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**ECOLOGICAL KNOWLEDGE OF LOCAL FISHERS, ECONOMIC IMPORTANCE,
MORPHOLOGICAL AND GENETIC VARIATIONS OF *Parachanna obscura* (GUNTHER,
1861) POPULATIONS IN THE CONTEXT OF CLIMATE CHANGE AND
ANTHROPOGENIC PRESSURES IN WEST AFRICA.**

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Public defense on 09th March 2022

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DEDICATION

I firstly dedicate this thesis to the almighty God for his grace in my life. I secondly dedicate this work to my mother, Eba KOUAO, and my late father, Amien AMOUTCHI. Dady, from where you are, know that your advices have guided me in my daily life, and today I am a full-grown man. I also dedicate this thesis to all my family members.

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TABLE OF CONTENTS

DEDICATION.....	i
ACKNOWLEDGEMENTS	ii
LIST OF TABLES	ix
LIST OF FIGURES.....	xi
LIST OF APPENDICES	xiii
LIST OF ABBREVIATIONS	xiv
ABSTRACT.....	xv
RÉSUMÉ	xvi
GENERAL INTRODUCTION.....	1
Background and justification	2
Objectives	6
Research hypothesis	6
CHAPTER I: Literature review	8
I.1 Major threats to freshwater biodiversity	9
I.1.1 Climate change	9
I.1.2 Habitat degradation or loss and flow modification	10
I.1.3 Overexploitation	11
I.1.4 Water pollution	12
I.1.5 Invasion by exotic species	13
I.2 Importance of fishers' local or indigenous ecological knowledge	13
I.3 Morphological variations in fishes	14
I.3.1 Origin and importance of morphological variation as tool for species adaptation	14
I.3.2 Tools for assessing fishes morphological variations	15
I.4 Genetic diversity and species adaptation	17
I.4.1 Definition and importance of genetic diversity	17
I.4.2 Genetic diversity as a potential for species adaptation to changes in environmental conditions	19
I.4.3 Tools for genetic diversity assessment	20
I.4.4 Principal parameters measured in population genetics	21
I.5 Review on <i>Parachanna obscura</i>	26
I.5.1 Description	26
I.5.2 Taxonomy, habitat, ecology and distribution	27
I.5.3 Diet and reproduction	28
CHAPTER II:.....	31

Fishers’ perceptions and experiences toward the impact of climate change and anthropogenic activities on freshwater fish biodiversity in Côte d’Ivoire.....	31
Abstract.....	32
II.1 Introduction.....	32
II.2 Material and methods.....	35
II.2.1 Study area.....	35
II.2.2 Sampling of fishers.....	35
II.2.3 Data collection.....	36
II.2.4 Statistical analysis of the data.....	38
II.3 Results.....	38
II.3.1 Socio-demographic background of respondents.....	38
II.3.2 Livelihood strategies of the fishers.....	39
II.3.3 Fishers’ perception of climate change, its drivers, and its impact on Ivorian freshwater fish abundance.....	39
II.3.4 Fishers’ perception of the Anthropogenic stressors on freshwater fish.....	43
II.3.5 Fish species locally under threat according to the fishers.....	46
II.3.6 Factors influencing fishers’ awareness of climate change and perception of change climate.....	46
II.3.7 Factors determining fishers’ perception of change in fish abundance.....	50
II.4 Discussion.....	52
II.5 Conclusion and perspectives.....	57
CHAPTER III:.....	59
Local fishers’ knowledge on the ecology, economic importance, and threats faced by populations of African snakehead fish, <i>Parachanna obscura</i>, within Côte d’Ivoire freshwater ecosystems.	59
Abstract.....	60
III.1 Introduction.....	61
III.2 Material and methods.....	63
III.2.1 Study area.....	63
III.2.2 Sampling procedure and data collection.....	64
III.2.3 Data analysis.....	67
III.3 Results.....	67
III.3.1 Local names for <i>P. obscura</i>	67
III.3.2 Habitats of <i>P. obscura</i>	68
III.3.3 Use of <i>P. obscura</i>	68
III.3.4 Market price.....	70
III.3.5 Respondents' willingness for introducing <i>P. obscura</i> in Aquaculture.....	70
III.3.6 Threats faced by <i>P. obscura</i> populations within Ivorian’s aquatic ecosystem.....	73

III.4 Discussion.....	77
III.4 Conclusion and recommendations.....	81
CHAPTER IV:.....	83
Morphological variations of <i>Parachanna obscura</i> fish populations along climate and habitat gradients.	83
Abstract.....	84
IV.1 Introduction.....	85
IV.2 Material and methods.....	87
IV.2.1 Field sampling and data collection.....	87
IV.2.2 Morphological data collection.....	88
IV.2.3 Data analysis.....	88
IV.3 Results.....	91
IV.3.1 Morphological variation among <i>P. obscura</i> populations.....	91
IV.3.2 Influence of geographical distance on morphological variations.....	96
IV.3.3 Climatic and habitat characteristics of collection sites of <i>P. obscura</i> populations.....	96
IV.3.4 Correlation between morphological variation and climate and habitat variables.....	99
IV.4 Discussion.....	101
IV.5 Conclusion.....	104
CHAPTER V:.....	105
Population genetics of the African snakehead fish <i>Parachanna obscura</i> along West Africa’s water networks	105
Abstract.....	106
V.1 Introduction.....	107
V.2 Materials and methods.....	109
V.2.1 Study area and collection of samples.....	109
V.2.2 Molecular genetics analyses.....	113
V.2.3 Statistical data analyses.....	114
V.3 Results.....	118
V.3.1 Genetic structure within populations.....	118
V.3.2 Genetic structure between populations.....	121
V.3.3 Detection of loci potentially under selection.....	126
V.4 Discussion.....	129
V.5 conclusion.....	133
GENERAL CONCLUSION, RECOMMENDATIONS AND PERSPECTIVES.....	134
REFERENCES.....	138
APPENDICES.....	1

LIST OF TABLES

Table I. I: Comparison of the properties and technique of the most common molecular markers.....	22
Table I. II: Common metrics of genetic diversity used in evolutionary and ecological studies (Hughes et al., 2008).....	23
Table II. I: Overview of the socio-demographic background of 381 respondents to a questionnaire on the perception of climate change and changes in fish biodiversity and their potential drivers in Côte d'Ivoire. 40	
Table II. II: Livelihood strategies of 381 respondents to a questionnaire on the perception of climate change and change in fish biodiversity and their potential drivers in Côte d'Ivoire.....	41
Table II. III: Monthly income of 381 respondents to a questionnaire on the perception of climate changes and changes in fish biodiversity and their potential drivers, from three Ivorian climatic zones.....	41
Table II. IV: Anthropogenic activities threatening Ivorian freshwater fish biodiversity according to fishers of the watersheds sampled.	45
Table II. V: Fish species locally threatened according to fishers of the sampled watersheds.	47
Table II. VI: Influence of socio-demographic factors on Ivorian fishers' awareness of climate change revealed by multinomial logistic regression.	48
Table II. VII: Influence of socio-demographic factors on Ivorian fishers' perception of climate change revealed by multinomial logistic regression.	49
Table II. VIII: Influence of socio-demographic factors on Ivorian fishers' perception of change in fish abundance revealed by multinomial logistic regression.	51
Table III. I: Fishers' knowledge regarding local names of the snakehead fish <i>P. obscura</i> according to the socio-linguistic and ethnic groups.....	69
Table III. II: Result of z-test comparing proportions of perceptions of fishers about each type of habitat of the snakehead fish among three climate zones.	71
Table III. III: Fishers' perception (N=381) about the market price of the snakehead fish of <i>P. obscura</i>	72
Table III. IV : The result of the significance of Z-tests comparing the proportions of threats faced by the snakehead population <i>P. obscura</i> in Ivorian freshwater ecosystems considering each climatic zone (N=271).	75
Table III. V: Relation between geographic and socio-demographic factors, and fishers' perception about decrease in abundance of the snakehead fish <i>P. obscura</i> , revealed binary logistic regression.....	76
Table IV. I: Sample size, standard length (SL, cm) and weight (g) of seven populations of <i>P. obscura</i> used in the study.....	90
Table IV. II: Mahalanobis distances (lower diagonal) and significance (upper diagonal) of pairwise comparisons by the canonical variate analysis performed between populations of the <i>P. obscura</i>	93
Table IV. III: Loadings of the 14 climate and habitat variables on the first two principal components explaining 76.2% of total variation and with Eigenvalues greater than 1.....	97
Table V. I: Samples sizes, basins, country and climate of locations of 15 samples <i>P. obscura</i> (with total sample size of 259 individuals).....	112
Table V. II: Microsatellite markers developed and used in this study for the population genetic study of <i>P. obscura</i> with details on primer sequences, fluorescent dyes, repeat motifs and expected PCR amplification size.	116
Table V. III: Composition of the PCR mix of the eight multiplex reactions performed for studying the population genetics of <i>P. obscura</i>	117
Table V. IV: Allelic variability across the 21 microsatellites developed and used for this studying the population genetics of <i>P. obscura</i>	119
Table V. V: Genetic diversity of <i>Parachanna obscura</i> fish from 15 sampling locations at 21 microsatellite loci.	119

Table V. VI: P-values of deviations from Hardy-Weinberg equilibrium population after correction by the false discovery rate for multiple tests.	120
Table V. VII: Matrix of pairwise F_{ST} between the 15 <i>P. obscura</i> locations (lower diagonal), and their P-values as obtained by G-tests (upper diagonal).....	122
Table V. VIII: Analysis of molecular variance for 259 <i>Parachanna obscura</i> individuals originating from 15 locations sampled in Côte d'Ivoire and Benin for this study.	122

LIST OF FIGURES

Figure 1. 1: Example of anatomic landmarks used in Geometric morphometric analysis.	18
Figure 1. 2: Illustration of truss network measurements performed from 10 truss landmarks on specimens of fish.....	18
Figure 1. 3: Lateral view of <i>P. obscura</i>	29
Figure 1. 4: Taxonomy range of <i>Parachanna obscura</i>	29
Figure 1. 5: Distribution map of <i>P. obscura</i>	30
Figure 2. 1: Study area map, showing the borders of Côte d’Ivoire, the main climate zones and the locations where surveys were conducted.....	37
Figure 2. 2: Distribution of the 381 Ivorian fishers interviewed according to their perception of the causes and factors of climate change.....	42
Figure 2. 3: 381 Fishers’ responses concerning their perception of (A) change in rainfall, (B) change in rainy season timing and (C) length, (D) change of temperature, and (E) change in flooding occurrence in Côte d’Ivoire.....	44
Figure 3. 1: Map of Côte d’Ivoire, showing the main climate zones and the locations where the study were conducted, and its position in West Africa.....	65
Figure 3. 2: Framework summarising the sampling procedure and data collection	66
Figure 3. 3: Perception of fishers about the types of habitats where <i>P. obscura</i> fish is caught or found according to their climate zone.....	71
Figure 3. 4: Reasons for the consumption of <i>P. obscura</i> by the 377 fishers who consume this fish.	72
Figure 3. 5: Chord diagram showing fishers’ perceptions regarding the threats faced by <i>P. obscura</i> fish populations within Ivorian’s freshwater according to the 271 fishers who reported a decrease in the species populations.	74
Figure 4. 1: Map of the study area, showing locations of populations from which <i>P. obscura</i> specimens were collected, and position of Côte d’Ivoire in West Africa.....	89
Figure 4. 2: Defined landmark points for collection of <i>P. obscura</i> body shape data.....	90
Figure 4. 3: <i>Parachanna obscura</i> shape variations corresponding to wireframe deformation along the first two CVA axes (CV1, CV2).....	94
Figure 4. 4: Scatter plot obtained of first two factors of the canonical variate analysis on 15 geometric morphometrics characters (landmarks).....	95
Figure 4. 5: Estimation of pairwise morphological distances between populations plotted against natural logarithm (ln) of pairwise Euclidean geographical distance (km).....	97

Figure 4. 6: Scatterplot of the projection of the populations, and habitat and climate variables (arrows) on the first two principal components explaining 76.1% of the total variation in climate and habitat variables.	98
Figure 4. 7: Pearson correlation plots between the first two CVA axes (CV1 and CV2), representing morphological variation among populations, and the first two PCA axes (PC1 and PC2), which represent variation in habitat and climate variables between sites.	100
Figure 5. 1: Map of the study area, showing sampling locations from which <i>P. obscura</i> specimens were collected, in Côte d'Ivoire (left) and in Benin republic (right down), and position of these countries in West Africa.	111
Figure 5. 2: Neighbor-joining dendrogram <i>P. obscura</i> fish from 15 sampling locations in Côte d'Ivoire and Benin, based on Prevosti's genetic distance.	123
Figure 5. 3: Axes 1 and 2 of the principal component analysis (PCoA) of 259 <i>P. obscura</i> individuals (dots) and inertia ellipses representing 15 sampling locations.....	124
Figure 5.4: Multi-locus estimates of pairwise genetic distances ($F_{ST} / (1-F_{ST})$) between fish from 15 sampling locations plotted against natural logarithm (ln) of pairwise Euclidean geographical distance (km).....	125
Figure 5. 5: Admixture analysis by STRUCTURE of <i>P. obscura</i> fish obtained from 15 sampling locations. (a) Line plot of successive ΔK from $K = 2-14$. (b) Bar plots of genetic clusters for $K = 3$ and $K = 9$ ancestral groups.	127
Figure 5. 6: Plot representing the BAYESCAN results for search of candidate loci under putative selection.	128

LIST OF APPENDICES

Appendix 1: Survey locations GPS coordinates	II
Appendix 2: Survey questionnaire on “Fishers’ perceptions and experiences toward the impact of climate change and anthropogenic activities on freshwater fish biodiversity in Côte d’Ivoire” on “Fishers' knowledge of local names, habitats, uses, market prices, population dynamics and threats faced by the African snakehead fish, <i>Parachanna obscura</i> , in Côte d'Ivoire"	II
Appendix 3: GPS Coordinates of the locations of <i>Parachanna obscura</i> populations used the study	V
Appendix 4: Climate and habitat variables from the locations of the seven <i>P. obscura</i> populations sampled. Values are averages from measurements during the dry and wet seasons.....	IV
Appendix 5: Proportion of missing genotypes among the 21 microsatellites (columns) in the 15 populations <i>Parachanna obscura</i> (rows). No individual with more than two missing genotypes where found, thus, all the 259 Individuals used for subsequent statistical analyses.	V
Appendix 6: Matrix of pairwise F_{ST} between the 15 <i>P. obscura</i> populations obtained using only the 19 microsatellite loci with low null allele frequencies.....	VI
Appendix 7: Output of BAYESCAN analysis for identifying candidate loci under selection. q-value: q-value for the model including selection. alpha: coefficient indicating the strength and direction of selection; A positive value of alpha suggests directional selection, whereas negative values suggest balancing or purifying selection. F_{ST} : the F_{ST} coefficient averaged over populations. Significant q-value (lesser than 0.05) are bolded.....	VII

