	1.36	48.3	2.23
February	2.00	2.12	3.67	1.32	37.2	2.05
March	1.95	1.83	3.33	1.27	55.2	1.75
April	3.77	1.35	9.38	0.91	89.3	1.25
May	7.81	1.29	14.0	0.56	82.9	1.17
June	4.58	1.18	10.9	0.54	40.9	1.08
July	3.90	0.76	10.8	0.52	25.3	0.79
August	6.34	0.73	12.1	0.47	27.8	0.82
September	6.25	0.95	13.1	0.46	37.1	0.91

River is approximately double that of the Amala River. Mean monthly discharge on the Mara River at Mara Mines is bimodal, with peaks in December and April–May (Table 3), corresponding to the periods of both the short and long rains.

More detailed characteristics of the flow regime are revealed in the indices quantified for each station (Table 4). Median monthly low flows follow the same general pattern as mean monthly flow. Median monthly low flows account for, on average, 72% of the mean monthly flows in the Nyangores River and for 52% in the Amala River, with higher proportions in drier months and lower proportions in wet months. Median monthly low flows in the Nyangores River were generally more than 100% higher than those in the Amala River (Table 4). At Mara Mines on the mainstem Mara River, median monthly low flows accounted for an average of 56% of mean monthly flows. The pattern of reduced flows in the Amala River relative to the adjacent Nyangores River continued for median extreme low peak (0.26 *vs* 0.81 $m^3 s^{-1}$); however, values for median small flood peak were roughly equal (26.4 *vs* 27.4 $m^3 s^{-1}$), and the median large flood peak for the Amala River was considerably higher than that for the Nyangores River (81.2 *vs* 34.9 $m^3 s^{-1}$). One to 90-day minima and maxima in the Amala River were consistently below those in the Nyangores (Table 4). Extremes on the mainstem Mara River ranged from a low of 1.51 $m^3 s^{-1}$ to a high of 921 $m^3 s^{-1}$.

Table 4 Median values ($m^3 s^{-1}$) of flow indices with coefficients of dispersion (CD), and mean values for select periods of flow with coefficients of variation (CV). (CD is calculated as [75th percentile – 25th percentile]/50th percentile; CV is calculated as standard deviation of all the daily flow values divided by the mean flow).

	Amala		Nyangores		Mara	
	Median	CD	Median	CD	Median	CD
Low flows						
October	2.64	1.68	7.29	1.13	14.0	1.60
November	1.52	1.26	5.20	0.91	14.8	2.00
December	1.08	1.30	3.84	1.45	18.5	3.29
January	0.63	3.79	2.14	1.56	14.1	2.53
February	0.52	2.34	1.32	1.67	8.88	4.54
March	0.62	2.93	1.67	2.18	13.7	4.10
April	1.64	1.92	5.70	2.47	50.8	2.27
May	3.67	2.02	13.45	0.91	56.6	1.60
June	2.57	1.38	9.85	1.09	28.0	1.28
July	2.89	1.26	8.76	1.13	21.7	0.88
August	5.73	0.85	11.2	0.82	22.7	0.93
September	4.80	1.02	11.7	0.84	28.9	0.84
Extreme low peak	0.26	0.79	0.81	0.63	1.51	1.03
Small flood peak	26.4	0.39	27.4	0.09	180	1.15
Large flood peak	81.2	0.36	34.9	0.11	921	0.34
	Mean	CV	Mean	CV	Mean	CV
1-day min	0.14	2.17	0.68	1.54	4.23	3.59
7-day min	0.17	2.06	0.94	1.27	5.77	3.64
30-day min	0.41	1.60	1.15	1.23	8.12	2.58
90-day min	0.74	2.36	2.02	1.33	14.5	1.7
1-day max	23.2	0.94	28.0	0.21	260	1.73
7-day max	18.3	0.95	26.0	0.25	173	1.77
30-day max	12.5	1.20	21.4	0.32	120	1.26
90-day max	6.10	1.63	15.2	0.49	80.2	1.18

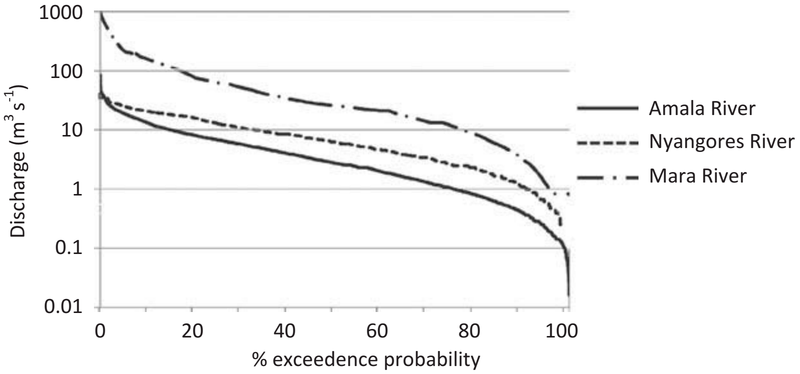


Fig. 3 Daily flow–duration curves for the gauging stations considered in the study. The shape of the headwater curves for Nyangores and Amala reflect the persistent higher flows in the Nyangores River but a wider variability of flow in the Amala River. The mainstem station at Mara Mine also reflects the high variability of flows at that site, ranging from less than 1 m^3 s^{-1} to just over 1000 m^3 s^{-1}.

