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Critically Small Contemporaneous Effective Population Sizes for Stocks of the African Bonytongue in West Africa

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Abstract: Inland capture fisheries play a critical role in supporting food security and livelihoods in West Africa. Therefore, it is important to evaluate genetic health of exploited fish populations. The African bonytongue, *Heterotis niloticus*, supports important commercial and subsistence fisheries in West Africa. Sharp declines of stocks have been reported, however. Herein, we estimate contemporary effective population sizes (*Ne*) of four *Heterotis* populations in Nigeria, three in Benin, and five in Cameroon using the Linkage Disequilibrium method with correction for age structure. *Ne* estimates were used to assess genetic short-term (i.e., inbreeding depression) and long-term (i.e., loss of evolutionary potential) risks. Analyses failed to obtain *Ne* point estimates for two populations. For the remaining ten populations, corrected *Ne* point estimates fell well below 500, the minimum recommended for populations to retain evolutionary potential; with eight populations below 100 (range 2.8–83.5), the minimum recommended to avoid inbreeding depression, one borderline (100–125), and one above this threshold (312–392). The lower 95% confidence interval bound of *Ne* for eleven populations was very small (0.7–14.6), and for the remaining population it was 44.2. Accordingly, all populations examined can be considered potentially at risk of inbreeding depression.

Keywords: effective population size; inland capture fisheries; West Africa; Heterotis

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Introduction

Inland capture fisheries in Africa comprise 28% of the global total (FAO, 2022) and provide a critical source of protein, micronutrients and income for people in Africa (Béné and Heck, 2005; De Graaf and Garibaldi, 2015; Funge-Smith, 2018; Funge-Smith and Bennett, 2019). Sustainability of these fisheries will be crucial for the food security of the rapidly growing human population of sub-Saharan Africa, which is projected to double by 2050 (United Nations-Department of Economic and Social Affairs-Population Division, 2019). Multiple threats, however, are imperiling native freshwater fish stocks in Africa, including overexploitation, habitat degradation, introduction of exotic species, and aquaculture (Abban, 1999; Lind et al., 2012; Marshall, 2016; Olaosebikan and Bankole, 2005). Therefore, it is important to conduct research that informs the sustainable use of these resources. Estimation of effective population size (*Ne*) is critically important for conservation and management of freshwater fish stocks. Overfishing, habitat destruction, and other threats can reduce *Ne* of fish stocks to levels that jeopardize population viability in the long-term and, in severe cases, short-term (Frankham et al., 2010).

Ne translates a population's census size into the size of hypothetical idealized population (i.e., one that fulfills several unrealistic assumptions including random mating) exhibiting the same rate of loss of genetic diversity as the real population under study (Husemann et al., 2016). *Ne* estimates the strength of genetic drift in a population, and thus, reflects the rate at which variation is lost from a population. Accordingly, *Ne* is used to predict the evolutionary potential of populations, or their ability to adapt to environmental change (Allendorf et al., 2012). The "50/500 rule" of Franklin (1980) proposes that a $Ne \geq 50$ for a single isolated population is required for short-term persistence, because it minimizes risk of deleterious effects from inbreeding depression (i.e., loss of fitness due to inbreeding). At $Ne < 50$, an isolated population can enter an "extinction vortex" (Gilpin and Soulé, 1986). $Ne \geq 500$ is needed for healthy evolutionary potential and long-term persistence (Allendorf et al., 2012). More recent work revised these numbers upward ($Ne \geq 100$ to avoid short-term collapse; $Ne \geq 5000$ to retain evolutionary potential) (Frankham et al., 2002; Frankham et al., 2014; Jamieson and Allendorf, 2012; Pérez-Pereira et al., 2022).

Inland capture fisheries are important in West Africa. Nigeria, the most populous (~225 million) country in Africa, ranked 9th in the world in 2020 for inland fisheries yield, accounting for ~11% of the total production in Africa. Nigeria is one of the seven countries that are driving most of the growth in global inland fisheries (Funge-Smith, 2018). This country is also one of nine countries that collectively will contribute more than half the projected growth of the global human population between 2019 and 2050 (United Nations-Department of Economic and Social Affairs-Population Division, 2019), and Nigeria could be one of the world's largest consumers of fish by that year (Chan et al., 2019). Inland fisheries have also been historically very important in neighboring Benin, a country with a much smaller population (13.7 million). In the period 1960–2013, the inland fishery sector of Benin produced an average 27,000 tons annually, employing 57,500 fishers and 40,000 women active in fish processing and marketing (Sonneveld et al., 2019). In 2001, Benin ranked 15th in the world in inland capture fisheries production per capita, and 17th in inland capture fisheries production per unit area (FAO, 2003).