LIST OF ABBREVIATIONS

AFLP	Amplified Fragment Length Polymorphism
AMOVA	Analysis of molecular variance
CAPS	Cleaved Amplified Polymorphic Sequences
CVA	Canonical Variate Analysis
CMIP	Coupled Model Intercomparison Project
DNA	Deoxyribonucleic acid
FAO	Food and Agriculture Organization
GCM	Global Climate Model
HWE	Hardy-Weinberg equilibrium
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
MLN	Multinomial Logit Regression
mtDNA	Mitochondrial DNA
NADH	Nicotinamide Adenine Dinucleotide (NAD) + Hydrogen (H)
PCA	Principal Component Analysis
PCoA	Principal coordinate analysis
PCR	Polymerase Chain Reaction
PIC	Polymorphism Information Content
RCP	Representative Concentration Pathway
RFLP	Restriction Fragment Length Polymorphism
SNP	Single Nucleotide Polymorphism
SRES	Special Report on Emissions Scenarios
SSR	Short Sequence Repeat
TDS	Total Dissolved Solids
UNESCO	United Nations Educational, Scientific and Cultural Organization
UNFCCC	United Nations Framework Convention on Climate Change
USAID	United States Agency for International Development
VNTR	Variable number of tandem repeats

ABSTRACT

This thesis aimed to contribute to the development of appropriate strategies to ensure the conservation and sustainable management of fisheries resources, in general, and *Parachanna obscura* in particular, under changing climatic conditions and expanding human activities, for future use in aquaculture in West Africa. We specifically investigated (1) fishers' perception of climate change, its drivers and other anthropogenic activities affecting freshwater fish biodiversity, as well as the species of fish locally threatened in the Ivorian freshwater ecosystems; (2) fishers' knowledge of the goods and services provided by *P. obscura*, and on local threats to populations of the fish in Côte d'Ivoire freshwater ecosystems; (3) morphological variation among populations of *P. obscura* according to climate and habitat gradient; (4) genetic diversity and structure of *P. obscura* populations from the West Africa region. Face-to-face interviews and a structured questionnaire were used for data collection from 381 fishers in the first two objectives. The morphological variation was assessed based on geometric morphometric (GM) method. We developed a set of 21 highly polymorphic microsatellite markers for studying genetic diversity and population structure. The result indicated a high proportion of fishers' awareness of climate change, and its drivers. The majority of fishers observed decreases in precipitation (87.9%) and increases in temperature (76.1%) over the past years. A significant decrease in fish abundance was also observed by fishers, with climate change and many anthropogenic activities pointed out as the main causes for this decline. Many fish species were listed as locally threatened within Ivorian freshwater ecosystems. Our results further showed that *P. obscura* is an economically important fish for local communities with consistent market price (the kg sold between 1.5 and 3 € on average). Fishers stated that the species is not yet produced in aquaculture, and expressed their willingness to support its introduction into aquaculture. A significant decrease in the abundance of this fish was observed, perceived mainly due to overfishing, lack of rainfall, and other anthropogenic activities. We found significant morphological variations among *P. obscura* populations, but only modest effects of climate and habitat variables on fish shape were obtained. Spatial distance and isolation among populations increased morphological distances, but this trend was likewise relatively weak. The results of genetic diversity showed a relatively low intra-genetic diversity in the fish populations, certainly attributable to the confinement of fish in segregated catchments, resulting in limited gene flow, and local adaptation processes. Additionally, a strong genetic differentiation ($F_{ST} > 0.5$) was found between most putative populations, reflecting the allopatric evolution in watersheds without hydraulic connectivity. The information obtained from this study constitutes a prerequisite for developing and implementing studies or policies aimed at mitigating and combating the negative effect of climate change and anthropogenic activities on freshwater ecosystems. Our results are also relevant for the sustainable management and conservation of *P. obscura* fisheries resources, and for deciding to cultivate the species in order to support the regional demand for fisheries products.

Keywords: climate change, anthropogenic activities, *Parachanna obscura*, goods and services, morphological variations, genetic diversity.

RÉSUMÉ

La présente thèse a eu pour objectif de contribuer au développement de stratégies appropriées pour assurer la conservation et la gestion durable des ressources halieutiques, en général, et de *Parachanna obscura* en particulier, dans des conditions climatiques changeantes et des activités humaines en expansion, pour son utilisation future en aquaculture en Afrique de l'Ouest. Nous avons spécifiquement étudié (1) la perception des pêcheurs du changement climatique, de ses facteurs et d'autres activités anthropiques ayant un impact sur la biodiversité des poissons d'eau douce, ainsi que les espèces de poissons localement menacées dans les écosystèmes d'eau douce ivoiriens ; (2) les connaissances des pêcheurs sur les biens et services fournis par *P. obscura*, et sur les menaces locales pesant sur les populations de ce poisson dans les écosystèmes d'eau douce de Côte d'Ivoire ; (3) la variation morphologique parmi les populations de *P. obscura* en fonction du climat et du gradient d'habitat ; (4) la diversité et la structure génétiques des populations de *P. obscura* de l'Afrique de l'Ouest. Des entretiens en face à face et un questionnaire structuré ont été utilisés pour la collecte de données auprès de 381 pêcheurs pour les deux premiers objectifs. La variation morphologique a été évaluée sur la base de la méthode morphométrique géométrique (GM). Nous avons développé un ensemble de 21 marqueurs microsatellites hautement polymorphes pour étudier la diversité génétique et la structure de la population. Les résultats ont indiqué une forte proportion de pêcheurs conscients du changement climatique et de ses facteurs. La majorité des pêcheurs ont observé une diminution des précipitations (87,9%) et une augmentation des températures (76,1%) au cours des dernières années. Une diminution significative de la quantité de poissons a également été observée par les pêcheurs, le changement climatique et de nombreuses activités anthropiques étant désignés comme les principales causes de ce déclin. De nombreuses espèces de poissons ont été répertoriées comme étant localement menacées dans les écosystèmes d'eau douce ivoiriens. Nos résultats ont également montré que *P. obscura* est un poisson économiquement important pour les communautés locales avec un prix de marché consistant (le kg vendu entre 1,5 et 3 € en moyenne). Les pêcheurs ont déclaré que cette espèce n'est pas encore produite en aquaculture, et ont exprimé leur volonté de soutenir son introduction en aquaculture. Une diminution significative de l'abondance de ce poisson a été observée, perçue comme principalement due à la surpêche, au manque de précipitations et à d'autres activités anthropiques. Nous avons observé des variations morphologiques significatives parmi les populations de *P. obscura*, mais seuls des effets modestes des variables du climat et de l'habitat sur variations morphologiques du poisson ont été obtenues. La distance spatiale et l'isolement entre les populations ont augmenté les distances morphologiques, mais cette tendance était également relativement faible. Les résultats de la diversité génétique ont révélé une diversité intra-génétique relativement faible dans les populations de ce poisson, certainement attribuable au confinement des poissons dans des bassins versants ségrégués, entraînant un flux génétique limité, et aux processus d'adaptation locaux. De plus, une forte différenciation génétique ($F_{ST} > 0.5$) a été observée entre la plupart des populations putatives, reflétant une évolution allopatrique des populations dans des bassins versants sans connectivité hydraulique. Les informations obtenues par cette étude constituent un prérequis pour le développement et la mise en œuvre d'études ou de politiques visant à atténuer et à combattre l'effet négatif du changement climatique et des activités anthropiques sur l'écosystème d'eau douce. Nos résultats sont également pertinents pour la gestion durable et la

conservation des ressources halieutiques de *P. obscura*, et pour la prise de décision concernant la culture de l'espèce afin de faire face à la demande régionale en produits halieutiques.

Mots clés : changement climatique, activités anthropogéniques, *Parachanna obscura*, biens et services, variation morphologique, diversité génétique.

GENERAL INTRODUCTION

Background and justification

More than 10,000 species of fish live in freshwater (Lundberg *et al.*, 2000), representing about 40% of the world's fish diversity and a quarter of the world's vertebrate species (Gatti, 2016). In addition, freshwater habitats support species of amphibians, aquatic reptiles (crocodiles, turtles, etc.), birds, and mammals (otters, river dolphins, platypuses, etc.). One-third of all vertebrates are confined to freshwater. Freshwater represents only 0.01% of the world's water and about 0.8% of the Earth's surface (Gleick, 1996), but this small fraction of the world's water is home to at least 100,000 species, or nearly 6% of all described species (Dudgeon *et al.*, 2006). Freshwater and inland water biodiversity is a valuable natural resource in economic, cultural, aesthetic, scientific and educational terms. In West Africa, freshwater fish production is very important for the food security of human populations (Pauly, 2017), with reservoirs, lakes and rivers throughout the region being important sources of protein and micronutrients (Abobi and Wolff, 2020). This Africa region has an average per capita fish consumption of 12.1 kg/year (Abobi and Wolff, 2020). Despite the economic value of freshwater ecosystems, the living organisms in these ecosystems are vulnerable to many pressures, including climate change, overexploitation, water pollution, invasion by exotic species, habitat degradation and flow modification. In the West African region, freshwater fish species have been reported to suffer greatly from climate change, water pollution, habitat loss due to deforestation, overfishing, and agriculture (Smith *et al.*, 2009). The extinction risk of the freshwater fish fauna in this region was assessed using the IUCN Red List categories and criteria and regional guidelines. The result showed that more than a quarter of all species (26.3%) are listed as threatened (Critically Endangered, Endangered or Vulnerable) and are therefore considered to be at high risk of extinction in West Africa (Smith *et al.*, 2009). In addition, the level of Near Threatened species was 10.7%, reflecting the number of species in the region that is close to reaching the thresholds of a threatened category.

Conservation and management policies are needed to ensure the sustainability of freshwater fisheries resources. Effective conservation and management policies are based on sufficient data, for example on the knowledge, experience and level of participation of indigenous or local fishers in the use of fisheries resources, which are important for planning, implementing and monitoring management and conservation. Management responsibilities are shared between communities and local government authorities. Co-management must respond to problems identified by the

communities, and decisions must be adapted to local conditions, which makes them unique. Local communities, for example fishers, who depend directly on the freshwater ecosystem for their livelihoods, are therefore well equipped to provide relevant information on threats to freshwater biodiversity, changes in fish numbers in recent years, or any other relevant information. In the aquatic conservation community, there is increasing interest in combining local and scientific knowledge to achieve management objectives (Berkström *et al.*, 2019). Fishers' knowledge encompasses all experiential knowledge, including ecological knowledge, based on resources, ecosystems, fishing practices, fishing communities and livelihoods, governance and markets, and their dynamic relationships (Fischer *et al.*, 2015).

Global fish production in West Africa has exploded in recent years, from 2 million tonnes in 2006 to 3 million tonnes in 2016 (FAO, 2016). This increase is due to rising harvest levels in both marine and inland capture fisheries. The increase in production occurred mainly in Sierra Leone, Benin, Burkina Faso, Guinea and Côte d'Ivoire, where production increased by 114%, 80%, 78%, 66% and 60%, respectively (FAO, 2016). Tilapiine species (*Oreochromis niloticus* and *Sarotherodon galilaeus*) of the family Cichlidae are the main freshwater fishery resources in most West African lakes and reservoirs (FAO, 2003). For example, in Nigeria, at Asejire Reservoir, 19 fish species from 16 genera and 13 families were recorded among which fishes of the family Cichlidae were the most dominant, with *Tilapia mariae* being the most common species (Ipinmoroti *et al.*, 2017). In Ghana, the target cichlid species accounted for 89%, 74% and 71% of the total catch composition (landed weight) in Tono, Bontanga and Golinga reservoirs, respectively (Abobi *et al.*, 2019). In Côte d'Ivoire, the catch composition of the Taabo reservoir showed a dominance of *Chrysichthys* spp. (58.4%) and tilapiine fish (35.8%). Other fish species such as *Clarias* spp. (2.5%), Mormyrids (1%), *Heterotis niloticus* (0.8%) and *Schilbe* spp. (0.7%) were represented in most West African reservoirs. In Côte d'Ivoire, In Ayamé lake, the most abundant families were Alestidae (36.61%), Cichlidae (34.19%) and Claroteidae (13.43%) (Cissé *et al.*, 2019) whilst in Buyo lake, Côte d'Ivoire, the fish biomass was dominated by Cichlidae (32.27%) and Claroteidae (26.35%) (Abobi and Wolff, 2020). Three countries dominate regional fisheries and aquaculture; Nigeria, Senegal and Ghana together account for 70% of all fish production in West Africa, followed Sierra Leone and Guinea (FAO, 2016). Ghana and Nigeria dominate aquaculture production, with Nigeria producing 16% of total African aquaculture production. It is worth noting that Nigeria ranks eighth (8th), among the world's 16 largest inland fisheries producers (FAO, 2016). In Côte d'Ivoire, Gambia,

Ghana and Sierra Leone, fish accounts for 50% or more of total animal protein consumption, while in Nigeria, Senegal, Togo and in Mali, Cape Verde, Liberia and Niger fish accounts for more than 30%, less than 15% animal protein (FAO, 2018). Despite the increase in fish production in many West African countries, the regional supply of locally/regionally produced fish only covered less than half of the demand in the region. As a result, West African countries as a whole import about 1.7 million tonnes of fish to cover their demand. Therefore, more actions and efforts are needed to fully cover the regional fishing demand. This can be done through the development of the aquaculture sector by cultivating more freshwater fish species, locally appreciated and with high potential economic values. Five hundred and fifty-three (553) species of freshwater fish are found in West Africa, of which about 300 are endemic to the region (Smith *et al.*, 2009).

Parachanna obscura constitutes one of the frequent freshwater fish species with high value for the people of Africa because of its high nutritional value and economic potential (Teugels *et al.*, 1984). *Parachanna obscura* is commonly known as the African snakehead due to the presence of large scales on its head and is native to Africa. It belongs to Channidae family, a family of freshwater fishes found in Asia (as *Channa* genus) and Africa (as *Parachanna* genus). *Parachanna* genus includes four species which are *Parachanna fayumensis*, *Parachanna insignis*, *Parachanna africana* and *P. obscura* (Bonou and Teugels, 1985). *Parachanna obscura* is generally distributed in the intertropical convergence zone where the water temperature ranges from 26 ° C to 28 ° C, principally in West Africa. Nevertheless, they are also distributed in the upper course of the White Nile, the Chad lake basin, and the Congo river basin (Bonou and Teugels, 1985). *Parachanna obscura* can constitute a potential supply for aquaculture sector. However, some information about the ecology, reproduction, biology, genetics, the market price of this species are needed before any attempt of cultivation of this fish. Some studies have been carried out on the species focusing mostly on *P. obscura* biology (Odo *et al.*, 2012; Bolaji *et al.*, 2011) and reproduction (Vodounnou *et al.*, 2017; Kpogue *et al.*, 2012b; Agokei and Hart, 2010). However, information is lacking regarding goods (market price) and services provided by the species to support the livelihood of local communities. Also, there is no study from the literature that addresses the genetic diversity of the species. In the context of past, current and future climate trends and the expansion of human activities, assessment of genetic diversity, morphological variation, and the trend of populations densities will be useful for knowing the species' ability to respond to changes in environmental conditions.