The flow regimes at all three sites are highly variable, as reflected in the coefficients of variation and coefficients of dispersion listed in Tables 3 and 4. Between the Amala and Nyangores rivers, however, the Amala is considerably more variable, with greater extremes at high- and low-flow levels. This is reflected in the daily flow duration curves of each river as well (Fig. 3). To illustrate the full variability of discharge over the entire flow record, we plotted four percentile ranges for each day of the year (Fig. 4). Applying thresholds similar to those in the IHA analysis, the range of Q5–Q10 corresponds to flood levels, Q10–Q75 represents high flows, Q75–Q95 represents low flows, and Q95 to the minimum flows represent the lowest flows at the site. Higher variability is apparent in the distribution of flows in the Amala and mainstem Mara rivers, whereas fewer extremes are evident in the Nyangores River. High flow and flood events during the short rains of October–December are reflected in the variability of both the Amala and Nyangores rivers, but do not produce strong responses in low flow (i.e. baseflows). The long rains of April and May, however, lead to clear increases in baseflows that persist during the following months (Fig. 4). By comparison, the mainstem Mara River experiences a predominance of high flows and extreme events in the period extending from December to May, most likely driven by seasonal flow in ephemeral, and ungauged, tributaries.

Measures of flow predictability and constancy derived from the IHA analysis (*sensu* Colwell 1974) indicate low predictability and constancy of Mara flows compared to broad classes of rivers from other parts of the world (Olden and Poff 2003, Kennard *et al*. 2010). Clear differences among stations were also noted. In the headwaters, flows of the Nyangores River were more predictable (0.42 *vs* 0.27, respectively) and constant (0.29 *vs* 0.17, respectively) than flows in the Amala River. Predictability (0.23) and constancy (0.17) of flow at Mara Mines are comparable with those of the Amala River, but also included the influences of ephemeral tributaries.

River hydraulics at select flow levels

Macro-channel geometry was fairly consistent between sites 1 and 4, which were incised on average by 8 m, with an average channel width of 50 m. Sites 5 and 6 also were incised by approximately 8 m, but channel width was much greater than upstream sites, ranging from 110 m at Site 5 to 90 m at Site 6 (Fig. 5). All sites were well constrained by terraces and none was connected to a distinct floodplain. Sites 2–6 had intermediate terraces, which would be rarely (less than once a year) inundated, and all cross-sections included flood benches that are annually inundated. All sites included mixtures of sand, gravel, and cobble-bed materials distributed according to hydraulic features such as riffles and pools; however, boulders were also prevalent at sites 2–6.

Hydraulic modelling produced relationships between flow and ecologically relevant variables of velocity, wetted perimeter, and depth (Fig. 6). Reach–scale relationships generally had characteristic shapes, steeper at low discharges with one or more inflection points. Model results for environmental flow components illustrate the range of conditions and habitat characteristics that aquatic species experience throughout the year. Median monthly low-flow conditions at Mara Mines station on the mainstem Mara River include consistent velocities ranging from 0.47 to 0.66 m s^{-1},