The African bonytongue, *Heterotis niloticus* (Cuvier, 1829), supports important commercial and subsistence fisheries in West Africa. Nigeria leads wild captures of this fish (Table 1) (FAO, 2021), totaling 409,784 metric tons between 1990 and 2021 (85.3% of the total caught in Africa during that period), of which 23,875 metric tons were caught in 2021 (86% of the total caught in Africa that year). Benin has ranked second for *Heterotis* yields, with 21,640 metric tons captured between 1987 and 2021 (5% of the total caught in Africa during that period), including 1,095 tons in 2021 (Table 1). In Cameroon, this fish naturally occurs in the Sudano-Sahelian zone (Far North and North regions), and has been introduced from there to other regions in the country (i.e., Centre, South, and Littoral), where it supports subsistence fishery (Brummett et al., 2010; Moreau, 1982). Although FAO does not have capture statistics for *H. niloticus* in Cameroon, it is an important capture species in the Nyong River (Centre region), where it was introduced in 1958 (Depierre and Vivien, 1977), with reports of 60 tons landed near Ayos in 1976 (Depierre and Vivien, 1977), approximately 616 tons/year prior to 1984 in Akonolinga, and ~240 tons/year in the 2004-2005 season in the middle Nyong River (reviewed in Brummett et al., 2010). Overexploitation and declines of *Heterotis* stocks have been reported for Nigeria (Mustapha, 2010), Benin (Adite et al., 2006), and other West African countries (Laë, 1995).

Table 1. Inland waters capture production in Africa, Nigeria and Benin of live weight.

	Production (average per year)				*** Yearly Production ***					
Region	**1980s**	**1990s**	**2000s**	**2010s**	**2017**	**2018**	**2019**	**2020**	**2021**	**Percentage of world's total for 2020**
Africa – inland	1.47M	1.89M	2.33M	2.87M	3.01M	3.02M	3.24M	3.21M	3.49M	28
Africa - Heterotis		5,961	12,653	23,876	31,815	29,257	28,649	27,818	27,777	
Nigeria – inland	100,513	104,173	210,970	350,175	420,078	392,188	373,344	354378	362,792	3
% of Africa	(6.8%)	(5.3%)	(9.01%)	(12.2%)	(14.0%)	(12.9%)	(11.4%)	(10.9%)	(10.4%)	(9th globally)
Nigeria –Heterotis		4,770	10,877	20,606	27,896	25,689	24,626	23,375	23,875	
% of Africa		(80.0%)	(86.0%)	(86.3%)	(87.7%)	(87.8%)	(86.0%)	(84.0%)	(86.0%)	
Benin - inland	31,823	31,830	28,664	28,969	33,415	28,900	28,775	28,815	29,000	
Benin - Heterotis	421	565	564	791	853	1398	925	1,085	1,095	

M = million tonnes of live weight.

Genetically differentiated populations of the African bonytongue, suggested to represent different conservation/management units, have been identified in Benin, Nigeria, and Cameroon (localities shown in Fig. 1). In Benin, large genetic differences were detected among: (1) a population from Malanville, Niger River, in the north; (2) a population from Mono River in the southeast; and (3) a population in the Oueme-Sô river floodplain system in the southwest (Hurtado et al., 2013). In Nigeria, large genetic differences were detected between fish from Kainji Lake, in the north, and fish from three southern locations (i.e., Epe Lagoon, Igbokoda River, and Ethiope River) (Oladimeji et al., 2022). Lower, yet significant, F_{ST} values (i.e., a measure of genetic differentiation among populations) were observed among the southern Nigerian samples (Oladimeji et al., 2022), and all populations examined to date face multiple threats (Oladimeji et al., 2022). In Cameroon, significant genetic differentiation is detected among five populations of *Heterotis*, including two native (one in Logone River, in the Far-North region, and one in Benoue River, in the North region), and three introduced (Nyong River, in the Centre region; Dja and Lobo Rivers, in the South region, and Nkam River, in the Littoral region), using the dataset of Wikondi et al. (2023). Herein, we estimate *Ne* for populations of *Heterotis* in Nigeria, Benin, and Cameroon, to assess genetic indicators of risks of inbreeding depression and loss of evolutionary potential.