The capacity of a species to cope with changed conditions depends on the ability for evolutionary adaptation via microevolution, e.g., the selection of local genotypes better adapted to changing environmental conditions (Canale and Henry, 2010; Hoffmann and Sgro, 2011). Individual fitness has been demonstrated to benefit from genetic diversity, since high levels of heterozygosity can boost fitness by counteracting the effect of deleterious mutations (Chapman *et al.*, 2009). Similarly, population stress tolerance and adaptive potential are positively related to the degree of total genetic diversity, with the loss of which being a hazard to the population or species in question (Frankham, 2005; Nowak *et al.*, 2007; Markert *et al.*, 2010; Pauls *et al.*, 2013). Thus, sustainable management in the wild and in culture of *P. obscura* fish will require information on genetic diversity. It will help in the identification of stocks in breeding programmes. It will also provide information on the ability of the fish population to cope with environmental changes and whether conservation actions are needed, and what kind of conservation is required. In addition to genetic diversity, morphological variation in fish populations, either due to genetic variation or phenotypic plasticity in response to different selection pressures or environmental conditions, may help species adapt to different environmental conditions. It may also help identify individuals with suitable morphological characteristics that can be useful for domestication and selection programmes.

Given the lack of information in the literature and from ministers regarding official landing data for *P. obscura* over the past years, the assessment of population density trends can only be done by assessing the knowledge of local fishers. Obtaining such information will help in the management of fishery resources in the reservoirs and in wild. Also, assessing the market prices of the fish will provide information about the economic importance of the fish as well as the contribution of the fish in sustaining the local communities' livelihood. This will help in making decisions relative to the potential cultivation of this fish.

Overall, achieving the points mentioned above will help in achieving objectives 1, 2, 12, 13 and 14 of UN sustainable development goals, which are no poverty, zero hangers, responsible consumption and production, climate action and life below water, respectively. The Sustainable Development Goals give the direction to be followed in all domains of activities including research to achieve a better and more sustainable future for all. These goals respond to the global challenges we face, including those related to poverty, inequality, climate, environmental degradation, prosperity, peace and justice.

Objectives

This thesis aimed to contribute to the development of appropriate strategies to ensure the conservation and sustainable management of fisheries resources, in general, and *Parachanna obscura* in particular, under changing climatic conditions and expanding human activities, for future use in aquaculture in West Africa. Four specific objectives are targeted:

1. To investigate fishers' perceptions of climate change, human activities expansion, and their impact on freshwater fish biodiversity;
2. To investigate local indigenous knowledge on the goods and services provided by *P. obscura*, and on local threats to populations of the fish in Côte d'Ivoire freshwater ecosystems;
3. To assess morphological variation among populations of *P. obscura* according to climate and habitat gradient;
4. To characterize the genetic diversity and population structure of *P. obscura*;

Research hypothesis

The current study is based on three main assumptions:

1. Throughout the generations, local fishers have fished in specific freshwater ecosystems and thus depend directly on the services provided by these ecosystems for their livelihoods. They have accumulated a vast amount of valuable knowledge about freshwater ecosystems. For example, the diversity of fish species, the areas where a particular fish species is caught, species population dynamics, reproduction, threats, ecological changes, etc. These knowledges are critical to their survival. Thus, we hypothesised that fishers have knowledge of the impact of climate change and human activities on freshwater fish biodiversity, as well as knowledge about the goods and services provided by *P. obscura* to local people and threats faced by this species populations.
2. Côte d'Ivoire is characterized by a diversified climate, subdivided into four major climatic zones: Guinean (sub-equatorial climate) in the south, Sudano-Guinean (transitional equatorial climate) in the middle and Sudanian (tropical climate) in the north. In addition, the country is endowed with a freshwater ecosystem characterised by a large and complex system consisting of four major river basins: Sassandra, Cavally, Bandana and Comoe.

Cavally River basin is 700 kilometres long and has its source in Guinea, north of Mount Nimba, at an altitude of about 600 metres. The Sassandra river is 650 kilometres long and rises in the Guinea. The Comoe basin is the longest river in the country with about 1,160 km and has its source at Banfora in Burkina Faso. The Bandana basin has its source in Côte d'Ivoire in the Boundiali region and is about 1050 km long. These rivers have many tributaries. In addition to these major rivers, the country has many coastal rivers such as the Tabou, San Pedro, Niouniourou, Boubo, Agneby, Bia and Me rivers, as well as two tributaries of the Niger River (the Bagoue and Baoule rivers). Many lakes are also present in Côte d'Ivoire. Therefore, we hypothesized there is high morphological variation among *P. obscura* populations, resulting from genetic variation caused by isolation, or phenotypic plasticity to local environmental conditions.

3. Complex climatic and geological events have caused a long history of geographical isolation followed by diversification for some and extinction for other populations, ultimately resulting in the diversified fauna of the African freshwater ecosystems (Darwall *et al.*, 2011, Amoutchi *et al.*, 2021). The evolution of Africa's fauna and landscapes has been influenced by the cycles between the Pleistocene and Pliocene dry and rainy eras (deMenocal, 2014; Maslin *et al.*, 2014; Steenberge *et al.*, 2020). These climatic shifts led to migration, extinction, and allopatric divergence, which resulted in the current diverse fish faunas (Tedesco *et al.*, 2005). Accordingly, we hypothesized that there is strong genetic differentiation in *P. obscura* populations, caused by long time geographical isolation, and local environmental conditions selection of genotypes adapted.

CHAPTER I: Literature review

I.1 Major threats to freshwater biodiversity

Freshwater biodiversity represents valuable natural economic, cultural, aesthetic, scientific, and educational resources. Despite the socio-economic importance of freshwater ecosystems, freshwater biodiversity and habitats have been widely recognized to be under serious threat that exceeds those of marine and any other terrestrial ecosystems (WWF, 2004; Millennium Ecosystem Assessment, 2005; Gatti, 2016). Climate change, overexploitation, water pollution, invasion by exotic species, habitat degradation, and flow modification, are recognized to be the main threats to global aquatic biodiversity (Bassem, 2020). However, in Africa, especially in West Africa, water pollution, habitat loss due to deforestation, overfishing, and agriculture were identified as the greatest threats to freshwater fishes (Smith *et al.*, 2009).

I.1.1 Climate change

The Intergovernmental Panel on Climate Change (IPCC) defined climate change as a change in climate over time, whether due to natural variability or anthropogenic activities which lead to an increase in emissions of greenhouse gases thereby causing global warming. In Africa, during the last 50 to 100 years, near-surface global air temperatures have increased by 0.5°C or more (Funk *et al.*, 2012; Nicholson *et al.*, 2013; Niang *et al.*, 2014). These temperatures were significantly higher during the period from 1995 to 2010 compared to the period 1979–1994 (Collins, 2011; Niang *et al.*, 2014). Africa's average near-surface air temperature is projected to rise faster than the global average increase during the 21st century (Sanderson *et al.*, 2011; James and Washington, 2013). Under the Representative Concentration Pathway 4.5 (RCP4.5) and 8.5 (RCP8.5) scenarios, the global average near-surface air temperature is projected to move beyond the average near-surface air temperature of 20th century, simulated variability by 2069 and by 2047, respectively (Mora *et al.*, 2013). However, in West Africa, these unprecedented climates are projected to occur 1 to 2 decades earlier than the global average. Its average annual temperature projections from both the CMIP3 GCMs (SRES A2 and A1B scenarios) and CMIP5 GCMs (RCP4.5 and RCP8.5) for the end of the 21st-century range between 3°C and 6°C above the late 20th-century baseline (Fontaine *et al.*, 2011; Diallo *et al.*, 2012). Concerning rainfall, most parts of Africa lack adequate observational data to conclude tendencies of annual precipitation over the past century (Niang *et al.*, 2014). However, increases in annual precipitation over parts of eastern and southern Africa, and decreases over the western and eastern Sahel region of northern Africa were likely observed over the past

century from sufficient data from these areas. Concerning future precipitation, various CMIP5 models indicate a wetter core rainfall season with a small delay to the rainy season by the end of the 21st century (Biasutti, 2013).

Freshwater ecosystems are recognized as extremely vulnerable to climate change, principally in Africa (Gatti, 2016). Precipitation-induced changes in hydrology and abiotic processes, and other anthropogenic pressures, are expected to have large effects on aquatic ecosystems by causing a loss of biodiversity (Gatti, 2016). Warming temperatures deteriorate water quality and will have adverse effects on all organisms, including benthic invertebrates and microorganisms like plankton communities (Woodward *et al.*, 2010). Distributions of fish and other aquatic organisms will probably move north, with some extinctions, under climate change. Overall, goods and services provided by the freshwater ecosystem are expected to deteriorate. The vulnerability of freshwater ecosystems to climate change can be elucidated by their relative isolation and physical fragmentation within a larger terrestrial landscape, already intensely exploited by humans for their livelihood (Woodward *et al.*, 2010).

I.1.2 Habitat degradation or loss and flow modification

Habitat degradation describes the set of reactive factors that can drive direct or indirect effects on the aquatic environment (Bassem, 2020). In Africa, dam construction, water abstractions, water transfer, and deforestation and sedimentation are the major drivers of habitat degradation and water flow modification (Darwall *et al.*, 2011).

Africa encompasses a large number of dams, with the Maghreb, southern and western Africa accounting for the largest number (Darwall *et al.*, 2011). Dams have been constructed for several purposes such as domestic, industrial, and mining water supply, crop irrigation, and hydroelectricity. Large dams are obstacles to the longitudinal exchange of nutrients and sediments along rivers. They constantly destroy upstream submerged habitats and block the migration pathways of some aquatic species. They also impact downstream by changing the flow regime, water temperature, and water quality.

Water abstractions are principally practised for urban, industrial, and agricultural uses purposes. This is illustrated by Lake Chad, whose volume has been reduced to around 5% since the 1960s due to drought and desertification caused by a deficiency of rainfall and excessive withdrawal and

diversion of water for agriculture, particularly rice production (Musa *et al.*, 2008; Darwall *et al.*, 2011).

The unequal distribution of rainfall in Africa left some parts of the continent rich in water resources whereas others do not have enough. The obvious resulting solution is to transfer water from the water-rich basin to water-limited areas. Water transfer is generally associated with certain problems, notably: flow reduction in the donor river, then increased flow in the recipient river, leading to loss of biodiversity, and changes in the physical and chemical status of the river water, which is likely to increase algal growth; inflow of fine sediments from one river to another, resulting in a loss of habitat; spreading of exotic fish species, floating aquatic plants and animal diseases and their vectors (Darwall *et al.*, 2011).

Deforestation alters surface runoff and increases river sediment loads, which may lead to aquatic habitat change. Habitat modification, caused by deforestation and associated increased sedimentation, is one of the most widespread threats to freshwater fishes in Africa. Indeed, loss of forest cover destroys several fish species' shelters and changes in water temperature (Brummett *et al.*, 2009; Fugère *et al.*, 2018). In many of western Africa's rivers, especially the Volta, Niger, and Senegal Rivers, deforestation is largely prevalent. Agricultural expansion constitutes a major root of this deforestation (Smith *et al.*, 2009). A part of disturbance in ecology of the aquatic system, deforestation, and sedimentation deteriorates the composition of fish assemblages and the availability of certain food items to aquatic species (Payne and Welcome, 2000).

I.1.3 Overexploitation

Overexploitation affects principally fishes, reptiles and some amphibians (Dudgeon *et al.*, 2006). Overfishing causes a decline in average fish size and lowers trophic levels of fish communities, which are in most cases followed by disappearance of larger fish species (Smith *et al.*, 2009). Overfishing can also cause the reduction of genetic diversity, especially when there is a deep reduction of the population from the initial or natural stock size. Changes in fish community structure and distributions, caused by overfishing have been observed in numerous western Africa's inland waters, particularly in those of the Volta system (Smith *et al.*, 2009). Another example of fish community disturbance caused by overfishing has been perceived in the Ouèmè river (Benin), where large predatory centropomids and catfishes have been replaced by cichlids, cyprinids and small catfish (Helfman, 2007).

I.1.4 Water pollution

The majority of aquatic organisms are highly sensitive to any change within their environment and sometimes may respond drastically by death. Few of them may respond by reduction of their reproductive capacity or even by the suppression of some enzyme systems involved in conventional metabolism (Bassem, 2020). Water bodies' pollution by physical, biological, chemical and radioactive pollutants results from many sources such as mining activities, industrial effluents, domestic sewage and agricultural runoff is considered the main threats to freshwater biodiversity (Malmqvist and Rundle, 2002; Bassem, 2020). Several aquatic environment pollutants affect significantly biodiversity. For instance, pollution from heavy metals (Zn, Cu, Cd, Pb and Hg) impacts all aquatic living organisms. Globally, agriculture and industries, and human settlements constitute the most known causes of water pollution. Africa's freshwater habitat has been polluted principally by eutrophication, and domestic, industrial and agricultural loads.

Eutrophication is the consequence of the release of nutrients, mostly from agricultural and urban areas, in excess into freshwaters ecosystem (Darwall *et al.*, 2011). 28% of all African lakes and reservoirs are eutrophic. Lake Victoria eutrophication is one of the well-known examples (Darwall *et al.*, 2011). Increases in phytoplankton, large-scale blooms of macrophytes, replacement of diatoms by cyanobacteria, eradication of species such as fish, and deoxygenation of the water column constitute the environmental impacts of eutrophication.

Rapid population growth observed during the past decades has resulted in the urban area, industrial and agricultural land use increase. Agricultural wastewater contains various pollutants including those from herbicides and pesticides. These pollutants have negative effects on the river and people consuming river water. Increases in the use of pesticides to control diseases have been an important source of contamination of African rivers and lakes. Pesticides' impact on Africa's inland aquatic fish and invertebrates have been documented (Lévêque, 1997; Perkins and Ramberg, 2004). Industrial effluents, which are mainly heavy metals, are also highly toxic. For example, mercury discharge in freshwater systems, generally from gold mining settlements, represents a problem in the Congo River. Another major freshwater pollution is from chronic discharges of oil. One unfortunate example is the destruction of about 6,000 fish ponds, which affected around USD100 million worth of fish, in Delta State (Nigeria), caused by oil spillage (Amaize, 2010). Considering the immense fish loss, environmental contamination, and damage to the fishing settlement where

over 2,000 families from different parts of the country make a living, the cost is undoubtedly high (Darwall *et al.*, 2011).

