



Sizes, condition factors and sex ratios of the scattered populations of the small cichlid fish, *Alcolapia grahami*, that inhabits the lagoons and sites of Lake Magadi (Kenya), one of the most extreme aquatic habitat on Earth

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Abstract *Alcolapia grahami* is a small cichlid fish that inhabits the scattered lagoons and sites of Lake Magadi (Kenya). Exceptional physiological, morphological, biochemical and behavioural adaptations allow the fish to tolerate the harsh environmental conditions that exist in the locations, the most extreme milieus occupied by a species of fish on Earth. The temperature of the water is inordinately high for a fish; large diurnal fluctuations in the levels of the partial pressure of oxygen occur, with acute hypoxia happening during the night and hyperoxia during the day; the salinity of the water is ~60% of that of seawater and; the pH may be as high as 11. Having an average adult body length of less than 6 cm and a body mass of ~5 g, the fish is very small in size. Here, body mass, body length, condition factors (CFs) and sex ratios (SRs) were determined on fish sampled from nine

accessible isolated populations. Except for the Cement Water Holding Tanks (CWHT) population, where the female-to-male SR was 4:1, overall, the number of male fish surpassed the female ones by a ratio of ~2:1. The male fish were heavier and longer compared to the female ones. The relatively lower ambient temperature in the CWHT (32 °C) may explain the female dominated population and the effect future increase in temperature may have on sex distribution in the various populations of *A. grahami*. In fish from the Fish Spring Lagoons B and D, the CFs were greater in the male fish relative to the female ones. Exhibiting poor-to-fair body states, the CFs of the different populations of *A. grahami*, that ranged from 1.1. to 1.8, were among the lowest that have been reported in fish living under natural setting. The skewed SRs and the markedly low

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CFs of *A. grahami* reported here may be ascribed to the harsh (stressful) environmental conditions the fish contends with. The values may signal prospective demise of the fish. Conservation measures are urgently needed to protect a very rare fish.

Keywords Sex ratio · *Alcolapia grahami* · Lake Magadi · Condition factor · Extreme environment

Introduction

'Lake Magadi, in the southern Rift Valley of Kenya, is arguably the most extreme aquatic environment on earth to support fish life.'

Pörtner et al. (2010).

Lake Magadi that covers a surface area of ~100 km² and lies at an average altitude of ~620 m above sea level (Baker 1958), is located between latitude 1°43'S to 2°10'S and longitude 36°00'E to 36°30'E [Fig. 1a] at the southern end of the Kenyan section of the East African Great (Gregory) Rift Valley. Situated in a closed hypersaline basin, the Lake comprises a vast evaporation salt pan that covers ~70% of its surface (McNulty 2017) [Fig. 1b, c]. During the late Pleistocene to mid-Holocene (~12,000 to ~10,000 years ago), the Lake Magadi region to the north and the larger Lake Natron to the south consisted of a vast paleo-lake called Lake Orolonga (LO) (Parkinson 1914; Bützer et al. 1972; Damnati 1993). It is speculated that the common lake contained a large population of freshwater cichlids, probably related to the modern day *Alcolapia grahami* (Boulenger 1912; Seegers and Tichy 1999; Tichy and Seegers 1999). LO was ~50 to ~60 m higher in elevation compared to the present Greater Lake Magadi and ~48 m above that of the present Lake Natron (Baker 1958; Bützer et al. 1972; Jones et al. 1977; Eugster 1980). The separation of LO into Lakes Magadi and Natron probably occurred ~13,000 years ago (Bützer et al. 1972; Tichy and Seegers 1999) from extreme climatic- and geological changes (Roberts et al. 1993; Damnati 1993; Hassan 1997; Broecker 2006; Clark et al. 2009). Further decrease in precipitation and increase of seismic activities lead to drop of the level of the prehistoric Lake Magadi, leading to its separation into the Greater Lake Magadi and the Little Lake Magadi (Fig. 1d). The maximum depth of the Little Lake Magadi is 1.2 m, it is 7 km long, covers a surface area of ~14 km² and signifying the past complex

geology and the intense seismic activity that has occurred in the Lake Magadi region lies ~100 m higher than the Greater Lake Magadi. At their closest proximity, the two lakes are only ~50 m apart (Fig. 1d). The past higher levels of the prehistoric Lake Magadi are now evidenced by columns of soda ash and alluvial deposits that stand high above the old dry lake bed (Eugster 1970) (Fig. 1e). Since no perennial rivers enter or leave Lake Magadi, the lagoons and sites that are inhabited by *A. grahami* are replenished by hot (geothermal) alkaline springs (Fig. 1f). Those at the Little Lake Magadi are as hot as 86 °C (Eugster 1970; Jones et al. 1977). In the different locations that are inhabited by *A. grahami*, the chemistry of the waters varies greatly (Eugster 1970; Wilson et al. 2000, 2004; Wood et al. 2013, 2016). With continuous accumulation of soda ash in Lake Magadi (Eugster 1970, 1980; Goetz and Hillaire-Marcel 1992), the fish was displaced to the more hospitable peripheral locations (Fig. 1). The conditions that *A. grahami* lives under are extreme: the pH of the water is as high as 11; the titration alkalinity ranges from 350 mEq.L⁻¹ to 1625 mEq.L⁻¹; the salinity of the water is ~60% of that of seawater; the osmolarity of the water ranges from 617 to 1689 mOsm.kg⁻¹; the water contains high levels of reactive O₂ species (>8 μ mol L⁻¹); the temperature of the water (in the hospitable areas) may be as high as 45 °C and; the partial pressure of oxygen (PO₂) changes from a day-time hyperoxia to severe night time hypoxia (Narahara et al. 1996; Wilson et al. 2004; Johannsson et al. 2014). Among fish, the thermal tolerance of *A. grahami* is only rivalled by the pupfishes (Cyprinodontidae: *Cyprinodon* spp.) of the Death Valley of Southern California and Nevada (Brown and Feldmeth 1971; Echelle et al. 2005; Lama 2008; Hausner et al. 2013; Carson et al. 2014; Martin et al. 2016; Jones 2017). There is consensus that *A. grahami* is an extreme animal (Talling and Talling 1965; Wilson et al. 2004; Pörtner et al. 2010; Kavembe et al. 2014, 2015, 2016a, b; Kavembe 2015; Schagerl and Burian 2016; Oduor and Kotut 2016; Bianchini et al. 2017).