Methods

We used published genotypic data (Hurtado et al., 2013; Oladimeji et al., 2022; Wikondi et al., 2023) for *Heterotis* populations in West Africa (Figure 1), including three localities in Benin (Niger River at Malanville, Mono River; and Oueme-Sô river floodplain system), four in Nigeria (Kainji Lake, Epe Lagoon, Igbokoda River and Ethiope River), and five in Cameroon (Logone River, Far-North; Benoue River, North region; Nyong River, Centre region; Dja and Lobo Rivers, South region; and Nkam River, Littoral region). For Cameroon, we first assessed genetic differentiation among the five populations using the software GenAlEx v. 6.51b2n (Peakall and Smouse, 2012), and found significant differences in all pairwise comparisons (Supplementary material, Table SM1). Contemporary *Ne* was estimated for all populations using the LDNe method (Waples and Do, 2008), as implemented in the program NeEstimator (Do et al., 2014). This method estimates *Ne* based on patterns of linkage disequilibrium between loci, and was shown to perform well relative to other methods when calculating *Ne* under scenarios of low *Ne* and low migration rates (Gilbert and Whitlock, 2015). *Ne* values were calculated assuming random mating and using the following alternate settings: minimum allele frequency (MAF) cutoff values of 0.05, 0.02, 0.01, 0+ (i.e., no alleles excluded), and excluding singleton alleles. Confidence intervals for *Ne* values were estimated using the parametric and jackknife methods (Waples and Do, 2008) implemented in NeEstimator. Because *Ne* estimates can be biased by age structure, we used the “two traits” formulas provided in Table 3 of Waples et al. (2014) to adjust our “raw *Ne*” estimates by incorporating information on the following two life history traits: age at maturity (α) and adult life span (AL); where $AL = \omega - \alpha + 1$; being ω maximum age. Moreau (1982) indicates maturity in this fish occurs at about 2 years, and the maximum age is between 5 and 10 years. Accordingly, we used $\alpha = 2$, with $\omega = 10$ and 5; which resulted in AL values of 9 and 4.