I.1.5 Invasion by exotic species

Widespread invasion and intentional release of exotic species increase threats to human physiological and chemical impacts in freshwater environments. This is partly because exotic species are more likely to invade freshwaters that are already modified or degraded (Gatti, 2016). In Africa, one of the famous example is the introduction of Nile perch on Lake Victoria in 1950s for boosting the fisheries industry (Gatti, 2016). The populations explosion of this species led to a halving of the lake's haplochromatic cichlid herd of about 500 species (Pringle, 2005). The reduction in species diversity and function resulted in a restructuring of the ecology of the lake; for example, the disappearance of zooplanktivorous haplochromines coincided with a dramatic sixfold increase in the biomass of the zooplanktivorous cyprinid *Rastrineobola argentea* (Pringle, 2005). The infestation of freshwater habitat by water hyacinth (*Eichhornia crassipes*) is another critical problem for the health of many systems in Africa. Experience from Lake Victoria, suggests that if rapid action is not undertaken to address the problem there will be serious economic, health, and environmental consequences (Smith *et al.*, 2009).

I.2 Importance of fishers' local or indigenous ecological knowledge

Indigenous and other long-established peoples in particular have significant accumulated knowledge that has enabled them to live in one place for countless generations and use the resources of their homeland in a sustainable way (Turner *et al.*, 2022). Johnson (1992) defined indigenous knowledge as “A body of knowledge built up by a group of people through generations of living in close contact with nature”. In general, such knowledge evolves in the local environment, so that it is specifically adapted to the requirements of local people and conditions. It is also creative and experimental, continually integrating external influences and internal innovations to respond to new conditions. Local fishers are a group of people depending directly on services provided by aquatic ecosystems for their livelihood. Their knowledge is developed in a socio-cultural and geographical context. In aquatic conservation community, there is substantial interest in combining local and scientific knowledge to achieve management objectives (Berkström *et al.*, 2019). In developing countries, where there is often a lack of data and financial resources,

many authors have highlighted the practical value of local ecological knowledge in generating valuable information (Taylor *et al.*, 2011; Silvano and Begossi, 2012; Thornton and Scheer, 2012). Because biologists do not always have the means or resources to directly gather knowledge about ecosystems, the traditional approach to natural resource management that relies solely on scientific evidence is doomed to fail (Davis and Ruddle, 2010).

Fishers can provide relevant information about the biology and ecology of species and help answer questions related to determining fish habitat use, breeding areas and species migrations, where such knowledge is scarce (Begossi *et al.*, 2016). Le Fur *et al.* (2011) showed that fishers in West Africa were able to collaboratively develop hatchery site maps with specific details for each estuary. In addition, the fishers identified the periods when mature adults migrated to the spawning grounds and the periods of recruitment of juvenile fish. This information is critical for fisheries management and can also be used to establish aquatic protected areas, particularly to determine the location and size of the protected area to maximize conservation, biodiversity and fisheries benefits. The local ecological knowledge was also compared to scientifically collected data, showing that the two datasets were similar (Le Fur *et al.*, 2011), highlighting the collaboration between scientists and fishers and the use of the local ecological knowledge as complementary information (Berkström *et al.*, 2019).

I.3 Morphological variations in fishes

I.3.1 Origin and importance of morphological variation as tool for species adaptation

When a species encounters novel environmental conditions, for example, during range expansion, climate change, habitat degradation, or host plant shifts, some phenotypic characters may develop differently. It has long been recognized that environmental perturbations of development have the potential to facilitate adaptive evolution and enable populations to reach new adaptive peaks (Mousseau *et al.*, 2000; Price *et al.*, 2003; West-Eberhard, 2003). Morphological differences between populations of a given species of fish are caused by genetic differences or processes of phenotypic plasticity in response to different selection pressures or environmental conditions (Barlow, 1961). Phenotypic plasticity, the capacity of a single genotype to produce multiple phenotypes in response to changes in the environment, has received renewed attention from the scientific community over the past years (Ghalambor *et al.*, 2007; Lande 2009, Machado-Schiaffino *et al.*, 2014). It has been suggested that phenotypic plasticity may play a key role in evolution by

promoting: (i) the emergence of new phenotypes, (ii) divergence between populations and species, (iii) the formation of new species, and (iv) adaptive radiation (Machado-Schiaffino *et al.*, 2014). West-Eberhard (2003) argued that phenotypic plasticity even if not under strict genetic control, plays an important role in creating the conditions that result in an adaptive genetic response. This suggests that environmentally induced non-heritable variation such as phenotypic plasticity is initially established in a population, and later becomes genetically assimilated such that the environmental stimulus previously required to produce the trait is no longer required (Ghalambor *et al.*, 2007). Genetic assimilation represents a kind of genetic accommodation where environmentally induced phenotypes gradually become canalized and develop in the absence of the triggering environmental stimulus (Pigliucci and Murrena, 2003; West-Eberhard, 2003).

In contrast to phenotypic plasticity which is not under genetic control, adaptive phenotypic variation is based on genetic divergence and is a heritable phenotypic variation sorted by natural selection into different environmental niches. Adaptive genetic variation is identified through an association between heritable phenotypic divergence and exploration of different niches (Timothy *et al.*, 2000). Adaptive morphological variation based on genetic divergence is more likely to develop and is maintained among spatially isolated populations (Rundle and Nosil, 2005).

I.3.2 Tools for assessing fishes morphological variations

Morphological variation in fish has traditionally been assessed using linear morphometry, which consists of linear measurement of morphometric or/and meristic traits, to represent the populations of a variety of exploited fish species (Tripathy, 2020). This method has been widely used to identify differences between fish populations (Cheng *et al.*, 2005; Buj *et al.*, 2008; Torres *et al.*, 2010). Naeem and Salam (2005) explained that morphometric and meristic studies are dynamic tools to measure the discretion of the same species. In early morphological research, particularly using the linear morphometric method, measurements were limited to selected body structures, (e.g., fin position) and provided little or no quantification of body shape (Winans, 1984). Traditional (or linear) morphometry relied mainly on measurements of shape indicators such as lengths, areas, angles and their ratios (Wainwright, 1988; Wikramanayake, 1990). The combination of multivariate and geometric methods according to Silva (2003) increased the chances of detecting small differences in morphometry at the intraspecific level, as expected since the geometric methods took

into account the geometry of the configurations and provided additional information about shape differences that is not available in the multivariate methods (Rohlf and Marcus, 1993).

Modern morphometry according to Rohlf (1990) and Bonhomme *et al.* (2014) considered the overall shape through approaches such as landmarks configuration and outline analysis. The power of landmark-based morphometry is to separate fish based on different body shapes, which supports the improvement of this technique for field-based diagnosis (Fitzgerald *et al.*, 2002). Among landmark-based morphometry methods, Lele and Bookstein (1999) reported geometric morphometry (Figure 1.1) as a statistical method for analysing shape variation and its covariation with other variables. This method is considered to be the most rigorous, least expensive, and most user-friendly technique. It captures information about an organism's shape from digital images with more powerful statistical analyses for species differentiation (Parsons *et al.*, 2003; Toscano *et al.*, 2010; Adams *et al.*, 2013). Toscano *et al.* (2010) showed morphometric variations between the hybrids of roach (*Rutilus rutilus* L.) and bream (*Abramis brama* L.) and their parent species inhabiting an Irish lake using geometric morphometry. Similar results were observed between hybrid of *Oreochromis niloticus* and *Sarotherodon melanotheron*, and their parent from Ebrié Lagoon, in Côte d'Ivoire, using geometric morphometry method (Bopo *et al.* 2018a). Bopo *et al.* (2018b), applying geometric morphometric, showed significant morphological variations in *Sarotherodon melanotheron* fish populations in relation to pollution gradient in Ebrié Lagune. Echem (2016), using geometric morphometric analysis, demonstrated shape variation of *Sardinella lemuru* and showed that shape variation is due to their genetics and evolutionary adaptation, where phenotypic plasticity allowed them to respond and adapt to environmental changes by altering their morphology and their behaviour has been modified by changes in morphology, reproduction, or survival that mitigate the effects of such environmental changes. This technique has been applied and found being efficient to detect shape variation in many morphometric studies on fish species (Clabaut *et al.*, 2007; Paknejad *et al.*, 2014; Vieira *et al.*, 2016).

A second method that has also proven to be efficient in assessing morphological variations in fish is truss network analysis (Figure 1.2). Unlike the linear or traditional morphometric measurements, which are redundant and most are along the longitudinal axis and have no geometric properties, the truss network provides measurements that cover the entire body and represent the shape of the animal. The truss is a system of horizontal, vertical and oblique distances measured between

preselected anatomical landmarks, which are points chosen to divide the body into functional units identified based on local morphological characteristics (Reyment *et al.*, 1986). The truss network method has advantages over traditional morphometric character sets, which typically include measurements of length, depth, and width. Many authors agree that truss dimensions including components of body depth and length along the long axis have theoretical advantages over classical morphometric characters to distinguish between groups (Winans, 1984; Currens *et al.*, 1989; Ryu *et al.*, 2001; Park *et al.*, 2004).

I.4 Genetic diversity and species adaptation

I.4.1 Definition and importance of genetic diversity

The variety of life on earth, including plants, animals, microorganisms, and the genes they carry, is referred as biodiversity or biological diversity. Biodiversity is investigated and described at three levels: ecosystem diversity, species diversity, and genetic diversity. Ecosystem diversity refers to the variety of habitats and the various forms of life existing within them. Species diversity represents the variety of species within a region. Finally, genetic diversity is defined as the intra-specific genes (basic units of hereditary information, which are transmitted from one generation to the next) diversity. Genetic diversity allows populations to adapt according to their environment and are important for natural selection (Verma, 2017). Generalized indications of evolution by natural selection in nature confirm the presence of genetic variation for traits that influence fitness and a direct corollary is that individual genotypes must vary in ecologically important ways (Hughes *et al.*, 2008). Genetic diversity provides the basis for any evolutionary change and is crucial for maintaining the ability of species to adapt to new environmental conditions, and is therefore the most fundamental level of biodiversity (Yannic *et al.*, 2014).

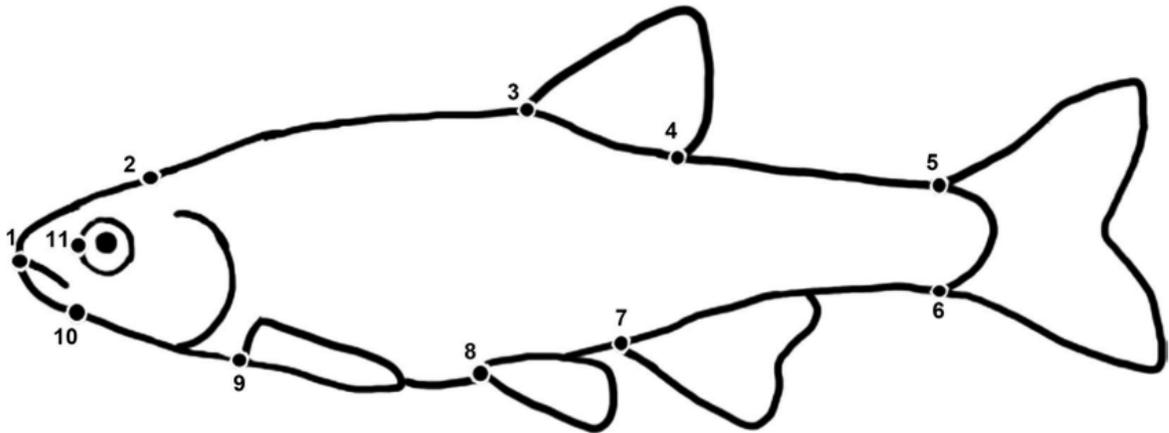


Figure 1. 1: Example of anatomic landmarks used in Geometric morphometric analysis.

Source: Jacquelin and Pyron (2016)

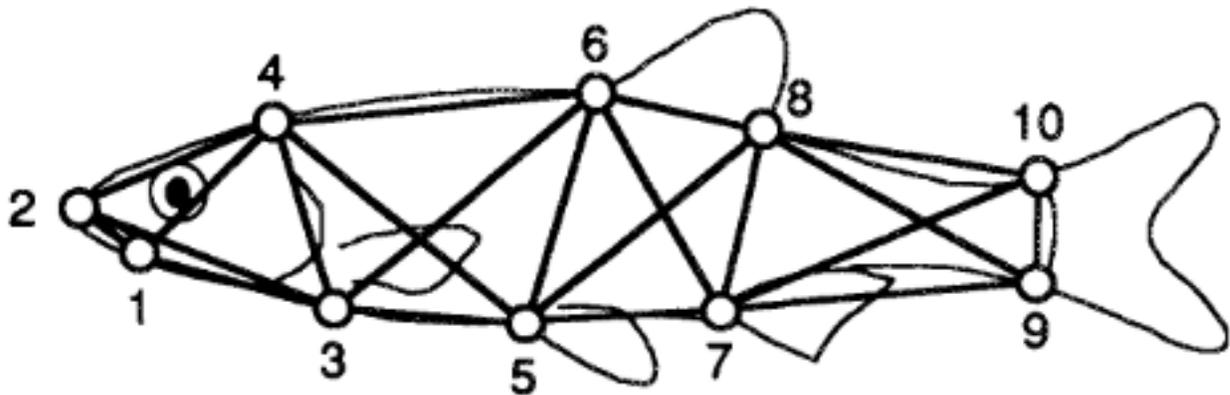


Figure 1. 2: Illustration of truss network measurements performed from 10 truss landmarks on specimens of fish.

Source: Wood and Bain (1995)

I.4.2 Genetic diversity as a potential for species adaptation to changes in environmental conditions

Numerous studies that assess the effects of climate change on biodiversity treat ecosystems and species as a whole, ignoring intraspecific genetic diversity. Species may respond to climate change by adapting locally or by avoiding the new conditions by shifting or reducing their range or doing a mix (Chen *et al.*, 2011; Yannic *et al.*, 2014). In any case, whatever direction a population, individuals or species take under climate change will influence the amount and distribution of genetic diversity, most often associated with a loss of genetic diversity.

Genetic diversity is relevant since it offers the basis for any evolutionary change and represents the greatest and essential level of biodiversity (May, 1994). In general, genetic diversity is recognized as critical for preserving ecosystem services, such as reducing pest and disease issues and boosting recovery from disturbance (Pauls *et al.*, 2013). Adaptive micro-evolutionary processes rely on sufficient genetic variation for natural selection to act and the likelihood of advantageous mutations being established (Hoffmann and Sgro, 2011; Peischel and Kirkpatrick, 2012). Adaptive micro-evolutionary mechanisms will tend to reduce genetic diversity at selected loci and, more significantly, in those portions of the genome that are hitchhiking with it in a degrading environment, such as climate change represents for many species (Via and West, 2008; Via, 2009). The hitchhiking process affects larger regions of the genome, the smaller the population is (Charlesworth *et al.*, 1997). As a result, quick increases in environmental stress and numerous degrees of stress can deplete a population's genetic diversity as it adjusts to them, decreasing the population's ability to respond to future selection pressures. A series of laboratory experiments with non-biting midges have suggested that exposure to one stressor over several generations can effectively reduce neutral genetic diversity through adaptation as well as increased genetic drift and reduce the possibility of adapting to a second stressor (Vogt *et al.*, 2007; Nowak *et al.*, 2009). Genetic variation with a phenotypic effect is therefore the most frequently occurring foundation for all evolutionary change and is essential for species' ability to adapt to changing environmental conditions. It's no surprise that the majority of research on the consequences of climate change on genetic diversity has concentrated on crops (Negrao *et al.*, 2008), commercially valuable fish (Bryant, 2009), forest trees (Parker *et al.*, 2000), or agricultural systems more broadly (Challinor *et al.*, 2009; Pauls *et al.*, 2013).