In biology, population structure talks to the prevailing and the past environmental conditions that an animal has experienced (Acevedo-Whitehouse and Duffus 2009; Milligan et al. 2009; Møller 2013; Bao et al. 2017). Reproduction is a very important life-history event (Charnov 2004; Beck and Agrawal 2010). It is influenced by various environmental factors (Crews and Bull 2009; Kumolu-Johnson and Ndimele 2010; Oso et al. 2011;

Stier et al. 2012). In more derived animals, even small but constant reductions in gamete production by either of the sexes causes population disruption, retrogression and eventual collapse (Conover and van Voorhees 1990; Miller et al. 2004; Pen et al. 2010; Wingfield 2013). The viability of a population is dependent on existence of critical numbers of male- and female animals (Conover and Van Voorhees 1990; Devlin and Nagahama 2002; Dyson and Hurst 2004). Sex ratio (SR) is an important demographic parameter that is pivotal to the evolution and the conservation of secondary sexual traits as well as the viability of a population (Valenzuela and Lance 2004; Dyson and Hurst 2004; Ospina-Álvarez and Piferrer 2008; Schacht and Smith 2017). Overall, SR specifies the growth rate, the reproductive health and the success of a population (Emlen and Oring 1977; Khalfalla et al. 2008; Terrell et al. 2011).

The primary goal of this study was to determine the sex distribution and the physical health of the scattered populations of *A. grahami* at Lake Magadi. Coe (1966) outlined the general reproductive biology of *A. grahami* at the Fish Spring Lagoons and Papah et al. (2013) examined the process of spermatogenesis in the male fish. The physical (body) condition (health) and the sexual reproductive status of *A. grahami* have not hitherto been investigated. The fish studied here were caught by a seine net at known accessible lagoons and sites of Lake Magadi (Fig. 1g) that comprised the Fish Spring Lagoon (Fig. 1h), the Cement Water Holding Tanks (Fig. 1i), the South Western Lagoons (Fig. 1j), the South Eastern Lagoons (Fig. 1k), the Western Lagoons (Fig. 1l) and the Little Lake Magadi (Fig. 1d). The tanks, that are located close to the factory, are used to store water that is used to ‘clean’ the trona (soda ash) which among others is used in industrial activities like manufacture of soap, paper, glass, dyes, drugs, cosmetics and fertilizers. *A. grahami* (Fig. 2a), exhibits air-breathing behaviour (Fig. 2b). At the Fish Spring Lagoon (D) (Fig. 1h), in a coordinated manner, at regular intervals (once every ~12 min), the fish *en masse* vigorously surged in a wave form from the lakeward parts of the lagoon towards the outer edge (Fig. 2c). Because no birds, which are the foremost predators, were anywhere close to where the fish were starting the ‘wave’, it was assumed that the created turbulence, which should have promoted the dissolving of oxygen in water, may have been provoked by hypoxia in the outlying waters. Lake Magadi is visited by large flocks of birds mainly from neighbouring lakes (Figs. 1j–l and 2d): egrets, herons, terns, gulls, pelicans

and flamingos comprise most of them. Presently, *A. grahami* is under extreme pressure from direct and indirect anthropogenic activities. It is urged that conservation measures be urgent instituted.

Materials and methods

The fish that were used in this study were collected from various lagoons and sites of Lake Magadi after approval of the study by the University of Johannesburg Animal Ethics Committee (Approval Reference Number Zoology/Fish/Maina-1950) and the animals were handled in compliance with NIH Guideline for Care and Use of Laboratory Animals, 8th Edition (Revised 2010). The Fish Spring Lagoon comprises four adjoining pools of water (Fig. 1h). The Fish Spring Lagoon A, which is the most peripheral one, is recharged by several highly productive hot springs. It is separated from the Fish Spring Lagoons B and C by a low cement wall but is connected to the Fish Spring Lagoon D by a spillway. The water in the Fish Spring Lagoon A could flow over the cement wall into the Fish Spring Lagoons B and C during heavy rains and/or when the pump (Fig. 1h), which removes water from the Fish Spring Lagoon A and delivers it to the Cement Water Holding Tanks, breaks down or is switched off for maintenance. The very small Fish Spring Lagoon B may be recharged by a hot spring. It was visibly green in colour from plentiful algal (cyanobacterial) growth. With the bottom comprising deep and dark soft mud, Fish Spring Lagoon (C) was large and very shallow. The Fish Spring Lagoon (D) was sizeable. Its inner (lakeward) edge comprised a ledge of trona. The Cement Water Holding Tanks (WHT) are fenced-off by wire mesh. They are located ~1 km away from the Fish Spring Lagoon A, close to the trona (salt) processing factory (Fig. 1). The tanks that are ~2.5 m deep are used to store water for processing the trona. The South Western Lagoons (Fig. 1j) consist of many shallow pools of water that are recharged by numerous highly productive hot water springs and the South Eastern Lagoons (Fig. 1k) comprise shallow, sprawling water pools. The Western Lagoons (Fig. 1l) are expansive very shallow water pools with thick black soft mud at the bottom. Under the present physical state of Lake Magadi, dispersal of fish between the lagoons and sites is impossible. Most of the locations are separated by long distances (Fig. 1), the surface of the Lake is covered by thick solid trona (salt) (Fig. 1b) and where the