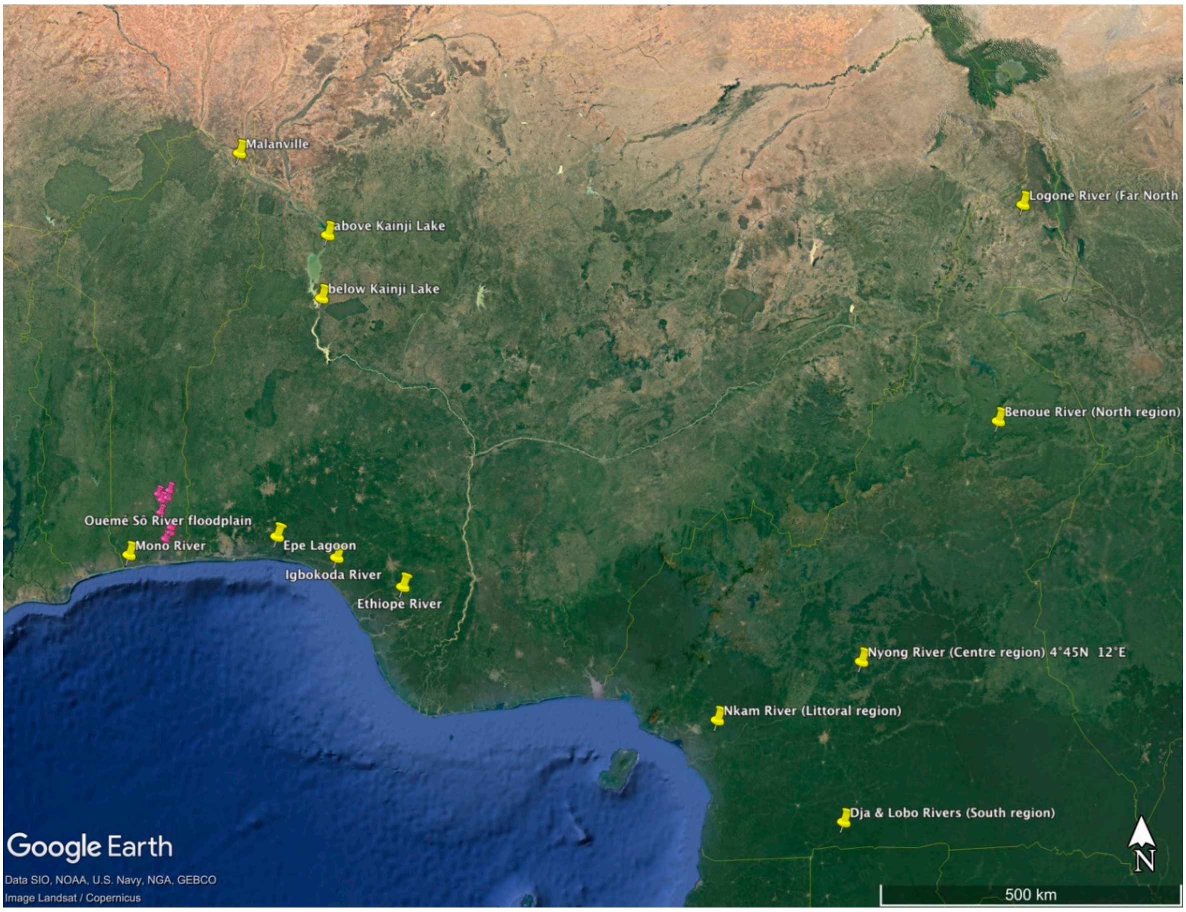

Figure 1. Map of the study area depicting sampled localities in Benin, Nigeria, and Cameroon. Collectively, the pink pins represent the Ouemé-Sô river floodplain system.

Table 3. Pairwise genetic differentiation for Cameroon populations of *Heterotis niloticus.*

Comparison		Genetic differentiation test					
Pop1	**Pop2**	**Fst**	**Gst**	**G'st(Nei)**	**G'st(Hed)**	**G''st**	**Dest**
Centre	South	0.041	0.024	0.047	0.079	0.101	0.057
Centre	Littoral	0.035	0.023	0.045	0.082	0.103	0.061
South	Littoral	0.049	0.031	0.060	0.097	0.124	0.068
Centre	North	0.047	0.035	0.068	0.162	0.191	0.132
South	North	0.083	0.066	0.124	0.264	0.309	0.212
Littoral	North	0.051	0.039	0.075	0.169	0.200	0.136
Centre	Far-North	0.088	0.076	0.142	0.320	0.368	0.264
South	Far-North	0.129	0.111	0.201	0.410	0.469	0.336
Littoral	Far-North	0.072	0.060	0.113	0.239	0.282	0.190
North	Far-North	0.059	0.046	0.089	0.244	0.278	0.207

P-values for Fst, Gst, G'st(Nei), G''st, Dest: p = 0.011 for Centre vs South comparisons; p = 0.001 for all other comparisons P-values for G'st(Hed): p = 0.002 for all comparisons.

Results

In Table 2 we report *Ne* estimates for populations in Nigeria, Benin, and Cameroon under three different assumptions: minimum allele frequency (MAF) = 0.05; MAF = 0.02; and excluding singleton alleles. As explained below, we chose MAF = 0.05 as the best cutoff value for our data, based on our interpretation of the results that appear to indicate that estimates for MAF ≤ 0.02 are driven by the presence of rare alleles. First, except for Kainji Lake, Ouemé-Sô river floodplain, and Benoue River, all *Ne* point estimations using MAF = 0.05 were identical to those that excluded singleton alleles. In the case of Kainji Lake and Benoue river, *Ne* point estimates using MAF = 0.05 (23.7 and 48.7, respectively) were very close to *Ne* point estimates excluding singleton alleles (27.7 and 56.2, respectively). Second, except for the Ouemé-Sô river floodplain population, all results for MAF = 0.01 and MAF = 0+ were identical to those obtained with MAF = 0.02. Third, the *Ne* point estimate for Kainji Lake based on MAF = 0.02 was approximately twice as large as the one based on MAF = 0.05. A similar pattern was observed in the Ouemé-Sô river floodplain, where the *Ne* point estimate based on MAF = 0.05 (92.1) was substantially lower than those based on MAF = 0.02, MAF = 0.01, MAF = 0+ and excluding singleton alleles (i.e., 179.5, 197.3 and 238.7, and 266.1, respectively).