I.4.3 Tools for genetic diversity assessment

The main technologies available for assessing genetic diversity are based on molecular genetic markers. The obtention of molecular markers can be based on isoenzymatic markers or DNA fragments. DNA markers are classified into DNA hybridization or amplification group according to the methodology used. RFLP markers (Restriction Fragment Length Polymorphism) and the Minisatellites or VNTR (Variable Number of Tandem Repeats) loci are markers related to the hybridization methodology, while RAPD (Random Amplified Polymorphism DNA), AFLP (Amplified Fragment Length Polymorphism), SSR (Short Sequence Repeat) or microsatellite, CAPS (Cleaved Amplified Polymorphic Sequence) or PCR-RFLP, SNP (Single Nucleotide Polymorphism) are markers revealed through DNA amplification (Grisolia and Moreno-cotulio, 2008).

DNA markers are either focused on nuclear or mitochondrial DNA. Mitochondrial DNA (mtDNA) is small circular DNA present in the mitochondria. mtDNA is characterised by maternal inheritance, absence of recombination, and faster evolutionary rate than nuclear sequences. These characteristics make mtDNA suitable for phylogenetic and phylogeographic analyses. One or more regions of the mitochondrial DNA molecule can be used depending on the study purpose. In general, the control region of mtDNA called D-loop region is most commonly used in population studies, whereas NADH genes, ribosomal, and cytochrome genes are more commonly employed in matters concerning the species as a whole and its distribution, as well as in intergeneric systematics (Perez-Sweeney *et al.*, 2003; Grisolia and Moreno-cotulio, 2008). Restriction enzymes (RFLP), SSCP (Single-stranded conformation polymorphism), and sequencing are some of the approaches that can be used to investigate genetic variation in mtDNA (Frankham *et al.*, 2002). According to the aim of the research, many regions of the molecule of the mitochondria DNA can be used.

Concerning nuclear DNA markers, although the availability of several types of markers, microsatellites are currently the most popular marker for ecological studies (Avise, 2004). Microsatellites are short DNA fragments of 10 to 100 base pairs (bp) that include repetitive elements with 1-6 bp tandem repeats, with the number of repeats varying, resulting in a high polymorphism information content (PIC). Microsatellites are abundant in the genome, have high mutation rates and are codominant meaning that heterozygotes can be distinguished from homozygotes (Ferreira and Grattapaglia, 1998). An important characteristic of microsatellites is that

primers generated for one species can be used for other species in related taxons (Grisolia and Moreno-cotulio, 2008). A summary of some key properties of the various approaches for marker analyses is provided in Table I. I.

I.4.4 Principal parameters measured in population genetics

I.4.4.1 Genetic diversity metrics

Genetic diversity is mostly assessed from estimates of heterozygosity and allelic richness. There are two types of heterozygosity, notably the observed heterozygosity and the expected heterozygosity. The observed heterozygosity is the frequency of heterozygotes individuals in a population, while the expected heterozygosity, also referred as gene diversity, is the probability that two gametes, randomly chosen from the gene pool, are of different alleles (Hughes et al., 2008). Allelic richness (A_R), also known as allelic diversity, is defined as the mean number of alleles per locus. The definitions of the common metrics of genetic diversity applied in evolution and ecology studies are summarised in Table I. II.

Table I. I: Comparison of the properties and technique of the most common molecular markers

Source: Grisolia and Moreno-cotulio (2008).

Variable	RFLP	PCR-RFLP	RADP	Microsatellite	SNP	AFLP
Quantity of DNA	10ug	50ng	50ng	50ng	50ng	500ng
Quality of DNA	Excellent	Reasonable	Reasonable	Reasonable	Good	Good
Based on PCR	No	Yes	Yes	Yes	Yes	Yes
Radioactivity	Yes	No	No	Yes/No	No	Yes/No
Multiplex	No	No	No	Yes	Yes	No
Ease of Use	No	Yes	Yes	Yes	Yes	No
Automation	No	Yes	Yes	Yes	Yes- high	Yes
Reproducibility	Good	Good	Low	Good	Good	Medium
Number of alleles per locus	Biallelic	Biallelic	Biallelic	Multiallelic	Biallelic	Biallelic
Gene expression	Codominant	Codominant	Dominant	Codominant	Codominant	Dominant
Abundance throughout the genome	High	High	Low	Medium	High	Medium
Cost by data	High	Low	Low	Low	Very low	Low

Table I. II: Common metrics of genetic diversity used in evolutionary and ecological studies

Source: Hughes et al. (2008).

Type of trait	Metric of diversity	Definition
Discrete allelic states	Allelic diversity	An index of molecular genetic diversity (e.g. Shannon–Wiener diversity) that incorporates information about the average number and relative frequency of alleles per locus. Allelic diversity is typically measured using molecular markers of putatively neutral loci.
	Allelic richness	The average number of alleles per locus.
	Genotypic richness	The number of genotypes within a population. Genotypic richness can be measured as the number of haplotypes using molecular markers, or it can be manipulated in experiments by varying the number of clonal genotypes or sib-families.
	Heterozygosity	The average proportion of loci that carry two different alleles at a single locus within an individual. Observed heterozygosity (H_o) can be estimated with co-dominant molecular markers, but estimates are biased by the number of individuals sampled within a population. Expected heterozygosity (H_e) can be estimated with both dominant and codominant markers when assumptions are made about the mode of inheritance, as well as the size and structure of populations.
	Mutational diversity and effective population size (Q)	A measure of nucleotide diversity that provides a combined measure of effective population size (N_e) and mutation rate. Q is typically calculated using Wattersons (1975) estimator ($h = 4N_e\mu$), which is equal to the expected number of segregating sites between two genotypes. Estimates of h assume an infinite number of nucleotide sites and no recombination.
	Nucleotide diversity (p)	The average number of nucleotide differences per site between two random individuals selected from a population.
	Percentage of polymorphic loci	The percentage of polymorphic loci.
Continuous traits	Coefficient of genetic variance (CV)	Genetic variance in a trait (V_G) corrected by the trait mean, calculated as $(V_G^{0.5}/\text{mean}_{\text{trait}}) \cdot 100\%$. Unlike genetic variance, CV is not biased by the magnitude of trait means and is arguably the best measure of genetic diversity for phenotypic traits when variance scales with the trait mean.
	Genetic variance (V_G)	The variance in a phenotypic trait among individuals due to genetic differences. Genetic variance is measured using parent–offspring regressions, controlled breeding designs that allow for sibling analyses or with detailed genealogical information. Total genetic variance can be further partitioned into additive and non-additive (dominant and epistatic) components of genetic variance. Genetic variance often scales positively with mean trait values.
	Heritability	The ratio of the genetic variance to the total phenotypic variance in the population. Heritability values are influenced by both genetic and environmental variance and therefore offer a poor estimate of genetic diversity.

I.4.4.2 Inbreeding and population differentiation

Breeding between relatives can occur in large populations as well as in small isolated populations where the number of possible partners is reduced. It can lead to inbreeding in the offspring with the possibility of having received two identical alleles per descent. An inbreeding coefficient is the probability that the 2 alleles at 1 locus of an inbred individual are identical alleles per descent (Gazal *et al.*, 2014).

The intra-population inbreeding coefficient (F_{IS}) measures the heterozygote deficiency compared to the expected value under the assumption of random crossing of gametes. It is usually estimated through the following formula:

$$F_{IS} = 1 - \frac{H_o}{H_e}$$

where H_o and H_e are the respective observed and expected frequencies of heterozygotes.

Genetic differentiation is the measured variation between two or more populations, demes or subpopulations. Genetic differentiation is mainly influenced by dispersal of individuals within populations (gene flow), isolation by distance and differential local adaptation (Praveen and Ram, 2022). When gene flow is restricted, it allows micro-evolutionary changes in local populations of the species to cope with climatic challenges. Many approaches have been developed to measure genetic differentiation. Among them, the most widely used are F_{ST} and G_{ST} . The F_{ST} approach was developed by Wright (1951, 1965) to partition genetic variation in a subdivided population. As a measure of genetic differentiation, he defined the F_{ST} , where S and T indicate the subpopulation and total population levels, respectively. The formula is the following:

$$F_{ST} = \frac{V(q)}{\bar{q}(1 - \bar{q})}$$

where q is the frequency of allele A2 at a biallelic locus and $V(q)$ is the variance over subpopulations. The F_{ST} ranges from 0 to 1.

The second approach is the G_{ST} proposed by Nei (1972), which is an estimate of F_{ST} for a locus with multiple alleles, assuming Hardy–Weinberg proportions, as follows:

$$G_{ST} = \frac{H_T - H_S}{H_T}$$

where H_S represents the average Hardy-Weinberg heterozygosity of the subpopulation and H_T is the total heterozygosity of the population. H_T is calculated from $H_T = 1 - \sum \bar{p}_i^2$, where \bar{p}_i is the average frequency of allele i over the subpopulations.

I.4.4.3 Hardy-Weinberg equilibrium (HWE)

The Hardy-Weinberg principle is a fundamental principle of population genetics and evolutionary biology. It describes how allele and genotype frequencies are linked, and how genetic variation can persist over generations in a randomly mating population. Consider a population where there is segregation between two alleles (A and B) at a single locus. The letters p and q stand for the frequency of alleles A and B, respectively. According to the Hardy-Weinberg principle, genotype frequencies will be p^2 , $2pq$, and q^2 after one generation of random mating. Genotype frequencies are expected to remain constant in the absence of additional evolutionary processes (such as natural selection), and the population is considered to be at Hardy-Weinberg equilibrium (Lachance, 2016). The Hardy-Weinberg principle is predicated on several assumptions, including random mating, the absence of natural selection, a very large population size (i.e., genetic drift is negligible), no gene flow or migration, no mutation, and the locus is autosomal (Lachance, 2016). Deviations from Hardy-Weinberg equilibrium may occur when these suppositions are violated. One of the useful statistical methods for testing whether a population is at Hardy-Weinberg equilibrium is the Chi-square (χ^2) test with one degree of freedom (Weir, 1996). This test begins by counting the observed numbers of individuals with each genotype. The allele frequencies are then calculated using these genotype frequencies (p and q). The total number of individuals sampled is multiplied by p^2 , $2pq$, and q^2 to determine the expected number of individuals with each genotype. When the observed and expected numbers of genotypes are known, the χ^2 statistics can be computed for each genotype using the equation $\chi^2 = \frac{1}{4} (\text{observed} - \text{expected})^2 / \text{expected}$. These values of χ^2 are summed, and if the overall χ^2 test statistic is above 3.84, the null hypothesis that the population is in Hardy-Weinberg equilibrium can be rejected (p-value lesser than 0.05).

I.4.4.5 Population bottleneck

In population genetics, the consequence of a temporary decrease in population sizes on genetic variation is called the bottleneck effect (Chakraborty and Kimmel, 2001). The bottleneck can be caused by a variety of events, such as environmental disasters, overhunting or overfishing, habitat destruction that results in the death of organisms, etc. The population bottleneck leads to a decrease in the population gene pool, since many alleles, or gene variants, found in the original population are lost. Subsequent to this event, the remaining population has a very low level of genetic diversity, which means that the population as a whole has few genetic characteristics.

The bottleneck phenomenon is sometimes studied in conjunction with the "founder effect", which influences the genetic makeup of a population initially formed by a small number of founders (Chakraborty and Kimmel, 2001). There is a close link between the genetic properties of these effects since in both cases contemporary members of the population can trace their ancestry back to a small number of common ancestors at some point in the past. Three models are mainly used for testing for populations bottlenecks: the infinite allele model (Kimura and Crow, 1964), the strict one-step stepwise mutation model (Ohta and Kimura, 1973) and the two-phase model (Di Rienzo *et al.*, 1994). The infinite allele model is recommended for allozyme data, while the strict one-step stepwise mutation model and the two-phase model are more appropriate when testing microsatellite loci (Piry and Luikart, 1999).

I.5 Review on *Parachanna obscura*

I.5.1 Description

Parachanna obscura is characterized by an elongated, fusiform and subcylindrical body, covered with cycloid scales of medium size (Figure 1. 3). The head is flattened anteriorly, long, and covered with cycloid scales that are bigger than those on the body and symmetrical on top. Its eyes are wide and lateral, has one anterior and tubulated pair of nostrils, and the mouth is large and protractile. The lateral line is solitary and usually has 65–78 scales. The dorsal and anal fins are elongated. The lower jaw is somewhat longer than the upper jaw and has 4 to 6 well-developed canines. All of their fins have soft fin rays that do not touch the caudal ones. The dorsal fin has 39–45 spiny rays and starts above the pectoral fins, whilst the anal fin has 26–32. The caudal fin contains 14 spiny rays and is gently rounded. The pelvic fins are located in the abdomen and are spineless, soft and close

to the pectorals (Teugels and Daget, 1984; Bonou and Teugels, 1985; Kpogue *et al.*, 2012a). The specimens of this species have five to eight dark spots on the flanks, more or less rounded or geometrical in shape. On the back, on each side of the dorsal fin, there are a few dark spots which tend to join those on the flanks. There is a dark band on the head and laterally, which widens from the posterior edge of the eye to the posterior end of the operculum. Small dark spots in the form of more or less visible oblique stripes can be seen on the fins, and a small, rounded black tarsus can also be seen just at the base of the caudal fin. The juveniles have an ochre background colouration with a black lateral stripe in the middle of the flank, running from the tip of the snout to the tip of the caudal fin (Bonou and Teugels, 1985).

This fish species has a remarkable growth performance, can reach a maximum total length of 56 cm, and maximum body weight of up to 1 kg. Its length-weight relationship established in different ecological areas showed that the values of the exponent “b” are close to 3, and allometric regression in favour of weight (Kpogue *et al.*, 2012a).

I.5.2 Taxonomy, habitat, ecology and distribution

Parachanna obscura Gunther is the fish species belonging to *Parachanna* genus and Channidae family (Bonou and Teugels, 1985). Channidae family fishes are freshwater fishes found in Asia (as *Channa* genus) and Africa (as *Parachanna* genus). *Parachanna* genus includes four species which are *Parachanna fayumensis*, *Parachanna insignis*, *Parachanna africana* and *P. obscura* (Bonou and Teugels, 1985). *P. fayumensis* is an extinct species of this genus known only as a fossil. The taxonomical classification of *P. obscura* is presented in Figure 1. 4.