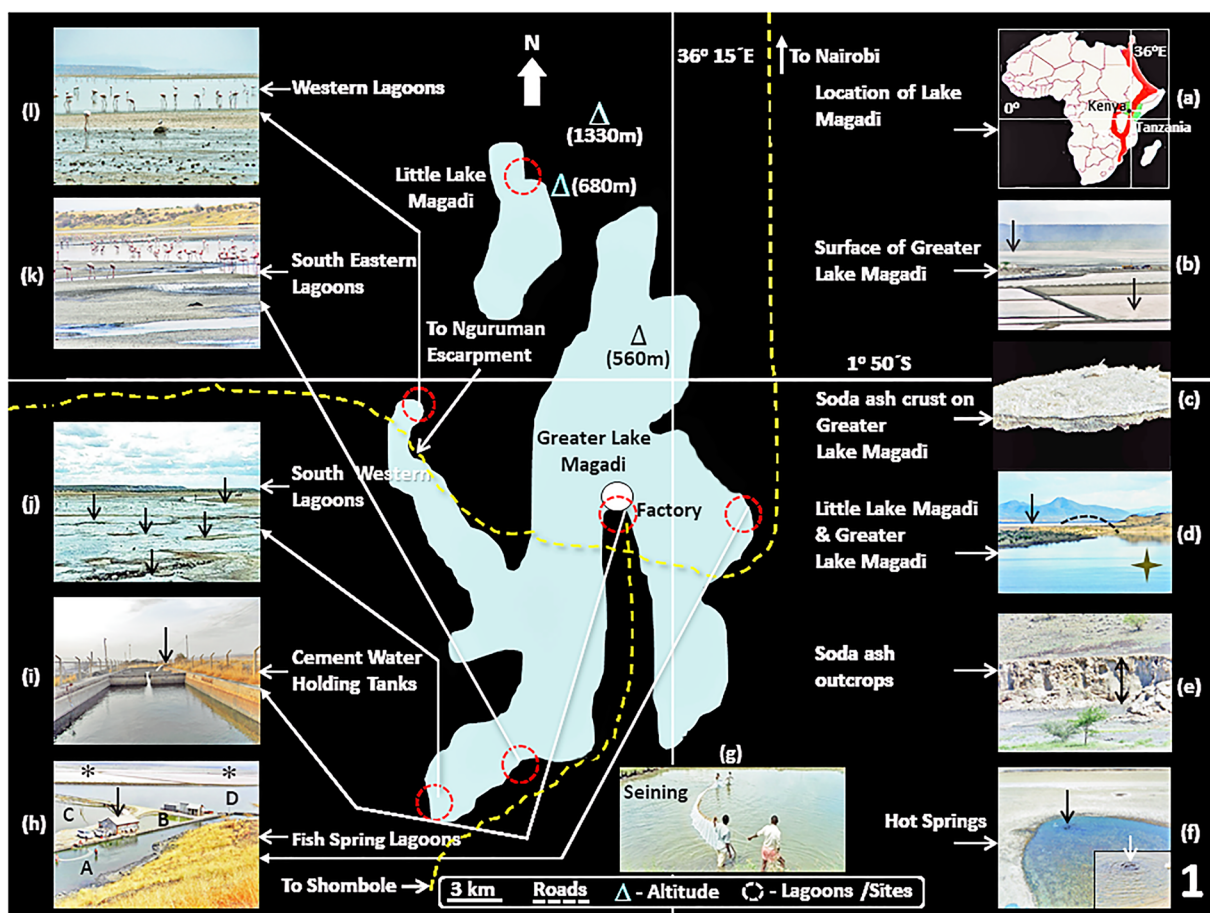


Fig. 1 Diagram showing the location of the Greater Lake Magadi (GLM) and the Little Lake Magadi (LLM), photographs of the lagoons and sites from where fish were sampled and other interesting physical features (inserts). Figure 1a. Map of Africa showing the location and extent of Great Rift Valley (highlighted in red). The approximate location of Lake Magadi in Kenya is shown by a spot. Figure 1b. Soda ash (salt = trona) covering the surface of the GLM (arrows). Figure 1c. A slab of soda ash peeled from the surface of drying brine in a pond of the GLM. Figure 1d. View of the LLM (star) with the GLM (arrow) in the distant background. At their closest proximity, the Lakes are separated by a narrow ledge of ground (dashed curved line); the LLM lies ~100 m higher in elevation relative to the GLM. Figure 1e. Column of soda ash and alluvial deposits (double sided arrow) on the dry floor of the prehistoric Lake Magadi. Figure 1f. Hot (geothermal) springs at the South Western Lagoons (arrows). Figure 1g. Except for the

Cement Water Holding Tanks where scoop nets were used to catch fish, at the lagoons and site, fish were caught by dragging a seine net across. Figure 1h. The Fish Spring Lagoon that comprises four water ponds (lagoons) A-D. Asterisks (*), trona covering the surface of the distant part of the GLM; arrow, pump house from where water is pumped to the Cement Water Holding Tanks. Figure 1i. One of the Cement Water Holding Tanks that is used to store water for processing ('cleaning') the trona. Arrow, water flowing into a tank from the pump at the Fish Spring Lagoon A, about a mile away. Figure 1j. South Western Lagoons which consist of shallow water pools (arrows) that are recharged by hot springs. Figure 1k. South Eastern Lagoon that comprises many shallow water ponds. The lagoons are visited by large flocks of birds, most of which are flamingos. Figure 1l. Western Lagoon that consists of large water ponds which are visited by large numbers of birds, with most of them being flamingos

trona is broken, the brine (water) is very hot and saline to support fish. It has been speculated that in the past, movement of fish between various locations and sites may have occurred during rare heavy rains and floods (White 1953; Coe 1966). No hard data are, however, available to corroborate the suggestion. It is nevertheless possible that mixing of the fish populations may have

been possible because the locations were closer to each other and the water may have been less hot and alkaline.

For this study, fish were caught about the same time of the day (~10:00) over a period of three weeks during the months of July and August, a relatively cooler and drier part of the year in Lake Magadi region. It was done by dragging a long seine net with dense meshwork

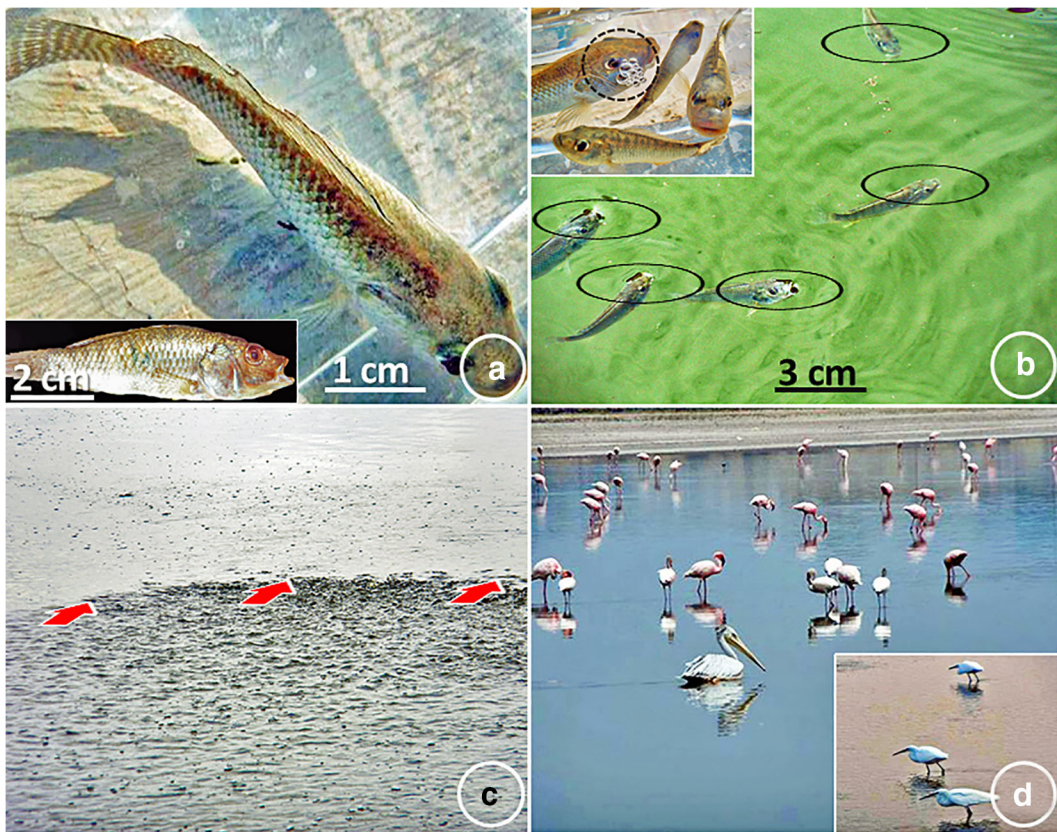


Fig. 2 Fig. 2a and insert: A live specimen of *Alcolapia grahami* seen in a container of water and a fixed specimen (insert). Figure 2b. Specimens of *A. grahami* in the Fish Spring Lagoon A shown skimming the surface of the water and breathing air (circles). Insert, four specimens of *A. grahami* in a laboratory container where one of them has just expelled air from the mouth/swimbladder into the surrounding water (dashed circle). Figure 2c:

The ‘waving’ behaviour of fish in the Fish Spring Lagoon D. At regular intervals, *en masse*, the fish vigorously swam towards the outer edge of the lagoon (arrows). It was presumed that the activity promoted the oxygenation of the water. Figure 2d: Birds at the Fish Spring Lagoon D. Most of them are flamingos. Insert: Egrets, *Egretta garzetta*)

across the lagoons and sites (Fig. 1h). In the Little Lake Magadi, the fish were caught at the north-eastern part of the Lake which was criss-crossed several times with the net. At the Cement Water Holding Tanks, fish were caught using scoop nets after prior request had been made to the management of the TATA Magadi Soda Company (the current proprietors of Lake Magadi) for have the pump to be turned off at the Fish Spring Lagoon A for several hours. Continued use at the factory at the factory made the level of the water in the tanks to drop to a level where fish could be caught easily. In those lagoons and sites where fish existed in large numbers, e.g., in the Fish Spring Lagoons A, B and D and in the Cement Water Holding Tanks, the fish that were caught were tipped directly from the net into eight sequentially numbered 20-l buckets in about equal numbers. A random number generator (www.excel-easy.com/examples/random-numbers.html - retrieved on

31-12-2018) was used to produce a number between 1 and 8 and the fish in the bucket that was determined were used in the study. The sampling procedure eliminated personal bias in obtaining the fish that were investigated. The rest of the fish in the other buckets were immediately returned to the same location where they had been caught. Because for most lagoons and sites considerable areas were ‘seined’, it was presumed that the numbers of fish that were caught were representative of the existing population. At a temporary outdoor laboratory, the fish were killed by quickly transecting the brain stem using a pair of sharp-pointed scissors, causing the animal to die instantly. Body mass and body length were determined at once and the condition factors (CFs) calculated by applying the eq. $K = 100BM.BL^{-3}$, where BM was the body mass expressed in grams and

BL the body length expressed in cm (Nash et al. 2006). The sexes of fish were determined after the coelomic cavity was opened and the gonads, ovaries for females and testes for males, were directly identified. For the very small specimens, sex determination was more difficult. In such cases, examination was performed under a dissection microscope. Fish were assigned a particular sex only after the gonads were categorically identified. Where it was not possible, the fish was placed under the 'sex unidentified' category shown on Table 1.

Temperature, pH and oxygen levels were measured at the lagoons and sites when fish were caught. (Table 2). The level of oxygen in water was determined as described by Johannsson et al. (2014) and the values of the alkalinity of the water in the various locations are those reported by Randall et al. (1989), Wilson et al. (2004) and Wood et al. (2002, 2016).

Statistical analysis

Correlations between environmental factors (in water), i.e., temperature, pH, alkalinity and PO₂, with biological factors, i.e., CF and SR, were determined using the Spearman's correlation coefficient, with the significance threshold set at $P < 0.05$.

Results

The overall mean body mass and body length of the fish (*A. grahami*) sampled from the various lagoons and sites of Lake Magadi were respectively 3.5 ± 3.4 g and 5.8 ± 1.7 cm (Table 1). The largest fish were found in the Cement Water Holding Tanks and the Fish Spring Lagoon D while the smallest inhabited the Western- and the South Eastern Lagoons and the Little Lake Magadi (Fig. 1; Table 1). Regarding the entire Lake Magadi fish population, the number of male fish was about twice that of the female ones and the male fish were heavier and longer than the female ones (Table 1). In fish from the Cement Water Holding Tanks, body mass and body length matched closely while notable differences existed between the two parameters in fish from the other locations, especially in the Western-, the South Eastern- and the Fish Spring Lagoons (B) as well as in the Little Lake Magadi (Table 1; Fig. 3). The SRs of the fish are shown on Fig. 4 and Table 2. Except for the fish from the Cement Water Holding Tanks, where the number of

female fish considerably exceeded the male ones by a ratio of 4:1, in the other populations, male fish greatly exceeded the female ones (Table 2; Fig. 4). The greatest male-to-female SRs occurred in the Little Lake Magadi and the South Eastern- and the Western Lagoons (Table 2; Fig. 4). The highest value of the CFs (1.8) occurred in the male fish from the Fish Spring Lagoon (B) and 1.6 in the female fish from the Cement Water Holding Tanks and the Fish Spring lagoons A and B (Table 2; Fig. 5). The fish population from the Western Lagoon had the lowest CF (1.1) (Table 2; Fig. 5).

The Spearman's correlation coefficients (r) between environmental parameters (temperature, pH, alkalinity and PO₂) with biological parameters (CFs and SRs) are shown on Table 3. The correlations were either positive or negative, strong or weak or significant or insignificant. For temperature, strong positive correlation was found with CF ($r = .433$) and a weak negative one with SR ($r = -.188$); for pH, the correlation with the CF was not significant ($r = 0.001$) and a negative one occurred with SR ($r = -.280$); for alkalinity, the correlation with CF was not significant ($r = -.022$) and a positive one existed with SR ($r = .256$) and; the PO₂ in water correlates positively with CF ($r = .260$) and the correlation with SR was not significant ($r = .068$). It is cautioned that the correlative statistics reported here should be treated as preliminary for the following reasons: a) for the reason that *A. grahami* has been declared a threatened species (Bayona and Akinyi 2006), it was necessary that a minimum number of specimens be investigated; b) since fish move all over the individual locations and in a highly tectonically active region environmental parameters, especially temperature, change greatly over short distances (depending on proximity to geothermal springs), the number of measurements of the predictor variables were limited, especially for the large places where the measurements were averaged out and; c) the number of lagoons and sites from which the fish were sampled was not adequate to warrant robust multilevel analysis.