Table 2. Effective population size (*Ne*) point estimates and 95% Confidence Intervals (CI) under three assumptions of allele frequencies: Minimum Allele Frequency (MAF) = 0.05; MAF =0.02; and no singletons. *Ne* point estimates corrected for age structure, under adult life span (AL) values of 9–4 (see text), are provided in parenthesis.

Population	**Raw N_e (Corrected N_e assuming AL = 9–4)** **95% CI Parametric of raw *Ne*** **95% CI Jackknife of raw *Ne***		
	MAF = 0.05	no singletons	MAF = 0.02
Nigeria Populations:			
Kainji Lake	23.7(25.6–32.3)	27.7(30.0–37.7)	44.3*(47.9–60.4)
	14.2–48.9	18.1–49.3	27.6–93.0
	9.3–278.0	11.6–281.0	20.9–333.7
Epe Lagoon	23.1(25.0–31.5)		18.1*(19.6–24.7)
	11.3–84.4		10.5–38.8
	8.4–∞		7.2–116.6
Igbokoda¹	∞	∞	∞*
	21.5–∞	21.5–∞	242.0–∞
	14.9– ∞	14.9– ∞	62.3–∞
Igbokoda²	288.0(311.6–392.3)		∞*
	18.5–∞		4703.4–∞
	11.6–∞		180–∞
Ethiope River	42.2(45.7–57.5)		56.5*(61.1–77.0)
	15.6– ∞		19.6– ∞
	8.2– ∞		13.7– ∞
Benin Populations:			
Ouemé–Sô River fldp.	92.1(99.7–125.5)	266.1(287.9–362.5)	179.5(194.2–244.5)
	69.5–125.8	196.5–390.4	131.3–262.9
	44.2–250.1	137.8–947.8	78.9–1031.0
Mono River	22.9(24.8–31.2)		28.7*(31.1–39.1)
	9.2–904.8		12.4–662.8
	9.1–2310.1		9.8–∞
Malanville	27.0(29.2–36.8)		25.5*(27.6–34.7)
	3.0–∞		4.7–∞
	2.1–∞		10.0–∞
Cameroon Populations:			
Benoue River (North)	48.0(51.9–65.4)	56.2(60.8–76.6)	63.7*(68.9–86.8)
	19.1–∞	21.6–∞	24.4–∞
	14.6–∞	17.3–∞	23.0–∞
Logone Riv. (Far-North)	61.3(66.3–83.5)		103.2*(111.7–140.6)
	17.1–∞		22.7–∞
	11.1–∞		17.5–∞
Nkam River (Littoral)	∞	∞	∞*

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	36.3–∞	82.9–∞	32.1–∞
	11.3– ∞	24.4– ∞	31.1–∞
Dja & Lobo Riv. (South)	2.6(2.8–3.5)		2.6*(2.8–3.5)
	1.2–18.3		1.4–11.9
	0.7–∞		1.3–14.7
Nyong River (Centre)	∞		∞*
	23.1– ∞		26.5– ∞
	12.6– ∞		15.7– ∞

* Results using MAF = 0.01 and 0+ were identical; [1] including all loci; [2] removing monomorphic locus *H45*.

After correcting for age structure, *Ne* point estimates using MAF = 0.05 ranged 25–37 for Kainji Lake, Epe Lagoon, Malanville, and Mono River; 45.7–57.5 for Ethiope River; 51.9–65.4 for Benoue River; 66.3–83.5 for Logone River; and 99.7–125.5 for Ouemé-Sô river floodplain. *Ne* point estimation for Igbokoda was inconclusive (infinite; see below) using all loci. However, when removing locus *Hn45*, which was monomorphic in southern Nigeria populations, corrected estimates ranged 311.6–392.3. For the other southern Nigeria populations, *Ne* estimations were identical including all loci and removing locus *Hn45* (not shown). The *Ne* point estimate for the introduced population of Dja and Lobo rivers was 2.8–3.5, and the analysis failed to estimate *Ne* for the other two introduced populations (Nyong River and Nkam River). The lower bound of the 95% CI for all populations, with the exception of Ouemé-Sô river floodplain, ranged between 0.7 and 14.6 using the jackknife method, which is less biased (Waples and Do, 2008); suggesting the *Ne* of these populations can be very small. The lower bound of the 95%CI jackknife for Ouemé-Sô river floodplain was 44.2. Upper 95% CI bounds for some populations were determined as infinite. When estimates of *Ne* are negative, which is caused by sampling error, the program reports them as infinite (Do et al., 2014).