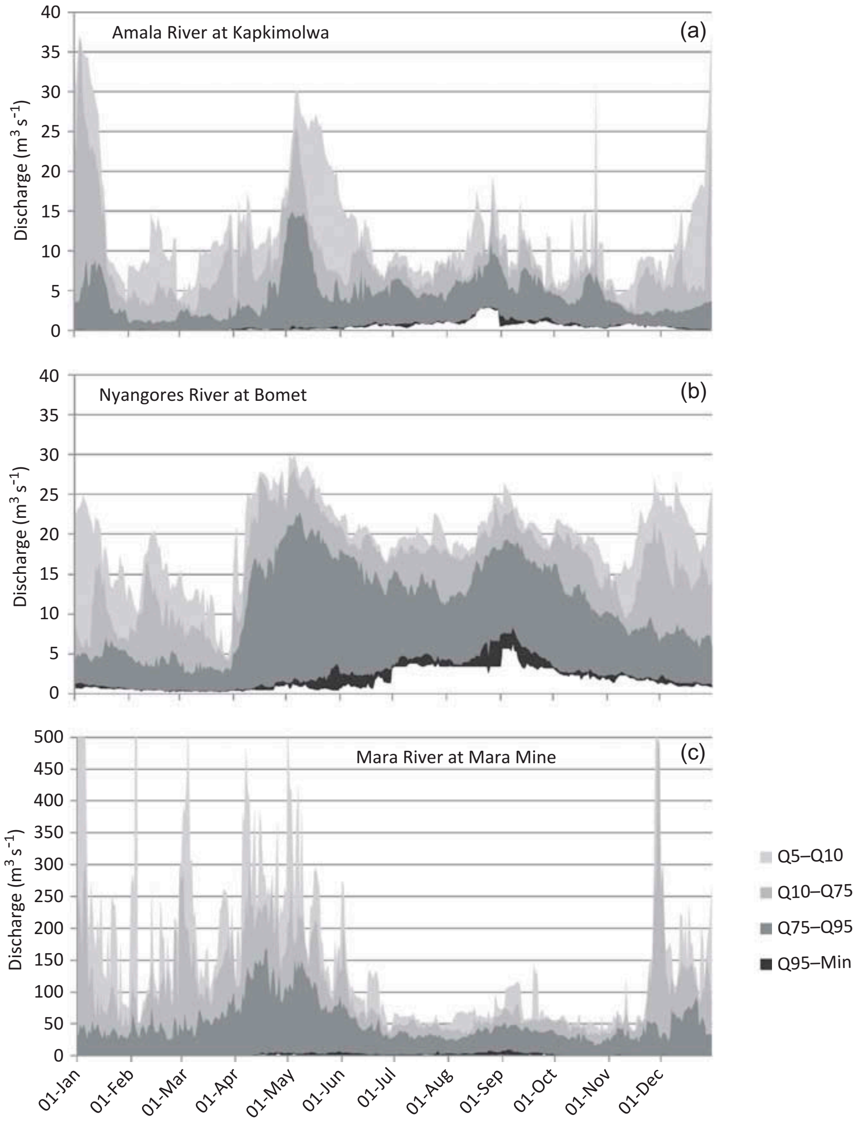


Fig. 4 Percentile flows for individual days of the calendar year over the duration of the discharge record for the three gauging stations. Thresholds were selected to approximate different environmental flow components from the IHA analysis; Q5–Q10 corresponds to flood levels, Q10–Q75 represents high flows, Q75–Q95 represents low flows, and Q95 to the minimum flows represent the lowest flows at the site. Note that the vertical axis is truncated at 500 m^3 s^{-1} in panel (c) to allow for more detail to be visible at lower flow levels.

maximum channel depths of 1.12–1.57 m, and wetted perimeters of 48.9–51.3 m. During median extreme low-flow conditions, velocity drops to 0.24 m s^{-1}, maximum depth is 0.58 m, and wetted perimeter is reduced to 28.9 m. Conversely, during median large-flood conditions, velocity increased to 1.82 m s^{-1}, maximum channel depth reaches nearly 8 m, and the wetted perimeter expands to 131 m. Annually, depths greater than 4 m persist, on average, for up to 3 days, and depths greater than 2 m may persist for 90 days or more. Depths also drop to less than 1 m for up to 30 days. At the stations on the Amala and Nyangores rivers, median low flows offer comparable velocities and depths, but wetted perimeter on the Nyangores is 50–200% larger. This relationship is consistent across other flow components, except for flooding conditions, when the wetted perimeter is similar between the sites and flow depths and velocities are higher in the Amala. These relationships are used to explore changes in habitats in the Discussion section of this paper.

Biological communities

Riparian vegetation Four distinct vegetation zones were recorded from the field surveys: Zone A —the aquatic zone, in which almost no macrophytes

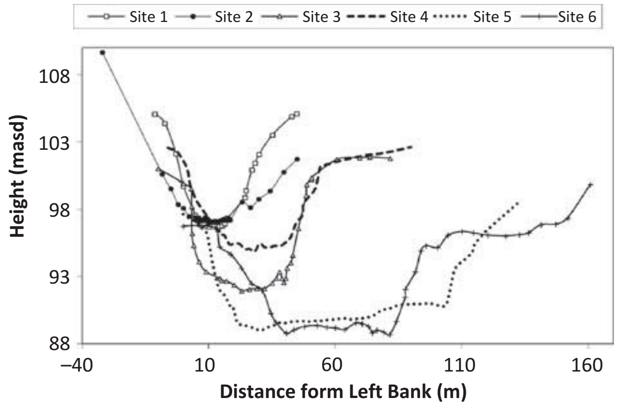


Fig. 5 Comparison of surveyed cross-sections from each sampling site illustrating a similar level of incision across all locations and increasing channel width along the river course. Levels expressed in metres above site datum (m a.s.d.).

were recorded; Zone B—the wet bank zone, dominated by grasses and sedges; Zone C—the lower dynamic zone at the edge of the macro-channel bank, dominated by shrubs and small trees; and Zone D—generally >30 m away from the river's edge. In upstream reaches (Site 1), the riparian zone was largely intact. In middle reaches, the riparian vegetation was less dense (Table 5). Site 3 had a deeply incised channel, possibly limiting riparian development on upper terraces. Site 4 was not as deeply incised, but was dominated by largely terrestrial grasses and shrubs. There were some woody plants present at each site, including *Prunus africana* (red stinkwood), *Diospyros abyssinica* (giant diospyros/ebony), *Warburgia ugandensis* (Sprague), and *Ficus* sp. At Site 5, in-channel sedges and grasses were present, but there were no riparian shrubs or trees. In lower reaches (Site 6), the riparian vegetation was more dense, despite some influence of settlements and over-grazing.

Aquatic macroinvertebrates A total of 24 786 macroinvertebrates belonging to 11 orders and 34 families were documented in the samples collected during low and high flows across all sites in the Mara River. Overall, Ephemeroptera (mayflies), Trichoptera (caddisflies), and Diptera (midges and flies) were the most dominant orders. Ephemeroptera and Trichoptera are generally considered to be orders that are sensitive to water quality. Across all sites, number of taxa, sensitivity, and diversity of macroinvertebrates generally were greater during high-flow compared to low-flow conditions (Table 6). In general, diversity increased from upstream to downstream throughout the basin. Diversity index values for sites 1–4 are considered low and indicative of disturbed conditions, whereas values for sites 5–6 reflect relatively high diversity (Table 6). Care must be taken in interpreting these results, because changes in diversity could be attributable to the difference across sites in sampling years and/or discharge levels during sampling, rather than site location. More detailed sampling over both space and time is necessary to confirm basin-wide trends.