Discussion

In this study, where the CFs ranged from 1.1 to 1.8 (Table 2), compared to species and groups of fish that have been investigated, especially those that phylogenetically proximate *A. grahami* (e.g. *O. niloticus*; Ighwela et al. 2011), the Lake Magadi tilapia species is

Table 1 The locations of lagoons and sites, the numbers of female and male fish and the mean body mass and body length of fish, *Alcolapia grahami*, in various locations of Lake Magadi

Lagoon	Lagoon global location: GPS coordinates	Fish	n	Mean Body Length \pm SD (cm)	Mean Body Mass \pm SD (g)
CWHT	01° 53' 40.0"S 36° 17' 24.4"E	Female (F)	20	7.0 \pm 1.8	5.6 \pm 3.3
		Male (M)	5	9.8 \pm 2.0	14.8 \pm 8.8
		Sample mean	25	8.4 \pm 2.1	10.2 \pm 5.8
FSL(A)	01° 53' 29.5"S 36° 18' 09.9"E	Female	23	5.6 \pm 0.8	2.9 \pm 1.6
		Male	44	5.9 \pm 0.9	3.1 \pm 1.4
		Sample mean	67	5.9 \pm 0.9	3.0 \pm 1.5
FSL(B)	01° 53' 27.4"S 36° 18' 09.8"E	Female	25	4.6 \pm 0.6	1.6 \pm 0.7
		Male	35	5.2 \pm 1.0	2.6 \pm 1.6
		Sample mean	60	4.9 \pm 0.9	2.1 \pm 1.4
FSL(C)	01° 53' 29.2"S 36° 18' 09.1"E	Female	17	6.1 \pm 1.4	3.8 \pm 2.9
		Male	28	7.0 \pm 1.1	5.4 \pm 2.9
		Sample mean	45	6.6 \pm 1.3	4.6 \pm 3.0
FSL(D)	01° 53' 30.0"S 36° 18' 09.9"E	Female	20	6.3 \pm 1.4	4.1 \pm 2.9
		Male	43	7.7 \pm 1.4	8.2 \pm 4.7
		Sample mean	63	7.0 \pm 1.5	6.2 \pm 4.6
LLM	01° 43' 39.3"S 36° 16' 50.7"E	Female	2	4.6 \pm 0.1	1.5 \pm 0.1
		Male	37	4.5 \pm 0.5	1.5 \pm 0.5
		Sex unidentified	12	4.3 \pm 0.5	1.1 \pm 0.3
		Sample mean	51	4.5 \pm 0.5	1.4 \pm 0.4
SWL	02° 00' 03.9"S 36° 13' 55.2"E	Female	42	5.6 \pm 1.0	2.7 \pm 1.3
		Male	59	6.1 \pm 1.8	3.9 \pm 3.5
		Sample mean	101	5.9 \pm 1.5	3.3 \pm 2.9
SEL	01° 59' 23.0"S 36° 15' 38.1"E	Female	9	4.2 \pm 0.3	1.1 \pm 0.3
		Male	42	4.5 \pm 0.6	1.3 \pm 0.4
		Sample mean	51	4.4 \pm 0.6	1.2 \pm 0.4
WL	01° 52' 20.2"S 36° 14' 39.7"E	Female	1	3.3	0.4
		Male	5	3.3 \pm 0.3	0.4 \pm 0.1
		Sex unidentified	25	2.9 \pm 0.3	0.3 \pm 0.2
		Sample mean	31	3.2 \pm 0.4	0.4 \pm 0.2
Total population		Female	159	5.6 \pm 1.4 ¹	3.1 \pm 2.4 ¹
		Male	298	5.9 \pm 1.7 ¹	3.8 \pm 3.9 ¹
		Total number	457	5.8 \pm 1.7 ¹	3.5 \pm 3.4 ¹

Names of the lagoons and sites from where fish were collected: CWHT, Cement Water Holding Tanks; FSL (A), Fish Spring Lagoon A; FSL (B), Fish Spring Lagoon B; FSL (C), Fish Spring Lagoon C; FSL (D), Fish Spring Lagoon D; LLM, Lake Little Magadi; SWL, South Western Lagoons; SEL, South Eastern Lagoons; WL, Western Lagoons

in a poor-to-fair body state. Condition factor (CF), a parameter that is also termed ‘coefficient of condition’, ‘Foulton’s CF’ or ‘K factor’, has been used in fishery research particularly after the subject was critically reviewed by Froese (2006). The index has been known and employed to assess the rate and the pattern of growth, the feeding intensity, the changes in nutritional

condition and the general health of fish (Fulton 1902; Charles-Barnham and Baxter 1998; Nash et al. 2006; Ighwela et al. 2011; Datta et al. 2013; Ayo-Olalus 2014; Otieno et al. 2014; Jin et al. 2015; Akintade et al. 2016). CF is also an important indicator of the productivity of a water mass and its capacity to support life (Charles-Barnham and Baxter 1998). Normally, fish with high

Table 2 Sex ratios, condition factors and measurements of different environmental parameters of the lagoons and sites of Lake Magadi from which fish were sampled

Physical and biological parameters				Environmental factors			
Lagoon/ Site	Sex	Sex ratios: Male to female fish	Condition factors \pm SD (g.cm^{-1})	Temperature* (°C)	pH*	Alkalinity* (mEqL^{-1})	Partial pressure of oxygen (mmHg)*.#
CWHT	Female	1:4	1.6 ± 0.6	32	9.86	378	733.9
	Male		1.4 ± 0.2				
FSL(A)	Female	1.9:1	1.6 ± 0.3	34	9.86	378	731.6
	Male		1.4 ± 0.3				
FSL(B)	Female	1.4:1	1.6 ± 0.3	33	9.86	392	733.3
	Male		1.8 ± 1.2				
FSL(C)	Female	1.6:1	1.5 ± 0.3	30	9.86	370	732.2
	Male		1.5 ± 0.3				
FSL(D)	Female	2.2:1	1.5 ± 0.3	34	9.78	412	738.9
	Male		1.6 ± 0.2				
LLM	Female	19:1	1.5 ± 0.1	42	9.32	1251	688.0
	Male		1.5 ± 0.1				
SWL	Female	1.4:1	1.4 ± 0.5	45	9.65	184	726.0
	Male		1.4 ± 0.5				
SEL	Female	4.7:1	1.4 ± 0.2	40	9.55	402	698.0
	Male		1.4 ± 0.2				
WL	Female	5:1	1.1 ± 0.3	36	9.13	350	801.0
	Male		1.1 ± 0.3				

Names of the lagoons and sites from where fish were collected: CWHT, Cement Water Holding Tanks; FSL (A), Fish Spring Lagoon A; FSL (B), Fish Spring Lagoon B; FSL (C), Fish Spring Lagoon C; FSL (D), Fish Spring Lagoon D; LLM, Lake Little Magadi; SWL, South Western Lagoons; SEL, South Eastern Lagoons; WL, Western Lagoons

*Measurements made in this study; * Values reported by Wood et al. (1994) and Wilson et al. (2000, 2004). # The partial pressures of oxygen were adjusted for the elevation (altitude) and the salinity of the Lake Magadi water

CFs display healthier body conditions compared to those with lower ones (Wootton 1996; Charles-

Barnham and Baxter 1998; Nash et al. 2006; Ighwela et al. 2011; Datta et al. 2013; Ayo-Olalus 2014; De