It is a benthopelagic and potamodromous fish mostly found in the creeks of swamps, ponds, streams, rivers, lakes, marshes and floodplains. *Parachanna obscura* prefers calm and muddy places with marginal vegetation to muddy areas in flowing waterways (Teugels *et al.*, 1992). It lives among aquatic vegetation and is often immobile as if sleeping, hence the name "sleeping fish" (Bonou and Teugels, 1985). Its favourite biotopes are marshes and rough banks. It is strictly tropical fish species supporting a water temperature range between 25 and 28° C and prefers a slightly acidic pH (6.5–7.5). Thanks to its cavity above the gill chamber, which functions as an accessory respiratory organ, *P. obscura* can withstand environmental conditions with poor levels of dissolved oxygen (Kpogue *et al.*, 2012a).

Parachanna obscura is generally found in the intertropical convergence zone in countries such as Benin, Burkina Faso, Cameroon, Central African Republic, Chad, Côte d'Ivoire, Equatorial Guinea, Ethiopia, Gambia, Ghana, Guinea, Guinea-Bissau, Mali, Niger, Nigeria, Senegal, Sierra Leone, Sudan and Togo (Teugels, 2003) (Figure 1. 5).

I.5.3 Diet and reproduction

Parachanna obscura is a voracious pelagic carnivore, a formidable predator, typically piscivorous or insectivorous (Paugy and Leveque, 2006). Larvae feed on algae and protozoa, while juveniles and adults consume smaller fish, insects, tadpoles, copepods and shrimps (Idodo-Umeh, 2003; Ekpo, 2004).

Parachanna obscura is a species with asynchronous iteroparous oogenesis carrying oocytes at different stages of development and its fecundity varies with stages III (ripening), IV (ripe) and V (spent). The relative fecundity is 19.46 oocysts/g body weight (Kpogue *et al.*, 2012a). The appearance of the partners changes during the breeding season. The male's colour changes from brown to bright blue with spots on the sides, which are usually a dark brown, becoming a deep, dark steel blue, while in female, the bright spots on the fins turn blue, and the brown spots on her body turn a deeper shade of brown. The pectoral fin tips of both males and females become silvery white (Balon, 1984). The couple forms circles on the water surface in an open area of the floating plant layer. The circular movements become more intense, and then the male starts to swim on the back of the female and wraps himself around her body. At this position, the genitals are side by side, the partners intertwine and remain in this position for 10 to 20 seconds, and the female lays eggs which are immediately fertilised by the male. The breeding process starts again after a short rest. Eggs are yellow and have a diameter of 1.33 mm, and are kept by both parents. The duration of egg incubation varies from 24 h to 48 h with temperature and photoperiod. Within 3 days after hatching, the larvae perform a continuous up-and-down movement for air-breathing and become free-swimming. They swim in groups like a "cloud" until they reach the size of 3.4 mm and enjoy this throughout the parental care period. They are large enough to feed on brine, shrimp, nauplii and micro worms after about a week (Kpogue *et al.*, 2012a).

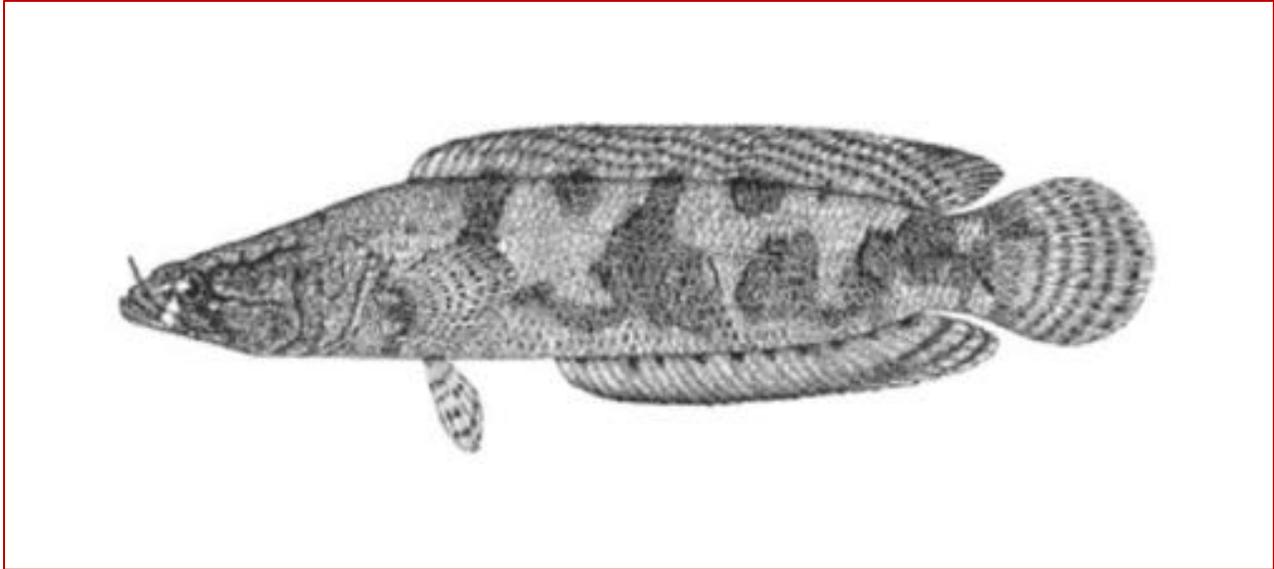


Figure 1. 3: Lateral view of *P. obscura*.

Source: Bonou and Teugels (1985)

Kingdom:Animalia
 Phylum:.....Chordata
 Subphylum:.....Craniata
 Kingdom:Animalia
 Phylum:Chordata
 Class:Actinopterygii
 Order:Anabantiformes
 Family:Channidae
 Genus:*Parachanna*
 Species: *Parachanna obscura*

Figure 1. 4: Taxonomy range of *Parachanna obscura*

Source : <https://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?id=304449>



Legend
 EXTANT (RESIDENT)

Compiled by:
 IUCN (International Union for Conservation of Nature) 2019

Figure 1. 5: Distribution map of *P. obscura* .

Source: Lalèyè (2020)

CHAPTER II:

**Fishers' perceptions and experiences toward
the impact of climate change and
anthropogenic activities on freshwater fish
biodiversity in Côte d'Ivoire.**

Abstract

Africa's freshwater ecosystems are impacted by many threats due to climate change and several anthropogenic activities. In Côte d'Ivoire, the economy relies mostly on agriculture, which covers around 64% of the land surface. This study aimed to investigate Côte d'Ivoire fishers' perception of climate change, its drivers and other anthropogenic activities impacting freshwater fish biodiversity. The fish species locally threatened in the Ivorian freshwater ecosystems were also investigated. Face to face interviews and a structured questionnaire were used. The data obtained were analysed using descriptive statistics such as frequency, percentage, means, and standard deviation, minimum and maximum. The multinomial logit regression was also applied to test factors that influence fishers' awareness and perception of climate change and their perception of change in fish abundance. The results show that around 72.7% of fishers were aware of climate change. Decreases of precipitation (87.9%) and increases of temperature (76.1%) were observed by fishers. Also, a significant decrease in fish quantity was observed by respondents. Climate change and anthropogenic activities such as gold mining, water withdrawal, use of small-mesh fishing nets, overfishing, industrial waste pollution, pesticides use for agricultural purposes along watersheds, obnoxious fishing practices and population growth, were highlighted as the main reasons for this decline. Species such as *Lates niloticus*, *Heterotis niloticus*, *Parachanna obscura*, *Malapterurus electricus*, *Sarotherodon galilaeus*, *Coptodon zillii*, *Polytyperus endlicheri* and *Labeo coubie* were listed by fishers as locally threatened within Ivorian freshwater ecosystems. Actions and policies are needed to be taken by local authorities to ensure the sustainability of fisheries resources. The information obtained from this study constitutes a prerequisite for developing and implementing studies or policies aimed at mitigating and combating the negative effect of climate change and anthropogenic activities on the Ivorian freshwater ecosystem.

Keywords: Anthropogenic activities, Climate change, Freshwater fish biodiversity, Fishers, Côte d'Ivoire.

II.1 Introduction

The United Nations Framework Convention on Climate Change (UNFCCC) defined climate change as “a change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable periods” (UNFCCC, 1992). Most aquatic organisms are very sensitive

to any variation in their environment. Combined effects of climatic factors, overfishing, increased human population growth, water pollution and alien invasive species, are amongst the stressors that contribute to the degradation of natural water resources, consequently threatening aquatic systems (Bassem, 2020). Recently, it was noted that aquatic biodiversity is threatened and subject to severe declines in many countries (Bassem, 2020). Among aquatic ecosystems, freshwater ecosystems are most sensitive to environmental disturbances (Liermann *et al.*, 2012). Freshwater organisms have the highest proportion of known species globally categorized as extinct or threatened in the International Union for Conservation of Nature (IUCN) Red List (Costello, 2015; Robert *et al.*, 2019). A report of the United Nations Educational, Scientific and Cultural Organization (UNESCO) indicated a faster decline of freshwater biodiversity than of terrestrial and marine biodiversity over the last three decades (UNESCO, 2003). The decline is expected to accelerate even further with warmer temperatures, reduced precipitation and increased water withdrawal for agriculture and other human use (Vörösmarty *et al.*, 2000; Xenopoulos *et al.*, 2005).

Africa harbours a diversified fish fauna resulting from a long history of complex climatic and geological events that resulted in geographic isolation followed by speciation for some populations, or extinction for others (Darwall *et al.*, 2011). African ichthyofauna shows numerous exceptional features compared to other continents. However, Africa's ichthyofauna shares affinities with those of both South America and Asia (Darwall *et al.*, 2011). Thus, Africa's freshwater fish biodiversity is reported to comprise more than 3000 species, more or close to that of Asia (more than 3600 species known) and South America (more than 4200 species known) (Lévêque *et al.*, 2008). Climate change and other anthropogenic perturbations such as dam construction, water extraction and overexploitation are some of the stressors impacting Africa's freshwater biodiversity (Darwall *et al.*, 2011, Smith *et al.*, 2009). Also, habitat modification, caused by various land uses and associated sedimentation is reported as one of the most widespread threats to freshwater fishes in Africa (Brummett *et al.*, 2009). Sediments cover submerged surfaces, increase turbidity, and reduce suitable habitats for breeding and feeding of many fish populations (Darwall *et al.*, 2011). Water pollution represents a problem for freshwater fish in several parts of Africa. Pesticides and fertilizers' impact on African's freshwater ecosystems have been well-documented (Darwall *et al.*, 2005; Smith *et al.*, 2009; Darwall *et al.*, 2011).

In Côte d'Ivoire, the economy relies mostly on agriculture, which covers around 64% of the land surface (World Bank, 2018). From 1960 to 2018, the country's rate of urbanization soared from 17.7% to over 50% (USAID, 2017). The high rate of urbanisation, combined with agriculture expansion, are susceptible to impact aquatic ecosystems, especially those of the freshwaters, in this country. Pollution of aquatic ecosystems from the discharge of untreated domestic, industrial, and agricultural wastes have been reported in the country (Ouattara *et al.*, 2021; Grogga *et al.*, 2012; Gueu *et al.*, 2021). Regarding the climate of this country, from the 1980s to 2000s temperature increased on average by 0.5 °C, and from 2001 to 2010 a temperature rise of 0.8 °C was recorded (Bernard, 2014). The decades 1950s and 1960s were recorded to be comparatively wetter than those from 1970 to 1990s which were drier. Moreover, according to the prediction of The Intergovernmental Panel on Climate Change in 2014 under RCP4.5 scenario, temperature will rise of 3 °C by 2100, over most of the country from north to south, and the daily precipitation will drop by 8% relative to its current amount during the season from April to July over the next hundred years (Bernard, 2014). Thus, climate change and human activities may constitute a real threat to freshwater fish biodiversity in this country. Consequently, there is an urgency to provide a scientific assessment of the impact of climate change and human activities on Côte d'Ivoire freshwater biodiversity, which will guide management strategies.

Over time, Indigenous peoples throughout the world have preserved distinctive understandings, rooted in cultural experiences, that guide relationships among human and non-human beings in specific ecosystems. These understandings and relationships constitute a system broadly identified as indigenous knowledge (Bruchac, 2014). Indigenous knowledge is part of the heritage of humankind. It is the library of knowledge that people have of the environments where they live (Vidal, 2019). Fishers are people depending directly on the services provided by the aquatic ecosystem for their livelihoods. Therefore, they are most affected by any environmental disturbance in this ecosystem, and also the key group well aware of the nature of the disturbance. Their perception of climate change (the existence, the impact, and causes) and knowledge of anthropogenic activities impacting freshwater fish biodiversity, being part of their indigenous knowledge, are essential for making and implementing decisions and policies related to the mitigation of these threats, and the management of freshwater fish biodiversity. Furthermore, fishers' knowledge and perception represent the baseline information for motivating and directing any research projects regarding this issue.

In this view, this study aimed to investigate Ivorian fishers' knowledge and perception towards climate change, its drivers, and human activities' impacts on freshwater fish biodiversity and the species locally vulnerable.

II.2 Material and methods

II.2.1 Study area

The study was carried out in Côte d'Ivoire, West Africa. The country is divided by latitude into three principal climatic zones, with a fourth zone being the particular climate of the mountain zone. Our study was carried out in three climatic zones within Côte d'Ivoire: Guinean in the south, Sudano-Guinean in the middle and Sudanian in the northern (Figure 2. 1). Guinean zone, also known as Attiean zone, is characterized by a sub-equatorial climate with two rainy seasons and two dry seasons. Its annual precipitation is estimated to be more than 1500 mm (Bernard, 2014). Fishers of Bia River (from Krindjabo, Bianou and Alliekro localities) and Ayame lake (Ayame locality), were randomly selected in this climate zone. Fishers from Faye locality fishing in Faye lake were also selected in Guinean zone. The Sudano-guinean or Baoulean zone is characterized by an equatorial transition climate between the Guinean and the Sudanian climates. This climate zone also has two rainy seasons and two dry seasons, with the annual precipitation comprising between 1200 and 1500 mm per year. Within this climate zone, fishers of Kan lake, Buyo lake and Nzo river, from Koubi, Dibobly and Guiglo localities were respectively selected for the study (Appendix 1). Within the Sudanian zone, the fishers of Bagoue river from Samorosso village were selected. The Sudanian zone is characterized by one rainy season and one dry season. The annual precipitation varies between 900 and 1200 mm.