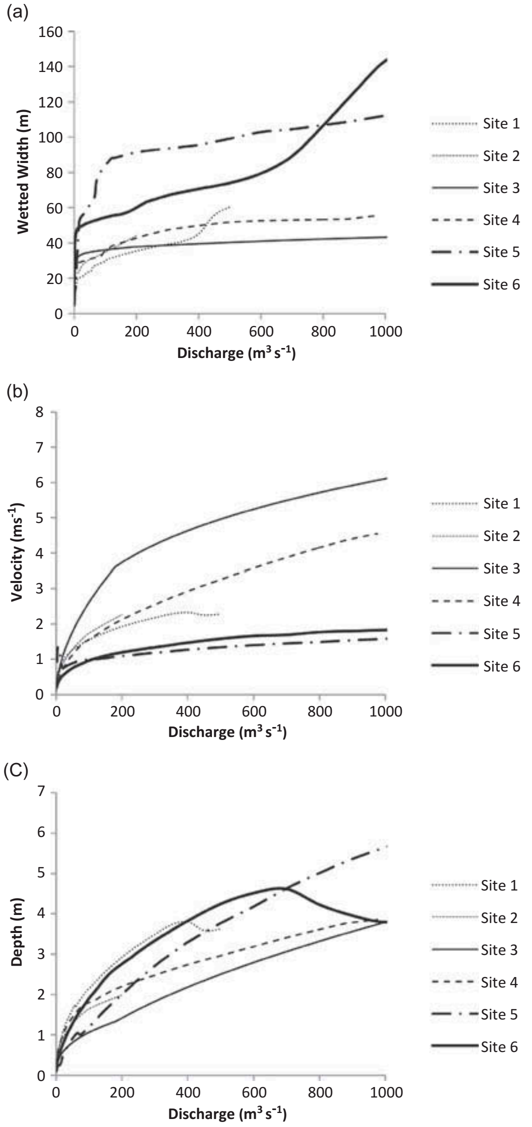


Fig. 6 Hydraulic simulations for EFA sites in the Mara River showing relationships between discharge and (a) wetted width, (b) velocity and (c) hydraulic depth. Simulations for Site 3 go to 2000 $m^3 s^{-1}$ and those for sites 4 and 5 to 1100 $m^3 s^{-1}$; however, discharge was abbreviated at 1000 $m^3 s^{-1}$ here to allow for better visualization.

Table 5 Riparian vegetation at each study site and inferred relationships to flow levels. No vegetation surveys were conducted at Site 2.

Study site	Vegetation zone	Vegetation type	Dominant species	Inferred relation to flow level
Site 1	A and B	Grasses and sedges	*Pennisetum clandestinum, Cyperus macrostachyos*	Sensitive to low flows
	C and D	Shrubs and small trees interspersed with herbs	*Syzygium cordatum, Vangueria madagascariensis, Rhus natalensis, Euclea divinorum, Erlangia cordifolia, Ocimum suave, Ageratum conyzoides*	Require shallow groundwater
Site 3	A and B	Grasses and sedges	*Cyperus macrostachyos* *Hyperrhenia cyambaria*	Sensitive to low flows
	C and D	Large trees and dry area shrubs	*Diospyros abyssinica, Prunus africana, Warburgia ugandensis, Lippia javanica, Croton dichogamus*	Common to moist, riverine forest
Site 4	A and B	Grasses	*Panicum maximum* *Cynodon dactylon*	Sensitive to low flows
	C and D	Few large trees, mostly dry area shrubs	*Acacia hockii, Ficus* sp., *Rhus natalensis, Croton dichogamus, Grewia bicolor, Carissa edulis*	Common to dry grassland with seasonal patterns of flooding and drainage
Site 5	A and B	Grasses and sedges	*Pennisetum purpureum, Cyperus articulates, Cyperus denudatus, Leersia hexandra, palm trees*	Sensitive to baseflow levels and seasonal flows
	C and D	No riparian trees present, only terrestrial shrubs	*Croton microtachys*	Low water demand, may occur despite insufficient baseflows
Site 6	A and B	Trees, shrubs, and sedges	*Cyperus articulates, Sesbania greenwayi, Ficus exasperata, Acacia xanthophloea*	Sensitive to low flows
	C and D	Large trees	*Ficus sur, Ficus lutea, Ficus exasperata, Trichilia emetic, Acacia xanthophloea, Acacia polyacantha, Sesbania greenwayi*	Sensitive to baseflow levels

Table 6 Aquatic macroinvertebrate diversity, sensitivity, and indication of water quality and habitat diversity at the six study sites in the Mara River basin. Data for low and high flows for sites 1–4 are from February 2009 and September 2008, respectively.

EFA site	Flow level	No. of Taxa	SASS 5 score	ASPT	Diversity index	Classification of water quality and habitat diversity
Site 1	Low	19	109	5.74	0.8	Fair
	High	15	88	5.87	0.96	Intermediate
Site 2	Low	17	106	6.24	0.84	Good
	High	18	110	6.11	0.97	Good
Site 3	Low	13	57	4.38	0.76	Poor
	High	15	81	5.14	0.87	Intermediate
Site 4	Low	14	72	5.14	0.86	Intermediate
	High	20	122	6.1	1.52	Good
Site 5	Low	10	73	7.3	1.63	Fair
	High*	–	–	–	–	–
Site 6	Low	14	107	7.64	1.74	Good
	High	19	126	6.63	2.19	Good

Note Interpretation of SASS 5 scores from Chutter (1998); interpreted as Good, Fair, Intermediate, or Poor.
*No macroinvertebrate data available for high flows at Site 5 due to an aggressive hippopotamus.