Fig. 3 Comparison of the mean body mass and the mean body length of the total number of female- and male fish of *Alcolapia grahami* that were sampled from the various lagoons and sites of Lake Magadi. Except for the fish from the Cement Water Holding Tanks, where body mass correlated with body length, in all the other cases, the parameters varied. FSL, Fish Spring Lagoons; SWL, South Western Lagoons; WL, Western Lagoons; CWHT, Cement Water Holding Tanks; SEL, South Eastern Lagoons; LLM, Little Lake Magadi

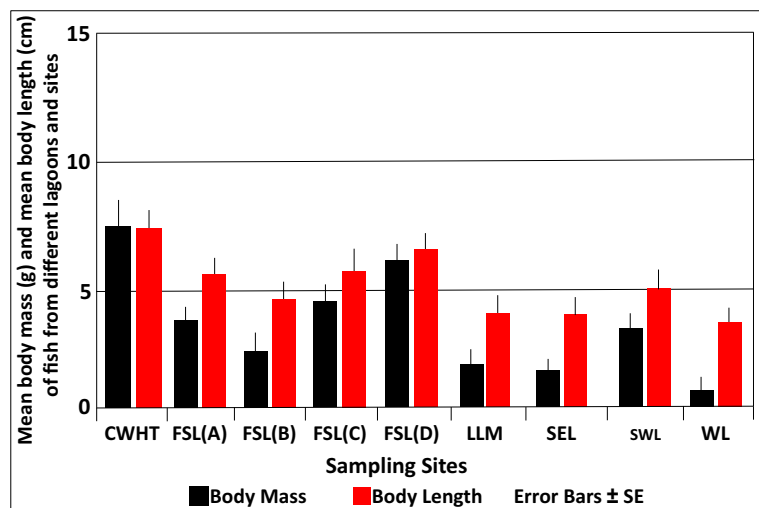
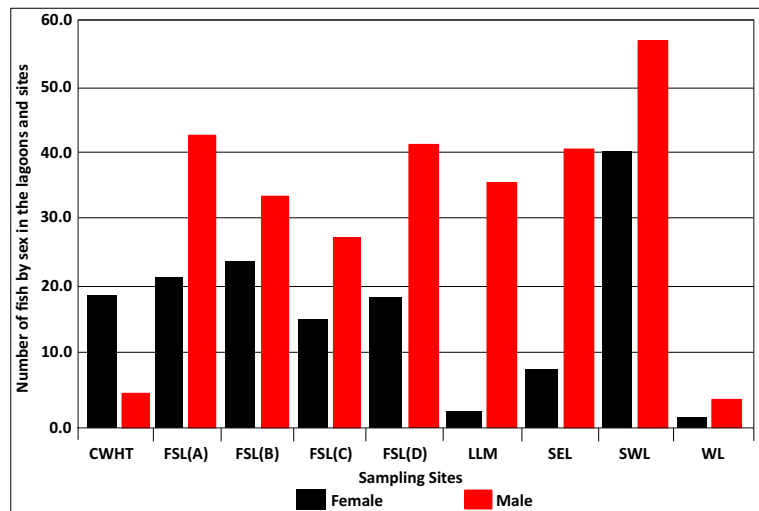


Fig. 4 Numbers of fish by sex in the lagoons and sites of Lake Magadi from which fish, *Alcolapia grahami*, were sampled. Except for the Cement Water Holding Tank (CWHT), where the number of female fish surpassed the male ones, in all the other cases, the number of male fish exceeded the female ones. FSL, Fish Spring Lagoons; SWL, South Western Lagoons; WL, Western Lagoons; CWHT, Cement Water Holding Tanks; SEL, South Eastern Lagoons; LLM, Little Lake Magadi



Giosa et al. 2014; Otieno et al. 2014; Ridanovic et al. 2015; Jin et al. 2015; Akintade et al. 2016; Fafioye and Ayodele 2018). The factor is influenced by factors such as shape, age and sex of fish, season, stage of maturation, fullness of the gut, type of food eaten, quantity of fat reserve and the degree of muscular development. For the reason that most of these features vary greatly between different species of fish, interpretation of the CFs should be made with discretion: comparison within a species is more meaningful than that between species.

According to Bagenal and Tesch (1978), for mature freshwater fish, CFs generally range from 2.9 to 4.8. Charles-Barnham and Baxter (1998) observed that salmonid fish with a CF of 1.60 presented excellent body condition, those with one of 1.40 were well-proportioned, fair state occurred in fish having a CF of 1.20 and respectively, fish with CFs of 1.00 and 0.80 showed poor and extremely poor body states. Anni et al. (2016) reported that all the specimens of *Tilapia mossambica* with a CF of 0.79 were in ‘high-quality’ physical

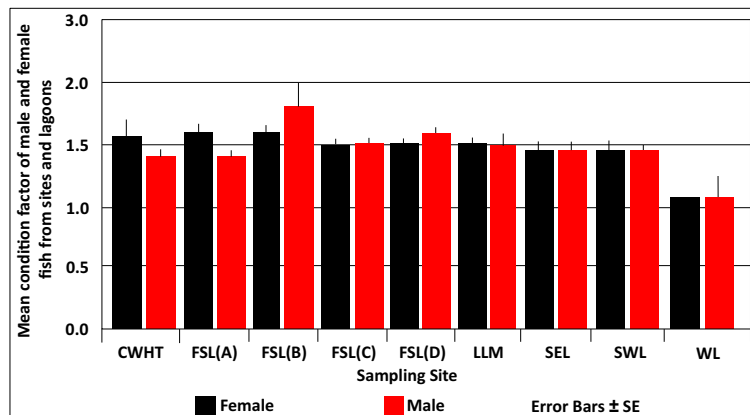


Fig. 5 The mean condition factors (CFs) of the male- and the female fish from the different lagoons and sites of Lake Magadi from which fish were sampled. For the female fish, the highest mean CF occurred in fish from the Fish Spring Lagoon A [FSL(A)], Fish Spring Lagoon B [FSL(B)] and the Cement Water Holding Tanks (CWHT) while the lowest values were in fish from the Western Lagoons (WL). For the male fish, the highest CF was in fish from the FSL(B) and FSL(D) while the lowest value was in

fish from WL. In fish from the FSL(B) and FSL(D), the CFs were greater in male fish compared to female ones while in the CWHT and the FSL(A), the CFs of the female fish surpassed those of males ones. For the other fish populations, the CFs were about equal in the sexes. FSL, Fish Spring Lagoons; SWL, South Western Lagoons; WL, Western Lagoons; CWHT, Cement Water Holding Tanks; SEL, South Eastern Lagoons; LLM, Little Lake Magadi

Table 3 Spearman's correlation coefficients between environmental parameters and biological parameters

Environmental Parameters	Biological parameters	
	Condition factor	Sex ratio
Temperature (°C)*	.433	-.188
pH*	.001	-.280
Alkalinity (mEqL ⁻¹)*	-.220	.256
Partial pressure of oxygen (mmHg)*	.260	.068