II.2.2 Sampling of fishers

A preliminary investigation was done in the three selected climatic zones with 90 fishers, to identify the proportion of them fishing or trading on *Parachanna* fish species among their global target species. The fishers selected were those who were familiar with *Parachanna* species and who had already been involved in fishing or trading on *Parachanna* species. These fishers were also involved in fishing or trading other common fish species found at the sampling sites. The survey was conducted among fishers in different types of freshwater ecosystems, including lakes, rivers and streams. The investigation resulted in the proportion of 60% of fishers fishing on

Parachanna among the globally interviewed fishers. This proportion was used in Dagnelie (1998) formula with a 95% confidence level to calculate the necessary sample size:

$$N = \frac{U_{1-\alpha/2}^2 p(1-p)}{d^2}$$

Where N = the total number of fishers to be surveyed; $U_{1-\alpha/2}^2$ represents the value of the normal random variable for a probability value of $1-\alpha/2 = 0.975$; $U_{1-\alpha/2}^2 = 1.96$; p represents the estimated proportion of fishers fishing on *Parachanna* fish species among their target species, obtained from the preliminary investigation ($p = 0.60$); d is the margin of error of a parameter estimated from the sample fixed at 0.05. From the formula, the sample size of 369 fishers was the minimum needed, but to be more accurate, 381 fishers were interviewed in this study.

II.2.3 Data collection

Face-to-face interviews were conducted using a structured questionnaire from October 2020 to February 2021. Fishers were randomly selected on each sampling site. Fish landing sites within each sampling site were used as collection sites. The questionnaire was divided into three sections (Appendix 2). The first section was structured to assess the respondent's general demographic background (e.g., age, sex, household size, education level, occupation, monthly income, etc.) and the second section was on the fishers' knowledge of climate change (e.g., awareness, causes and drivers, perceived change in variables, etc.). The last section was linked to respondents' perception of the impact of climate change and human activities on freshwater fish biodiversity (e.g., change in fish quantity, how climate change drew change in fish biodiversity, major human activities threatening freshwater fish biodiversity and locally threatened fish species).

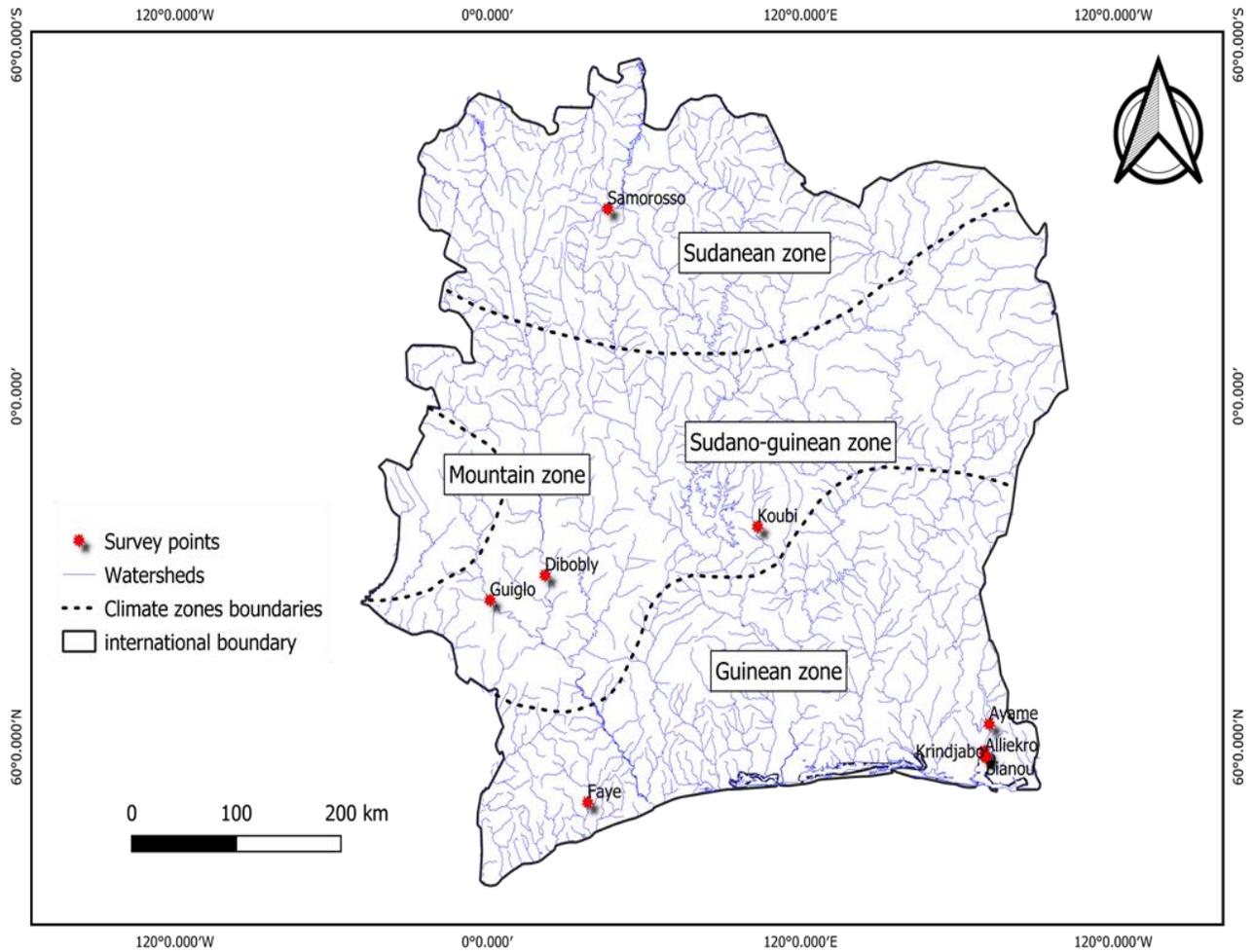


Figure 2. 1: Study area map, showing the borders of Côte d’Ivoire, the main climate zones and the locations where surveys were conducted.

II.2.4 Statistical analysis of the data

Descriptive statistics (frequency, percentage, means and standard deviation, minimum and maximum) were calculated to analyse fishers' demographic information, their perception related to climate change and its impact on freshwater fish biodiversity and their perception of human impact on fish biodiversity. The multinomial logistic regression model (MLN) was applied to analyse factors that influence fishers' awareness of climate change, their perception of climate change, and their perception of change in fish abundance. This model has been widely used in many studies to test factors that influence individual knowledge of climate change, climate adaptation and climate change risk perception (Agwu *et al.*, 2018; Owusu *et al.*, 2019). Multinomial logit regression is used to predict the probability of category membership of a dependent variable based on several independent (predictor) variables. The MLN model is a simple extension of the binary logit regression that allows for more than two categories of dependent or independent variables. In this model, the independent variables can either be nominal or ordinal (Starkweather and Moske, 2011). MLN uses maximum likelihood estimation to evaluate the probability of categorical membership in a dependent variable based on multiple predictor variables. In this study, we considered sociodemographic variables (e.g., age, gender, education level, household size, ethnic group) of fishers as the predictors and perception variables (e.g., awareness of climate change, perceived change in climate or fish quantity) as dependent variables. The MLN results reflect the expected change in the probability that fishers perceive climate change or fish quantity change or be aware of climate change with respect to a one-unit change in a predictor variable, keeping all the other predictors constant. Alpha (α) lesser than 0.05 was considered statistically significant. SPSS version 2.2 software was used for the descriptive statistics, while the multinomial logit regression was implemented in R 3.6.3 software.

II.3 Results

II.3.1 Socio-demographic background of respondents

A total of 381 questionnaires were successfully completed. 81.9% of respondents were males and 18.1% were females. Most (63%) of the respondents were between 30 to 49 years old, followed by those belonging to the ages ranging from 50 to 59 (17.8%), and 20 to 29 (13.6%). Only 5.5% of the respondents were 60 years and above. Among interviewed people, 84.5% were married, 15.2% single and 0.3% divorced. The household sizes of respondents were principally between 1 to 10

persons (85.5%), followed by 11 to 15 persons (12.1%), 16 to 20 persons (1.0%), then 26 persons and above (1.3%). The largest proportion of the respondents (43.3%) were illiterates (no formal education). Then, 28.6%, 23.1% and 3.4% had primary, high school and university education, respectively (Table II. I). Fishers interviewed in this study were belonged 14 ethnic groups. The ethnic groups with the highest proportion were Agni (19.7%), Baoule (17.1%) and Bozo (16.5%).

II.3.2 Livelihood strategies of the fishers

Whereas 80% of the respondents were engaged in fishing as their main occupation, 14.2% were only engaged in fish trade. The remaining percentage was shared among farming, teaching and shopkeeping. Regarding the secondary occupation, respondents were mostly involved in farming (59.1%), followed by fishing (3.9%), fish trading (2.6%), livestock farming (1.6%), and others (11.8%). Around 21% of respondents were not engaged in any secondary activities.

Concerning fishers' monthly incomes, the arithmetic mean monthly income was about 130 €, with a minimum of 15 € and a maximum of 763 €. However, it varied among the climate zones. Thus, Guinean climate zone fishers had the highest mean monthly incomes of about 145€. Comparatively, Sudano-Guinean climate zone fishers recorded the middle monthly mean income (126 €), more than those of Sudanian climate zone with the lowest one (93 €). The complete results of the interviewees' livelihood are presented in Tables II. II and II. III.

II.3.3 Fishers' perception of climate change, its drivers, and its impact on Ivorian freshwater fish abundance

About 72.7% of fishers were aware of climate change, whereas 27.3% were not. Of the total percentage of the respondents who were aware of climate change, 53% and 24% believed that the drivers of climate change are deforestation and greenhouse gas emissions, respectively, whereas 20% of the respondents attribute the cause of climate change to the will of God, 2% believe that natural processes such as volcanic eruptions are the main cause of climate change, and 1% did not know (Figure 2. 2). A decrease in precipitation (87.9%) and an increase in temperature (76.1%) were observed by respondents. Additionally, interviewees testified to having observed delay in the onset of the rainy season and its length shortening (Figure 2. 3). Concerning the occurrence of floods, 55.6, 3.7, and 40.7% of the respondents observed an increase, decrease and no change respectively (Figure 2. 3).

Table II. I: Overview of the socio-demographic background of 381 respondents to a questionnaire on the perception of climate change and changes in fish biodiversity and their potential drivers in Côte d'Ivoire.

Respondents	Frequency	Percentage	Respondents	Frequency	Percentage
Gender			Ethnic group		
Female	69	18.1	Abron	1	0.3
Male	312	81.9	Agni	75	19.7
Total	381	100	Apollo	4	1
Age			Bambara (Mali)	17	4.5
[20–29]	52	13.6	Baoulé	65	17.1
[30–39]	119	31.2	Bozo (Mali)	63	16.5
[40–49]	121	31.8	Dioula	8	2.1
[50–59]	68	17.8	Guéré	57	15
≥ 60	21	5.5	Keke (mali)	3	0.8
Total	381	100	Koroboro (Mali)	7	1.8
Marital status			Samogo	57	15
Married	322	84.5	Senoufo	14	3.7
Single	58	15.2	Songhaï (Mali)	9	2.4
Divorce	1	0.3	Tagbana	1	0.3
Total	381	100	Total	381	100
Household size			Watershed		
[1–5]	154	40.4	Bia river	58	15.2
[6–10]	172	45.1	Lake Ayame	58	15.2
[11–15]	46	12.1	Lake Buyo	48	12.6
[16–20]	4	1	Lake faye	55	14.4
≥ 26	5	1.3	Lake Kan	64	16.8
Total	381	100	River Bagoue	54	14.2
Education level			River Nzo	44	11.5
No formal education	165	43.3	Total	381	100
Primary	109	28.6	Climate zone		
Junior high school	63	16.5	Guinean climate	171	44.9
Senior high school	25	6.6	Sudano-guinean climate	156	40.9
University	13	3.4	Sudanian climate	54	14.2
Koranic school	6	1.6	Total	381	100
Total	381	100			

Table II. II: Livelihood strategies of 381 respondents to a questionnaire on the perception of climate change and change in fish biodiversity and their potential drivers in Côte d’Ivoire.

Respondents	Percentage	Respondents	Percentage
Main occupation		Secondary occupation	
Fishing	80	Fishing	3.9
Fish Trading	14.2	Farming	59.1
Farming	3.4	Fish Trading	2.6
Teaching	0.3	livestock farming	1.6
Shopkeeping	2.1	None	21
Total	100.0	Other	11.8
		Total	100

Table II. III: Monthly income of 381 respondents to a questionnaire on the perception of climate changes and changes in fish biodiversity and their potential drivers, from three Ivorian climatic zones.

Climate zone	Mean	Standard Deviation	Minimum	Maximum	% of Total N
Monthly income (€)					
Guinean climate	145	7.34	15	610	44.9%
Sudano-guinean climate	126	8.24	17	763	40.9%
Sudanian climate	93	7.63	15	183	14.2%
Total	130	4.91	15	763	100.0%

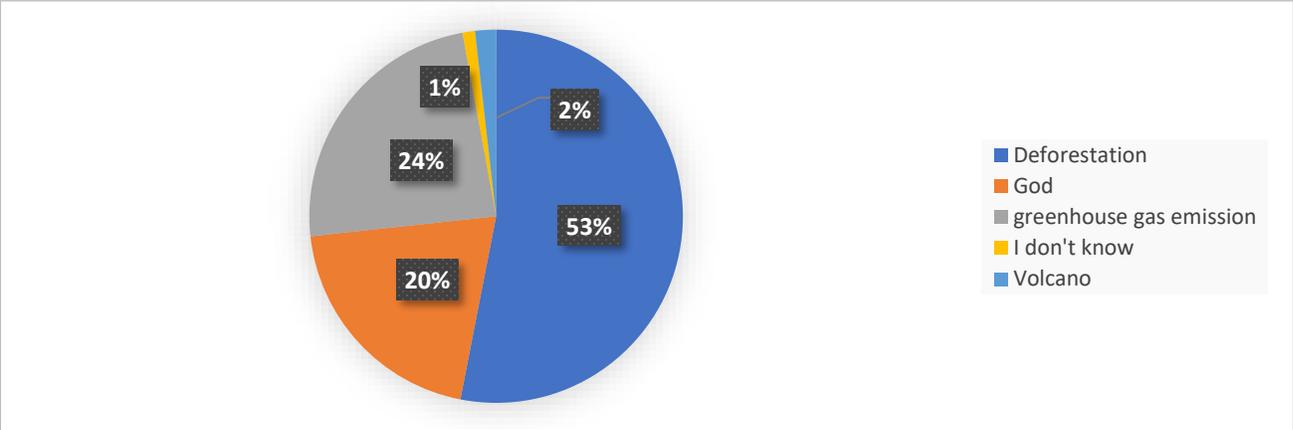


Figure 2. 2: Distribution of the 381 Ivorian fishers interviewed according to their perception of the causes and factors of climate change.