Fish Surveys at Sites 1–4 documented 339 individuals of fish belonging to six families and 15 species. Surveys at sites 4–5 captured 345 individuals from nine families and 18 species. The total number of species documented in the Mara by our sampling is 25, although including data from previous fish surveys conducted in the Tanzanian reaches of the Mara River increases the total number to 34 (Wandera *et al.* 2006, Chitamwebwa 2007, Tamatamah *et al.* 2010). At sites 1, 3, and 4, during both 2007 and 2009, the dominant species was *Barbus altianalis* (41%), followed by *Clarias liocephalus* (25%). At Site 2, only one species, *Clarias liocephalus*, was documented, likely due to the presence of the Tenwek Dam and natural waterfall just downstream of the site that prevents upstream migration of other fish species. At sites 5 and 6, the dominant species was *Petrocephalus catostoma* (24%), followed by *Barbus paludinosus* (23%). *Labeo victorianus* was one of the few species

Table 7 Catch per unit effort, as an indicator of abundance, and Shannon-Wiener diversity index values for fish surveys at the study sites. Data for sites 1–4 are from the 2009 field assessment.

EFA site	No. of species	Catch per unit effort		Shannon-Wiener diversity index
		Gill nets	Electroshocker	
Site 1	7	5.3	118	1.38
Site 2	1	0.3	66	0
Site 3	9	3.3	154	1.84
Site 4	9	2.7	52	1.87
Site 5	6	5.2	21	1.47
Site 6	16	14.5	69	2.1

common across all sites (except Site 2), accounting for 15–18% of the total catch.

Diversity generally increased from upstream to downstream, with sites 1 and 2 having the lowest diversity, and sites 3, 4, and 6 having the highest (in that order). Site 5 had a lower diversity than expected. Catch per unit effort (CPUE, no. of individuals per hour), an indicator of relative abundance, showed no strong basin-scale patterns across the sites (Table 7). Site 2 had the lowest CPUE (0.3) and Site 6 had by far the highest (14.5), but the other sites were fairly close to one another (2.7–5.3).

Fish in the Mara comprise two major communities, each consisting of different ecological guilds (Welcomme *et al*. 2006, Table 8). There was only one species documented in the riffle guild (at Site 3), which is considered most sensitive to flow levels; however, the majority of species in the upper and middle reaches were in either the pool or lotic guilds, which are considered moderately and highly sensitive, respectively, to flow levels. In contrast, at sites 5 and 6 in the lower reaches of the river, the majority of the species were in the eurytopic guild, which is considered to have a low sensitivity to flow levels. Site 6 also had the only representative from the lentic guild, or floodplain migrants.

Upon capture fish were examined for their reproductive status. In 2007, approximately 50% of the adult individuals of the most numerous fish species in the Mara River—*Barbus*, *Labeo*, and *Mormyrus*—had ripe gonads, indicating recent reproductive activity. In all species there were more adult individuals with ripe gonads in March 2007 than in July 2007, suggesting higher flow levels were linked to reproductive periods in these species. In 2009, 14 of the 15 species and over 23% of all adults had ripe gonads. There was also a relatively large number of immature and juvenile fish present, besides males and females with recently spent gonads, suggesting spawning activity had been triggered by high flows that occurred in December 2008 and January 2009. In 2009, about 57% of adult individuals captured at sites 4 and 5 had ripe gonads, and more adults had ripe gonads in February 2012 than in May 2012. These data combined with the capture of large numbers of spawning/spent females in February 2012 suggest that spawning might have been associated with high flows in December 2011/January 2012.

DISCUSSION

The results of this study identify ecologically relevant components of the Mara River flow regime, translate flow levels into dynamic aquatic habitat characteristics (velocity, depth, wetted perimeter) along select channel cross-sections, and document aquatic and riparian species living among these habitats. Specific environmental flow recommendations have

Table 8 Number of fish species of each ecological guild documented in six study sites in the Mara River basin.

Fish community type	Ecological guild	Number of species by site						Representative genera in the Mara River	Sensitivity to flow
		Site 1	Site 2	Site 3	Site 4	Site 5	Site 6		
Rhithronic communities	Riffle guild	–	–	1	–	–	–	*Chiloglanis*	Critical
	Pool guild	3	–	3	3	1	3	*Small Barbus, Brycinus*	Moderate
Potamonic communities	Lotic guild	3	1	2	2	1	3	*Labeo, Large Barbus, Schilbe, Clarias*	High
	Lentic guild	–	–	–			1	*Afromastacembelus*	Low
	Eurytopic guild	1	–	3	4	4	9	*Clarias, Tilapia, Oreochromis, Mormyrus, Petrocephalus, Synodontis*	Low

been formulated for each study site in a parallel process that involved water authorities and other stakeholders (GLOWS 2013). Our aim in this paper is to use our study as a starting point to begin to explore relationships between ecological processes in the river and the flow regime.

Spatial and temporal characteristics of the Mara flow regime

Our focus was on the perennial reaches of the river basin, recognizing that ephemeral tributaries also influence the flow regime of the middle and lower reaches of the mainstem Mara River. Insight into the relative flow contributions of different parts of the basin can be found in a simple comparison of the combined seasonal discharge of the perennial headwater tributaries (Amala and Nyangores) with that of the mainstem Mara River at Mara Mines. Although the combined catchment area above the headwater gauging stations is just 13% of the total catchment area of the Mara Mine station (Table 2), their combined median monthly low flows account for between 14% and 75% of the mainstem median monthly low flows downstream of all major ephemeral tributaries (Fig. 7). This influence might be somewhat less given recent data suggesting that the mainstem below the confluence of the Amala and Nyangores is a losing reach (Dutton 2012), but it is likely that headwater flows from the Mau Escarpment are disproportionately important throughout the year. This is almost certainly the case in the period between the end of the long rains in June and the beginning of the short rains in October. The results suggest that ephemeral tributaries take on increased importance during and following the short rains period of October–January.