* Measurements made in this study; * Values reported by Wood et al. (1994) and Wilson et al. (2000, 2004)

condition. In the four cichlid species examined by Anene (2005), the very high CFs, that ranged from 4.30 to 5.38, were ascribed to living in a very productive and stable ecosystem. For the African pike, *Hepsetus odoe*, Oso et al. (2011) determined a mean CF of 1.17 for the males and one of 0.86 for the females: the low values were attributed to poor productivity of the dam. With the CFs of the Nile tilapia, *Oreochromis niloticus*, fingerlings ranging from 1.64 to 1.79, Ighwela et al. (2011) noted that the fish displayed above average body condition. In three cichlid species investigated by Ayaode and Ikulala (2007), a mean CF of ~1 was found while for the 21 fish species examined by Kumolu-Johnson and Ndimele (2010), the values ranged from 0.12 in *Polydactylus quadrifilis* to 16.29 in *Eutropius niloticus*. For the former species, ~86% of the CFs fell out of the range that was considered optimum for mature freshwater species in the tropics. In the six species of fish examined by Ahmed et al. (2011), the CFs ranged from 0.51 in *Clarias lazera* to 3.42 in *O. niloticus*: ~83.3% of the CFs fell outside the range deemed good enough for mature tropical freshwater fish. For *Argyrops spiner* and *Epinephelus coioides*, Raeisi et al. (2011) reported that the CFs ranged from 1.022 to 1.079. According to Devlin and Nagahama (2002) and Valenzuela and Lance (2004), exacting environmental conditions may cause low CFs. Fish inhabiting such habitats have to mobilise various energetically costly physiological and biochemical counter measures in order to maintain homeostasis and execute vital activities. The routine metabolic rate of *A. grahami* is very high (Wood et al. 1994, 2016; Franklin et al. 1995; Narahara et al. 1996): ~50% of its energy reserves are expended on acid-base regulation (Wood et al. 2002). Fish from the South Western Lagoons that were investigated by Wood et al. (2016) had high upper critical temperature ($C_{t_{max}}$) of

45.6 °C, the greatest measurement that has ever been recorded in a fish. For *A. grahami*, the routine rates of O₂ consumption (MO₂) and swimming performance at temperatures of 25-, 32- and 39 °C are the highest metabolic performances ever recorded in a fish (Wood et al. 2016): they fall within the basal range of a small mammal of equivalent body mass. Mainly comprising microphytes, protozoa, invertebrates, insect larvae, the tilapia fish (*A. grahami*) and many piscivorous birds (Coe 1966; Javor 1989; Krienitz and Schagerl 2016; Krienitz et al. 2016; Mengistou 2016; Yasindi and Taylor 2016; Bianchini et al. 2017), a simple but highly productive food web exists in Lake Magadi (Harper et al. 2016; Oduor and Kotut 2016; Schagerl and Burian 2016; Bianchini et al. 2017). Struggle to survive in a severe environment may explain the generally small size of *A. grahami* in its natural setting (Lake Magadi) (Table 1). Indicating that its diminutive size is not a genetic feature, in the laboratory (Maina, unpublished observations) and even in the Cement Water Holding Tanks of Lake Magadi (this study), where the degree of predation is much less or non-existent because the tanks are fenced off (Fig. 1j) and heavy human traffic between the factory and the Magadi Township exists, the fish grow to larger sizes (Table 1). Here, correlative analysis showed that the CF and the SR of *A. grahami* are affected differently by various environmental factors (Table 3).

The temperature of the water in the hospitable parts of the lagoons and sites of Lake Magadi ranges from 30 °C to ~45 °C (Wilson et al. 2004) (Table 2). The largely male-dominated fish populations of *A. grahami* can be attributed to the high water temperatures in the locations occupied by the fish (Maina et al. 1996; Wilson et al. 2004; Johannsson et al. 2014; Wood et al. 2016) while the female dominated fish population at the Cement Water Holding Tanks can be ascribed to the relatively lower average water temperature (32 °C) compared to the higher one of 34 °C in the Fish Spring Lagoon A, localities areas which are connected by a water pipe. Correlative analysis showed that temperature influences CF and SR (Table 3). Interestingly, because the male-to-female SR of 1.4:1 at the relatively hotter South-Western Lagoons (~45 °C) was equal to that in the cooler Fish Spring Lagoons B (33 °C) (Table 2), an average temperature differential of 12 °C, other environmental factors may determine sex distribution in *A. grahami*. Temperature is an important sex determining environmental factor in fish (Valenzuela et al. 2003; Valenzuela and Lance 2004; Ospina-Álvarez and Piferrer 2008). First reported

in the Atlantic silverside, *Menidia menidia* (family Atherinopsidae), by Conover and Kynard (1981), it has since been reported in many other species of fish, mostly cichlids (Conover 2004; Ospina-Álvarez and Piferrer 2008). Except for *M. menidia* and *M. peninsulae* (Conover 2004) and *Cobitis elongatoides* (Bohlen et al. 2008), where temperature dependent sex determination has been reported in wild populations, most of the investigations have been done under laboratory conditions (Conover and Van Voorhees 1990; Valenzuela et al. 2003; Conover 2004; Ospina-Álvarez and Piferrer 2008). For the genus *Oreochromis*, Bezault et al. (2007) observed that high temperature causes masculinisation of genetic females. Study of the eggs of *M. menidia* have showed that during the thermosensitive period, a 2 °C change of temperature alters SRs from 50% to 69% for males (Conover 1984). In the Argentinian silverside, *Odontesthes bonariensis*, a temperature rise of 1.5 °C increased the percentage number of males from 50 to 73% (Cornejo 2003); in absolute terms, the SR changed from a ratio of 1:1 to that of 3:1. Bohlen et al. (2008) attributed the male-biased SR in *Sabanejewia balcanica* to the harsh thermal regimes in the hot springs the fish inhabited. Temperature treatments of *Oreochromis niloticus* at 36 °C increased the ratio of males-to-females from 33 to 81% (Baroiller et al. 1995). As a critique of our study and the methodology applied, it should be pointed out that because of the existing sexual size difference between the fish, where male fish were larger than female ones, possibility of more male fish being caught during seining compared to female ones and also more female fish being sucked up and pumped from the Fish Spring Lagoon A to the Cement Water Holding Tanks cannot be totally ruled out.