Discussion

Ne point estimates of all *H. niloticus* populations examined herein (Table 2) fall well below the minimum recommended for populations to retain evolutionary potential [original criterion *Ne* ≥ 500, recently revised to *Ne* ≥ 1000; (Frankham et al., 2014)]. Furthermore, all populations of *H. niloticus* examined can be considered potentially at risk of inbreeding depression. All corrected *Ne* point estimations for Kainji Lake, Epe Lagoon, Malanville, and Mono River populations (range = 25–37) were below the original benchmark of *Ne* ≥ 50 recommended for avoiding the potential deleterious effects of inbreeding depression; whereas corrected *Ne* point estimates for Ethiope River, Benoue River, and Logone River (range = 46–83.5) were below the benchmark of *Ne* ≥ 100. According to Frankham et al. (2014), an *Ne* = 50 is inadequate for preventing inbreeding depression over five generations in the wild, with *Ne* ≥ 100 being required to limit loss in total fitness to ≤ 10%. In addition, the lower 95% CI (jackknife) bound for all populations examined, except Ouemé-Sô river floodplain, indicates that the *Ne* of these populations may be very small (range 0.7–14.6). Corrected *Ne* values for Ouemé-Sô river floodplain were at the 100 threshold (using AL = 9), or slightly higher (125.5 for AL = 4); and the lower 95% CI (jackknife) bound (44.2) indicates *Ne* of this population may be below the 50 threshold.

The *Ne* point estimate of the introduced Dja and Lobo rivers population was the smallest (2.8–3.5). Although *Ne* point estimates of the other two introduced populations were inconclusive, their lower 95% CI values indicate they also can be very small (11.3 and 12.6 for Nkam River and Nyong River, respectively). Low *Ne* estimates of introduced populations are probably related to bottlenecks experienced during introductions. According to Depierre and Vivien (1977), *Heterotis* was introduced from northern Cameroon populations to a fish farming station in Melen, a suburb of Yaounde, in 1955, and from there ~20 fries were released into the Nyong River in 1958. Subsequently, in 1961, an accidental spill from a fishpond released several hundred fries into the Nyong River. These authors also indicate that *Heterotis* appeared in the Lower Sanaga River (Littoral region) around 1968, probably from the lower course of the Nyong, as the two rivers are connected in the mouth of the Sanaga through mangrove channels during periods of high water. It is possible that from the Sanaga, *Heterotis* colonized other rivers in the Littoral region, such as the Nkam; and that the Dja and Lobo rivers were also colonized by individuals related to the Nyong population. Indeed, STRUCTURE analyses of the five Cameroon populations found two main clusters, one corresponding to the native populations and the other to the introduced populations; suggesting a common origin for the introduced populations (Wikondi et al., 2023).

The cutoff value of MAF = 0.05 has been recommended in simulation analyses to ensure *Ne* estimations are not being driven by the presence of rare alleles (Gilbert and Whitlock, 2015; Hamilton et al., 2018; Waples and Do, 2010). Nonetheless, if MAF ≤ 0.02 were deemed more appropriate for our data, most of the corrected *Ne* point estimates would still fall below the critical thresholds (Table 2). All corrected *Ne* values, assuming MAF ≤ 0.02, were below 50 for Epe Lagoon, Mono River, and Malanville (range = 19.6–39.1), and below 100 for Kainji Lake (range = 47.9–60.4), Ethiope River (range = 61.1–77), and Benoue River (range = 60.8–76.6). Furthermore, the lower 95% CI bounds for the above populations, as well as Logone River and the introduced populations (range 1.3–31), indicate these stocks may be very small. We also note that the Benin samples used to estimate *Ne* were collected between 2008 and 2009, and the ones from Nigeria were collected in 2018. Thus, it is possible that current *Ne* of populations are even smaller than estimated, especially values for Benin stocks that were estimated with samples collected more than a decade ago, and considering that factors responsible for reducing *Ne* (e.g., overfishing and habitat destruction) have likely continued operating or increased in intensity.