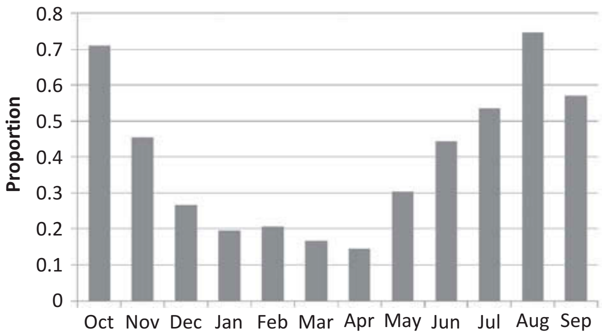
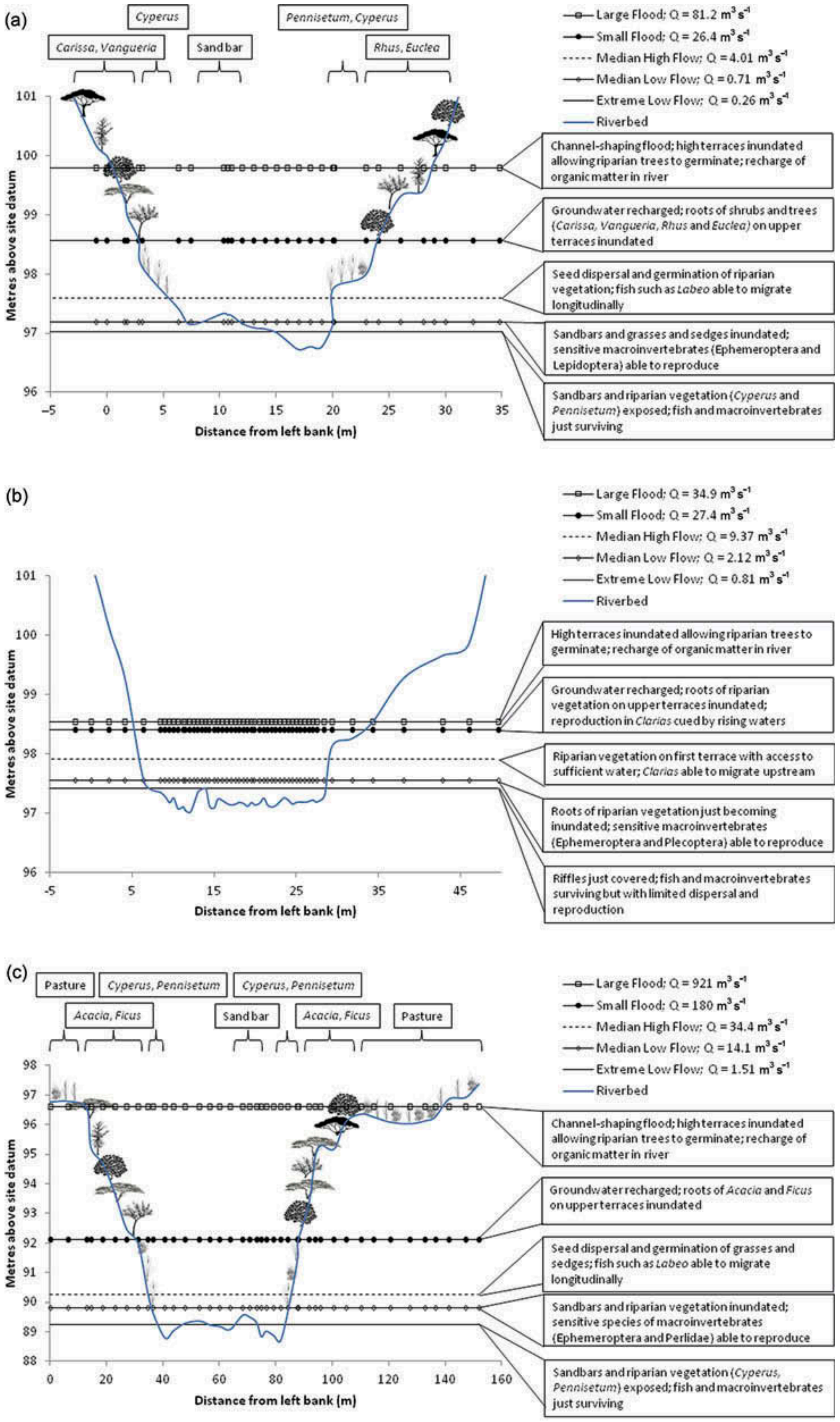


Fig. 7 Comparison of the combined monthly low flows of the Nyangores and Amala rivers with those of the mainstem Mara River at the Mara Mine station, represented as a proportion of mainstem low flows. The graph illustrates the disproportionate contribution of headwater tributaries to the mainstem low flows, especially in the period June–October.