Diaz and Rosenberg (1995) defined hypoxia as dissolved oxygen (DO) levels between 0 mg.L⁻¹ (anoxia) and 2.8 mg of O₂ L⁻¹. Hypoxic waters are extreme environments (Wourms and Lombardi 1992; Goodwin et al. 2002). Along with directly killing fish, hypoxia impairs and/or alters reproduction, growth and behaviour (Wu 2002, 2009, 2010; Reardon 2009; Thomas and Rahman 2009a, b; Cheek et al. 2009). Under natural conditions (Thomas et al. 2007; Landry et al. 2007; Thomas and Rahman 2011) and laboratory ones (Shang and Wu 2004; Richmond et al. 2006; Shang et al. 2006), hypoxia determines sex development and differentiation, producing more male- than female fish (Wu 2002; Wu et al. 2003; Thomas et al. 2006; Thomas and Rahman 2011). Under normoxic condition, 61% of zebra fish

(*Danio rerio*) spawned into males while under hypoxic conditions, the number of male fish increased to 74.4% (Shang et al. 2006; Cheek et al. 2009). For the Atlantic croaker, *Micropogonias undulatus*, a male-biased SR comprising as many as 63% males developed in hypoxic sites (Thomas and Rahman 2009a, b). At the Fish Spring Lagoon A of Lake Magadi, dramatic fluctuation of the PO₂ occurs, with extreme hypoxia existing during the night [when photosynthesis by the cyanobacteria (blue-green algae) has ceased and respiration by living matter continued] and hyperoxia happens especially during sunny days when photosynthesis is greatest (Narahara et al. 1996; Johannsson et al. 2014). It should be pointed out that hyperoxia in water only occurs during sunny days and that during dull days, the fish may experience different levels of hypoxia. Although similar data are lacking on the other locations from which fish were sampled for this study, similar changes may occur there. At night, *A. grahami* strives to obtain oxygen from water while during the day it has to resist the injurious effects of the reactive oxygen species (ROS) in water (Johannsson et al. 2014). The high levels of ROS in water, where maximum daytime values range from 2.53 to 8.10 µM H₂O₂, may instead of hypoxia (as commonly assumed) elicit air-breathing in *A. grahami* (Johannsson et al. 2014). The fish skim the well-oxygenated top layer of water ventilating the gills and gulp air into the mouth and then force it into a well-vascularized physostomatous swimbladder where gas exchange occurs (Maina et al. 1996). Here, in *A. grahami*, correlative analysis showed that CF and SR are affected in different ways by the PO₂ in water. In fish, air-breathing is a costly and risky behaviour (Kramer 1987): crucial activities like feeding and mating as well as social interactions have to be temporarily halted. It is probably for this reason that among the 25,000 extant species of fish, only ~400 species, i.e., 16%, air-breathe (Graham 1997; Chapman and McKenzie 2009). *A. grahami* imperils itself to predation, especially from piscivorous birds, when breathing air, especially during the day.

Concluding remarks

The population of *A. grahami* at Lake Magadi is small and declining (Bayona and Akinyi 2006). The challenges that the fish is currently facing from environmental perturbations and those it is likely to contend with in the future such a global warming (Lebreton 2011) are broadly discussed by Kavembe (2015), Kavembe et al. (2016a, b), Oduor and Kotut (2016),

Schagerl and Burian (2016) and Harper et al. (2016). Dismissed to be of no commercial- or food value since it is deemed to be too small and salty to eat, *A. grahami* is an important part of the Lake Magadi food chain. Directly and indirectly, it supports many other organisms and animals that populate or visit the Lake. The existence of the lagoons and the sites and by default that of fish in them is perilously dependent on the rate the locations are recharged with water by from the underground aquifer(s) through the geothermal springs. The process moderates the temperature and the alkalinity of the water, making the lagoons and sites hospitable to the fish. To meet the industrial-, irrigation-, drinking- and household needs for water by the increasing local population, boreholes are being sunk in the arid-to-semiarid Lake Magadi region. Extraction of water from the aquifer(s) which are situated under or close to Lake Magadi will reduce the renewal of the water in the areas inhabited by the fish. It will lead to inordinate increase in temperature, pH and alkalinity, conceivably making the lagoons and sites inhospitable. Permanent settlement near the Lake should be stopped or carefully regulated. Of late, new and more urgent threats to the survival of *A. grahami* have arisen. One of them is that believing that the hot and soapy water in the Lake Magadi lagoons may confer good health and even have curative effects on some skin diseases and afflictions (www.nation.co.ke/news/Lake-Elementaita-vast-ecosystem-threatened-pollution/1056-5172460-n1kplvz/index.html - accessed 28-06-2019), human traffic to the lagoons, especially to the relatively hotter and more isolated (private) shallow South Western Lagoons, has greatly increased. Microbial agents and even parasites that are foreign to the fish as well as heavy metals such as silver and mercury, that are contained in the oils and ointments commonly applied on the human body, are being introduced into a very delicate ecosystem as visitors sit in the lagoons for hours. Human activities at the lagoons should be stopped or very closely monitored and regulated. They will have short- and long-term injurious effects on the fish. Very recently, a more urgent and certain threat to Lake Magadi in general and *A. grahami* in particular has arisen. Massive ecological degradation from human activities, mainly from cutting tree for agriculture and infrastructural development (e.g. road construction) in the upper- and the lower catchment area of the Lake Magadi basin, has caused massive soil erosion (<https://spaceforgiants.org/2018/08/02/siltation-chokes-life-out-of-lake-magadi/> - accessed on 21-08-2019):

~8000 t of soil are being dumped into the Lake Magadi basin during every rain storm. The fish are literally being buried alive! Consideration the enormity of the crisis at Lake Magadi, albeit the now well-known ecological risks of introducing new species into a new habitat where it might become an invasive species [the ecological disaster from the introduction of the Nile perch (*Lates niloticus*) into Lake Victoria of East Africa to improve the fishery industry in the 1950's and 1960's that resulted in displacement and extermination of many indigenous species (Barel et al. 1985; Ogutu-Ohwayo 1990; Marshall 2018) is a good example], it seems like there are few possibilities of saving *A. grahami*. Translocation of the fish to the nearest lakes and dams without indigenous fish are options worthy considering. Previously, specimens of *A. grahami* were moved to the neighbouring Lake Nakuru (Vareschi 1979) and probably to Lake Elementaita (Okeyo 2006) but the success or failure of the initiative and the impact it might have had on the indigenous animal life, if any, were unfortunately not evaluated. We suggest that *A. grahami*, a unique animal that inhabits an extreme habitat, could be marketed as part of the 'wildlife diversity campaign' of Kenya, a country world-famous for its diversity of animal life. Funds raised from tourism could be used in the conservation of the fish. The situation at Lake Magadi is, however, not hopeless. *A. grahami* has been placed on the Red List Category and Criteria of the International Union for Conservation of Nature (IUCN) and listed as a threatened species (Bayona and Akinyi 2006) while the East African Salt Lakes have been conferred a World Heritage site status and protected by the Ramsar Convention (<https://www.ramsar.org/sites/default/files/documents/library/manual6-2013-e.pdf> - accessed on March 13, 2019). Although these steps might have come too late for *A. grahami*, the initiatives are critical steps of protecting the rare Great Rift Valley fauna and flora. As pointed out by Marton-Lefèvre (2006), 'human intervention is crucial to resolving the global problem of loss of biodiversity which is important not only to ensure the survival of endangered species but also that of humankind itself'.

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