According to Waples and Do (2010) precise estimates for relatively small (*Ne* < 200) isolated populations can be obtained with the LD method; and small populations are not likely to be mistaken for large ones. Gilbert and Whitlock (2015) used simulations to compare the performance of seven methods to estimate *Ne* under different scenarios of migration with three different *Ne* values (50, 500 and 5000), and found that the LD method implemented in NeEstimator v2.0 outperformed the other methods in conditions of isolation for *Ne* = 50 and 500. This method also performed well in scenarios of low migration and small *Ne*. Accordingly, because the *Heterotis* populations studied herein exhibit genetic differentiation consistent with isolation (Hurtado et al., 2013; Oladimeji et al., 2022), the small *Ne* estimations we obtained are likely reflective of the true *Ne*.

We used reported information on age of maturity and maximum age that allowed for bias corrections of our estimations due to overlapping generations. There was, however, not a single value for the maximum age in this fish, and for this reason we conservatively used the two extremes of the reported maximum age (ω) values (10 and 5), which resulted in AL values 9 and 4. Corrected N_e were larger than raw N_e estimates, and those using AL = 9 resulted in the lower values that were more similar to raw values than those using AL = 4. Considering reports of aquarium-housed fish living between 10–20+ years (e.g., Fish Laboratory, 2021), AL = 9 may represent our best approximation. *Ne* estimates assuming AL > 9 would be smaller and closer to the raw estimates. Similarly, we used age at maturity (α) = 2, however α = 1 has been reported for fish in aquaculture (Wikondi et al., 2023). Because correction formulas employ the ratio AL/α, designation of α = 1 would result also in smaller corrected *Ne* estimates (i.e., closer to the raw estimates) than those using α = 2. We note that in the case of the smaller raw point estimations (all, except for Ouemé-Sô river floodplain system and Igbokoda populations), the differences between raw and corrected estimations were small (2–15) with either AL value. That difference was also small using AL = 9 for the Ouemé-Sô river floodplain (8 individuals), Benoue (5 individuals), and Logone (5 individuals); with Igbokoda exhibiting the largest difference (24 individuals).

Ne estimations of *Heterotis* populations in West Africa are much lower than those reported for the region's wild populations of Nile tilapia (*Oreochromis niloticus*), an important species supporting capture fisheries and aquaculture production (Lind et al., 2019). Over 50 % of Nile tilapia samples from 23 localities across West Africa, including eight countries representing the major catchments of the Volta, Niger, Senegal, and Gambia River basins, had *Ne* in excess of 100 and none below 50. Nonetheless, all populations of Nile tilapia were below the threshold for long-term genetic risks (range: 56–352 individuals), whereas ten (43.5%) were below the revised threshold of 100 for short-term genetic risk; and 14 (60.9%) had lower 95% CI bounds below 100 (the lowest was 30.3). The *Ne* point estimate for Nile tilapia at Malanville was ~10 times larger (*Ne* = 236), than that for *Heterotis* from the same location (*Ne* = 23). Nile tilapia at Malanville might be part of a more widely distributed metapopulation, whereas *Heterotis* at this locality might correspond to a more isolated population. Nile tilapia from Malanville and Mopti (Mali), another locality in the Niger River separated by ~1,400 km, show high genetic similarity, suggesting high levels of gene flow. Nile tilapia *Ne* estimated at Mopti is very similar (*Ne* = 289) to that in Malanville; thus, it is possible that such *Ne* estimates reflect the *Ne* of a broader metapopulation. According to Waples and England (2011), "LD estimates of *Ne* accurately reflect local (subpopulation) *Ne* unless $m \geq 5$–10%. With higher *m*, *Ne* converges on the global (metapopulation) *Ne*". For *Heterotis*, high genetic differentiation appears to occur at comparatively shorter distances within the Niger River, i.e., between Malanville and Kainji Lake (~230 km), and between Kainji Lake and the lower Niger portion (~700 km).