Seasonal patterns in runoff for the Mara basin are consistent with other rivers in the region, although comparable data are not available for detailed indices describing variability in the flow regime. Runoff from other Western Kenya rivers (Nzoia and Yala) draining the Mau Escarpment include peaks in mean monthly discharge in May and August, similar to the headwater stations in the Mara (Githui *et al*. 2009, Kiluva *et al*. 2011). Peaks in mean monthly discharge associated with short (OND) and long (MAM) rains characterize the Mkomazi River in northeastern Tanzania, as at the Mara Mines station, but seasonal discharge transitions to a more unimodal pattern with distance to the south in the Pangani and Great Ruaha Rivers (PBWO/IUCN 2006, Kashaigili *et al*. 2007). The flow percentiles in Fig. 4 indicate that high flows and floods may occur at nearly any time between November and June at the Mara Mines site, but are far less frequent between July and October when baseflows depend most on runoff from the Mau Escarpment. High flows and floods do occur over this period in the Amala River, but are attenuated before reaching the Mara Mines site. Differences in mean annual flow between the Nyangores and Amala rivers are likely attributed to gradients in rainfall and possible rainshadow effects, as annual precipitation becomes more abundant with proximity to Lake Victoria (Camberlin *et al*. 2009). An explanation for the pronounced differences in predictability and constancy of flows is not yet apparent and requires additional research; however, the available discharge record indicates that riparian and riverine species of the Mara Basin live in a highly dynamic hydraulic and hydrological environment.

Indications of flow–ecology relationships

Biological sampling at each site documented species considered sensitive to the flow regime of the Mara River and the changing hydraulic conditions. The deeply incised channels and high terraces characteristic of much of the basin have resulted in a highly vertically stratified riparian vegetation community (Fig. 8). The in-channel grasses and sedges (e.g. *Pennisetum* and *Cyperus*) depend on low flows of sufficient magnitude to keep their roots inundated (Ellery *et al*. 2003), whereas the trees and shrubs on



Channel-shaping flood; high terraces inundated allowing riparian trees to germinate; recharge of organic matter in river

Groundwater recharged; roots of shrubs and trees (*Carissa, Vangueria, Rhus* and *Euclea*) on upper terraces inundated

Seed dispersal and germination of riparian vegetation; fish such as *Labeo* able to migrate longitudinally

Sandbars and grasses and sedges inundated; sensitive macroinvertebrates (Ephemeroptera and Lepidoptera) able to reproduce

Sandbars and riparian vegetation (*Cyperus* and *Pennisetum*) exposed; fish and macroinvertebrates just surviving

High terraces inundated allowing riparian trees to germinate; recharge of organic matter in river

Groundwater recharged; roots of riparian vegetation on upper terraces inundated; reproduction in *Clarias* cued by rising waters

Riparian vegetation on first terrace with access to sufficient water; *Clarias* able to migrate upstream

Roots of riparian vegetation just becoming inundated; sensitive macroinvertebrates (Ephemeroptera and Plecoptera) able to reproduce

Riffles just covered; fish and macroinvertebrates surviving but with limited dispersal and reproduction

Channel-shaping flood; high terraces inundated allowing riparian trees to germinate; recharge of organic matter in river

Groundwater recharged; roots of *Acacia* and *Ficus* on upper terraces inundated

Seed dispersal and germination of grasses and sedges; fish such as *Labeo* able to migrate longitudinally

Sandbars and riparian vegetation inundated; sensitive species of macroinvertebrates (Ephemeroptera and Perlidae) able to reproduce

Sandbars and riparian vegetation (*Cyperus, Pennisetum*) exposed; fish and macroinvertebrates just surviving

Fig. 8 Cross-section diagrams for (a) Site 1, (b) Site 2, and (c) Site 6 in the Mara River Basin, showing the riverbed level, critical discharge levels and their ecological significance, and vegetation survey results (surveys not carried out for Site 2). The macro-channel extended to 106 m a.s.d. for Site 1 and to 110 m a.s.d. for Site 2, but upper portions of the channel not hydrologically active are not shown here.

the middle and upper terraces (e.g. *Syzigium*, *Warbugia*, and *Ficus*) require high flows to allow them access to water and occasional large floods to enable seed germination (Ellery *et al*. 1993). When baseflows are insufficient to maintain these riparian communities, their decline and disappearance may lead to greater erosion, less stabilized river banks, and more channel widening (Abernethy and Rutherfurd 2000, Langendoen *et al*. 2009).

The two dominant macroinvertebrate orders in the Mara were Ephemeroptera and Trichoptera, which can be sensitive to water-quality conditions, such as sediment load, low dissolved oxygen, temperature, and conductivity. These parameters are often linked with decreases in discharge, and Ephemeroptera-Plecoptera-Trichoptera (EPT) taxa have been found to decline in response to decreasing flow levels (Dewson *et al*. 2007, Miller *et al*. 2007, Walters and Post 2011). At all but one of our study sites, the number of taxa, sensitivity, and diversity of macroinvertebrates decreased during low flows compared to high flows. Median low flows at sites 1, 2, and 6 were sufficient to inundate most or all of mid-channel bars, thus increasing the available habitat for macroinvertebrates (Fig. 8). These observations, when combined, suggest the river system needs regular high-flow periods as well as freshes during low flows to prevent declines in water quality and the accompanying loss of more sensitive taxa.

The majority of the fish captured in the upper and middle portions of the basin were in the pool and lotic guilds, which are sensitive to changes in the flow regime that affect habitat availability, dissolved oxygen levels, and mobility (Welcomme *et al*. 2006). Lotic guild species in particular, e.g. *Labeo victorianus*, are longitudinal migrants that are cued by rising water levels to travel upstream for spawning (Rutaisire and Booth 2005). Depths associated with median high-flow levels at sites 1 and 6 are considered sufficient to enable upstream migration of *Labeo*, and the same is inferred for other sites in the study (Fig. 8). The one exception is Site 2 where no *Labeo* were found, presumably due to the natural waterfall and small dam just downstream of the study site at Tenwek. At Site 3 we also documented a member of the riffle guild (*Chiloglanis*), which has the highest sensitivity to flow levels due to its need for fast-flowing, highly oxygenated water (Kadye 2008, Kadye and Moyo 2008, Rashleigh *et al*. 2009). At the Mara Mines site, we documented one lentic species (*Afromastacembelus*), which is a floodplain migrant (Welcomme *et al*. 2006), as well as several Mormyrids (e.g. *Hippopotamyrus*), which spawn by attaching eggs to emergent vegetation (Lévêque 1997). These species likely migrate between the lower reaches of the river and the Mara Swamp, which is also dependent on the timing of higher flows that make emergent vegetation and other floodplain habitats accessible for a sufficient period of time. Across all sites, gonadal maturation appears to be cued by first high flows, suggesting fish in the Mara time their spawning to coincide with rising flows and floods, as is common for many fish species in the tropics (Lowe-McConnell 1975, Ochumba and Manyala 1992, Ikomi 1996, Kirschbaum and Schugardt 2002).

Although much work remains to better describe and quantify flow–ecology relationships in the Mara River system, these findings emphasize the importance of flow variability in maintaining fish diversity in the Mara. Although species numbers are fairly low in this system, two species recorded in this study, *Synodontis victoriae* and *Labeo victorianus*, are native to the Lake Victoria basin. *Synodontis victoriae* is also listed as near threatened by the IUCN Red List, and three more species recorded from other studies in the lower Mara are listed as endangered (*Brycinus jacksonii*) and critically endangered (*Oreochromis variabilis* and *Oreochromis esculentus)* (Wandera *et al*. 2006, Chitamwebwa 2007, IUCN 2013). Furthermore, reaches of the Mara River near Lake Victoria have been documented to provide critical refuges to native species of fish suffering severe population declines in Lake Victoria due to the introduction of non-native species, overfishing, and eutrophication (Rosenberger and Chapman 1999, Chapman *et al*. 2002). Thus, the fish species of the Mara River, although limited in number, have important conservation significance.

MANAGEMENT IMPLICATIONS

The ecological systems of the Mara River basin have evolved under a dynamic hydrological regime, and alterations to this regime, such as the loss or dampening of hydrologic variability, could have serious consequences for the flora and fauna communities of the Mara River. A reduction in high flows could deprive riparian vegetation on higher terraces of sufficient water, leading to decreased growth and reproduction, or even mortality. At the same time, disappearance of critical low-flow events would prevent the colonization of newly exposed habitat, such as emergent sandbars, which could provide important in-stream habitat when water levels rise. Lack of periodic freshes and floods could lead to declines in water quality, which would result in the loss of sensitive macroinvertebrate taxa and their replacement by more tolerant ones. Lack of rising flows and floods accompanying the rainy seasons could fail to cue spawning in resident fish, leading to population declines in flow-sensitive species. In short, the most important component of the Mara's hydrology is its variability, as each component of the hydrograph likely plays a different role in maintaining the ecological health of the system.

Indications of the importance of hydrological and hydraulic variability for the ecological health of the river basin have clear implications for current and future management. Kenyan and Tanzanian water laws explicitly call for allocating sufficient flows—the Reserve Flow—in part to "protect aquatic ecosystems" and enable ecologically sustainable water resources development. In the absence of system-specific knowledge, however, the Kenyan water authority suggests that the minimum flow for the Reserve be set at Q95 (WRMA 2009). This is equivalent to drought flow conditions and, if sustained, is not sufficient to meet the protection of aquatic ecosystems that is intended in the water law. The allocation of the Reserve Flow should include various environmental flow components, including mean monthly baseflows that vary seasonally according to the natural flow regime and select high flows and floods. Environmental flows have been prescribed for the basin in a process run parallel to this study (GLOWS 2013). They have also been incorporated into sub-catchment management plans, so the emphasis now should be on implementation by basin water authorities as part of a long-term and adaptive management strategy (WRMA 2009).

The most important water management challenges in the Mara are expected in the next 10 years, as plans are under way for large increases in water use and the construction of three dams that will regulate flows in critical reaches of the river. Although plans have not been finalized, initial figures call for two multipurpose reservoirs (hydropower and water supply) on the Mau Escarpment, one each on the Amala and Nyangores Rivers, with a combined storage of 135×10^6 m^3 (J. Terer, personal communication). Based on our calculations, this is equivalent to approximately 35% of the combined annual historical runoff of these two rivers. Another dam and water supply reservoir are planned near the Mara Mines site, with a potential capacity of 20×10^6 m^3, or just over 1% of the annual historical runoff in this section of the river. The headwater dams, when combined with increased water consumption by irrigated agriculture, could have significant effects on the timing and amount of flows to downstream communities and conservation areas, especially Masai Mara National Reserve and Serengeti National Park. The dam on the lower reach of the river will have a smaller relative effect on flows to the Mara Wetland, but will impact upstream migrations of fish from the wetland complex. Choices about the design and operation of these dams, if constructed, will profoundly impact the ecological sustainability of the river system and dependent terrestrial systems (i.e. the annual wildlife migration).

The dynamic relationships among flow regime, channel hydraulics, and riverine ecology described for the Mara are illustrative of rivers throughout equatorial East Africa (Masese and McClain 2012), and the challenges of conserving riverine ecosystems in the face of increasing water resources development are similar to those in river basins across many regions of sub-Saharan Africa (McClain 2013, McClain *et al.* 2013). The Mara thus has potential to serve as a model for ecohydrological research examining flow–ecology linkages in East African environments, and applied research into approaches to protect ecosystems while sustainably developing water resources.

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