We note that heterozygosity and allelic diversity are poor predictors of short- and long-term genetic risks, underscoring the importance of *Ne* estimations. Heterozygosity in Kainji Lake was highest among all populations (*uHe* = 0.72), with second highest allelic diversity (Na = 8.33), yet *Ne* was only 24. Similarly, for Nile tilapia, the locality with the highest estimated *Ne* had comparatively low heterozygosity and allelic diversity among Nile tilapia populations examined. Severe declines in *Ne* can occur without significant loss of genetic diversity (Lonsinger et al., 2018).

Implications for Conservation and Management

Overfishing and habitat destruction likely pose the greatest threat for *Heterotis* stocks in Benin and Nigeria. This species is highly sought because of its high protein content and firm flesh (Agbugui et al., 2021). Overfishing has been documented in Kainji Lake (Abiodun, 2002; Yem et al., 2007), Malanville (Hauber et al., 2011), Ouémé–So river-floodplain system (Allan et al., 2005), Mono River (Lederoun et al., 2018), and Epe Lagoon (Olukolajo and Hillary, 2012). Illegal fishing activities exacerbate this problem. In Kainji Lake, illegal practices include the use of prohibited gear (e.g., small mesh size nets and destructive fishing gear), fish poisoning, and explosives (Mshelia et al., 2005). In the Ouémé–So river-floodplain system, fish traps are placed near active *Heterotis* nests to capture brooding adults (Adite et al., 2006). Pollution also impacts *Heterotis* stocks in some regions (Akinsanya et al., 2020a; Akinsanya et al., 2020b; Arojojoye et al., 2021; Ikomi and Arimoro, 2014).

Our results indicate that *Ne* values for populations of *Heterotis niloticus* in Nigeria, Benin, and Cameroon are below the recommended thresholds to avoid short- and long-term genetic risks. Indeed, high inbreeding (F_{IS}) was suggested previously for four of the local stocks (Hurtado et al., 2013; Oladimeji et al., 2022): Igbokoda (F_{IS} = 0.18; the highest inbreeding among Nigerian populations); Malanville (F_{IS} = 0.20); Mono River (F_{IS} = 0.13); and Ouemé-Sô river floodplain (F_{IS} = 0.13). Our *Ne* estimates are comparable to those of endangered species (Frankham et al., 2010; Palstra and Ruzzante, 2008). For example, *Ne*, heterozygosity, and F_{IS} values estimated for populations of an endangered snake (Sovic et al., 2019) were similar to estimates for West African *Heterotis*. Small *Ne* estimates of genetically differentiated *Heterotis* populations indicate that conservation and management actions are urgently needed, with special consideration of risks associated with inbreeding depression (but see Wood et al., 2016).

Heterotis niloticus is currently listed as a species of *Least Concern* by the International Union for Conservation of Nature (IUCN) (Diouf et al., 2020). It is important that future assessments of this species consider: (1) that this species is comprised of multiple genetically differentiated populations with small ranges relative to the species' global distribution, many of which face multiple threats (i.e., overexploitation, habitat destruction, pollution); (2) populations examined to date reveal *Ne* estimates below the critical long-term threshold of 500 for retaining evolutionary potential, and most are below the critical short-term threshold of 50 and 100 for preventing inbreeding depression; and (3) all *Ne* estimations had lower 95% CI values, suggesting *Ne* of these wild populations may be very small, thus highly vulnerable to inbreeding depression.

Growth of isolated populations may allow their *Ne* to increase (Kamath et al., 2015), and fishing restrictions may be required to allow stocks to recover (Pita et al., 2017). Gene flow between populations may also boost *Ne* (Frankham, 2022); however, given that stocks are genetically differentiated, gene flow could result in outbreeding depression (Allendorf et al., 2012). Translocation of stocks erodes distinct population genetic structures, which runs counter to a goal of the Convention on Biological Diversity's post-2020 global biodiversity framework (Hoban et al., 2023). Future research should examine genetic diversity of other *Heterotis* populations in West Africa as well as monitor *Ne* of genetically distinct populations. *Heterotis* is just one of several fishes important for subsistence and commercial fisheries in West Africa, and the genetic diversity of other fish species also needs to be investigated.

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