Most of the fishers reported significant decreases in fish abundance (81.6%), while 10.0, 3.4, and 5% observed little, moderate and no decrease, respectively. Concerning the impact of climate change on fish abundance, the respondents stated that temperature change has mainly led to a decrease in fish abundance (65.9%), while 3.4% of the respondents argued that change in temperature has led to an increase in fish abundance, 22.8% observed no effect and 7.9% did not know. As far as the effect of change in precipitation on the fish abundance is concerned, 71.1% of the respondents specified that it has led to a decrease, 8.1% to an increase, and 5% did not know. For the remaining 15.7%, change in precipitation has not affected fish abundance.

II.3.4 Fishers' perception of the Anthropogenic stressors on freshwater fish

Table II. IV shows the perception of interviewees on the impact of human activities on the Ivorian freshwater fish. Gold mining, water withdrawal for human needs, use of small-mesh fishing nets, overfishing, industrial waste discharge, pesticides use for agricultural purposes along watersheds, obnoxious fishing practices and increase in human population, were identified by Ivorian fishers as the major anthropogenic perturbations affecting Côte d'Ivoire freshwater fish biodiversity. Specifically, fishers of Bia River argued that the river is mainly impacted by obnoxious fishing practices (44.8%), overfishing (31.0%) and gold mining (22.4%). The use of small-mesh fishing nets (1.7%) was also identified as a stressor for the fish biodiversity of this river. Fishers in Ayame artificial lake, resulting from the construction of the hydroelectric dam on Bia River, identified in decreased order, gold mining (44.8%), overfishing (41.4%), water withdrawal and obnoxious fishing practices as stressors of the fish biodiversity in this lake. Use of small-mesh fishing nets, water withdrawal and industrial waste discharge were recognised as factors threatening fish diversity of Faye lake. Pesticides used for agricultural purposes along watersheds were implicated as the main human activity that threatens Buyo lake and Nzo River fish communities. Regarding Kan Lake located within the Sudano-Guinean climate zone and Bagoue river located in the Sudanian climate zone, overfishing was perceived to be the principal factor of fish biodiversity decline.

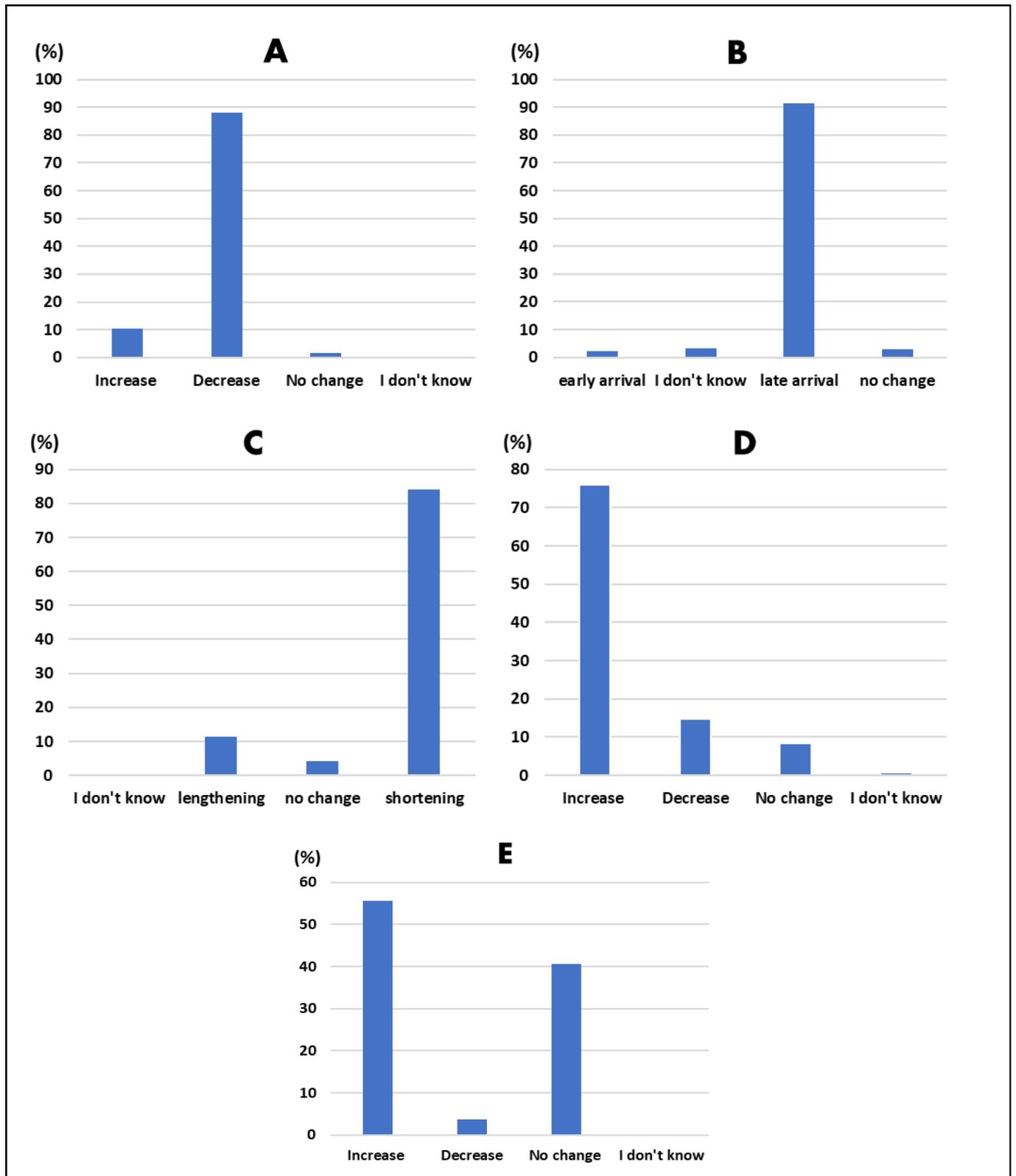


Figure 2. 3: 381 Fishers’ responses concerning their perception of (A) change in rainfall, (B) change in rainy season timing and (C) length, (D) change of temperature, and (E) change in flooding occurrence in Côte d’Ivoire.

y axis is the respondent percentage, x axis represents the categories of responses in the considered change climate attribute.

Table II. IV: Anthropogenic activities threatening Ivorian freshwater fish biodiversity according to fishers of the watersheds sampled.

Watershed	Stressor	Percentage (%)
Bia river (N=58)	Obnoxious fishing practices	44.8
	Gold mining	22.4
	Overfishing	31.0
	Use of small-mesh fishing nets	1.7
	Total	100
Lake Ayame (N=58)	Gold mining	44.8
	Overfishing	41.4
	water withdrawal for human needs	6.9
	Obnoxious fishing practices	6.9
	Total	100
Lake Faye (N=55)	Use of small-mesh fishing nets	16.4
	Water withdrawal for human needs	14.6
	Industrial waste discharge	12.7
	Overfishing	10.9
	Hydrological dams	1.8
	None	43.6
	Total	100
Lake Buyo(N=48)	Pesticides use for agricultural purposes along watersheds	66.7
	Overfishing	10.4
	Water withdrawal for human needs	4.2
	Obnoxious fishing practices	4.2
	I don't know	14.6
	Total	100
Nzo river(N=44)	Pesticides use for agricultural purposes along watersheds	97.7
	I don't know	2.3
	Total	100
Lake Kan (N=64)	Overfishing	40.6
	Pesticides use for agricultural purposes along watersheds	18.8
	None	40.6
	Total	100
River Bagoue(N=54)	Overfishing	42.6
	Obnoxious fishing practices	20.4
	Increase in population growth	3.7
	None	20.4
	I don't know	12.9
	Total	100

II.3.5 Fish species locally under threat according to the fishers

This section summarizes the fish species within Ivorian freshwaters for which fishers perceived drastic population declines, such that they are considered to be very scarce over the past years. *Coptodon zillii* and *Malapterurus electricus* were the principal fish species listed as threatened by Bia River fishers, while those of Ayame lake mainly identified *Heterotis niloticus* and *Parachanna obscura*. *Labeo cubie*, *Parachanna obscura* and *Coptodon zillii* species were mostly reported threatened within buyo Lake. Meanwhile, *Heterotis niloticus* was the only species reported threatened by Faye Lake fishers. About 89.1% of the interviewees from the area surrounding Kan Lake identified *Coptodon zillii* as under threat in this lake. Regarding River Bagoue and lake Nzo, no species was identified by the fishers as being threatened in these water bodies (Table II. V).

II.3.6 Factors influencing fishers' awareness of climate change and perception of change climate

Tables II. VI and II. VII present the results of the multinomial logit regression models concerning the variables that influence respondents' awareness and perception of climate change.

Variables such as climatic zone, household size and education level were significantly associated with respondents' awareness of climate change. Positive relationships between respondents' education level and awareness of climate change were found, meaning that respondents' awareness increased with high education level. The same positive relationship was found with respondents' household size, which increased fishers' awareness of climate change. However, a negative relationship was obtained between fishers' awareness of climate change and the climate zone. Thus, respondent awareness of climate change decreased when going from the Guinean forest zone to the Sudanian savanna zone.

Concerning fishers' perception of climate change, age, household size, gender, and education level were strongly influencing fishers' perception of change in rainfall. A decrease in rainfall was mainly observed by young adults, males, and low education level fishers. Perceived change in temperature was significantly influenced by fishers' fishing watersheds and ethnic groups. Perception of temperature decreases decreased when going from Bia River, Lake Ayame, Lake Buyo, Lake Faye, Lake Kan, Bagoue River to Nzo River fishers. Perceived change in flooding was significantly determined by watersheds, ethnic group, main occupation and household size.

Table II. V: Fish species locally threatened according to fishers of the sampled watersheds.

Watershed	<i>Heterotis niloticus</i>	<i>Coptodon zillii</i>	<i>Malapterurus electricus</i>	<i>Lates niloticus</i>	<i>Parachanna obscura</i>	<i>Sarotherodon galilaeus</i>	<i>Labeo cubie</i>	<i>Polypterus endlicheri</i>	None species	Total (%)
Bia river (N=58)	-	36.2	27.6	10.3	8.6	3.5	-	-	13.8	100
Lake Ayame (N=58)	50	8.6	3.5	-	31	1.7	-	-	5.2	100
Lake Buyo (N=48)	22.9	-	-	-	27.1	-	39.6	2.1	8.3	100
Lake Faye (N=55)	12.73	-	-	-	-	-	-	-	87.27	100
Lake Kan (N=64)	-	89.1	-	-	1.6	-	-	-	9.4	100
River Bagoue (N=54)	-	-	-	-	-	-	-	-	100	100
River Nzo (N=44)	-	-	-	-	-	-	-	-	100	100

Values are given in percentage (%) per total number of respondents (N) in the specific sampling site.

Table II. VI: Influence of socio-demographic factors on Ivorian fishers' awareness of climate change revealed by multinomial logistic regression.

Explanatory variable	Awareness of climate change
	Coef ^{Sig} (St. Err)
Climatic zone	-0.730* (0.287)
Fishing watershed	-0.012 (0.101)
Age	0.119 (0.146)
Ethnic group	-0.068 (0.051)
Gender	0.016 (0.445)
Household size	0.411* (0.189)
Education level	0.580** (0.104)
Main occupation	0.036 (0.276)
Residual Deviance	361.11
AIC	379.11

* $\alpha < 0.05$; ** $\alpha < 0.01$

Significant correlations are in bold, with the level of significance indicated by stars, and standard errors in brackets.

Table II. VII: Influence of socio-demographic factors on Ivorian fishers' perception of climate change revealed by multinomial logistic regression.

Explanatory variable	Perceived Change in rainfall		Perceived Change in temperature		Perceived Change in flooding	
	Increase	Decreased	Increase	Decreased	Increase	Decreased
	Coef ^{Sig} (St. Err)	Coef ^{Sig} (St. Err)	Coef ^{Sig} (St. Err)	Coef ^{Sig} (St. Err)	Coef ^{Sig} (St. Err)	Coef ^{Sig} (St. Err)
Climatic zone	-3.117 (2.384)	-0.907(2.307)	0.478 (0.401)	0.671(0.628)	-1.445** (0.302)	0.519 (0.819)
Fishing watershed	-0.539 (0.514)	-0.733 (0.486)	0.214 (0.175)	-0.641** (0.248)	0.670** (0.106)	-0.370 (0.328)
Age	-1.235 (0.690)	-1.527* (0.663)	0.458 (0.238)	-0.069 (0.309)	-0.230 (0.141)	-0.245 (0.337)
Ethnic group	0.543 (0.398)	0.616 (0.392)	-0.280** (0.069)	-0.197* (0.089)	-0.302** (0.049)	-0.039(0.120)
Gender	12.139** (0.412)	14.398** (0.412)	1.884(1.342)	3.366** (1.388)	0.271 (0.416)	1.115 (1.182)
Household size	-2.195** (0.821)	-1.773** (0.762)	0.140 (0.330)	0.496 (0.397)	0.261 (0.188)	0.695* (0.344)
Education level	-1.814* (0.728)	-1.530* (0.717)	-0.016 (0.127)	-0.053 (0.161)	-0.058 (0.089)	0.141 (0.198)
Main occupation	-0.066 (0.794)	-0.870 (0.764)	-0.319 (0.460)	-0.007(0.463)	0.305 (0.204)	-12.793** (0.00002)
Residual Deviance	236.66		421.86		483.83	
AIC	272.66		475.86		519.83	

* $\alpha < 0.05$; ** $\alpha < 0.01$

Significant correlations are in bold, with the level of significance indicated by stars, and standard errors in brackets.

II.3.7 Factors determining fishers' perception of change in fish abundance

Change in fish abundance was significantly associated with respondents' age, education level, ethnic group and climate zone. Perceived decrease in fish abundance (low, moderate, and significant) increases with an increase in respondents' ages. Positive relationships between fishers' education level and their perception of a significant decrease in fish abundance were observed (Table II. VIII). Fishers' perception of a significant decrease in fish abundance increased when going from the Guinean climate zone to the Sudanean zone.

Table II. VIII: Influence of socio-demographic factors on Ivorian fishers' perception of change in fish abundance revealed by multinomial logistic regression.

Explanatory variable	Perceived Change in fish abundance		
	Low decrease	Moderate Decrease	Significant Decrease
	Coef ^{Sig} (St. Err)	Coef ^{Sig} (St. Err)	Coef ^{Sig} (St. Err)
Climatic zone	0.156(1.041)	0.378(1.160)	2.364* (0.965)
Fishing watershed	-0.294 (0.301)	-0.851 (0.483)	-1.009** (0.274)
Age	1.604** (0.556)	1.909** (0.646)	1.607** (0.532)
Ethnic group	0.219 (0.164)	0.858** (0.227)	0.123 (0.156)
Gender	1.633 (2.231)	0.249 (3.157)	-1.205 (2.175)
Household size	-0.430 (0.539)	-1.123 (0.855)	0.100 (0.479)
Education level	0.365 (0.240)	0.083 (0.347)	0.491* (0.220)
Main occupation	-3.218 (2.427)	0.222 (2.906)	1.708 (2.165)
Residual Deviance		334.245	
AIC		388.245	

* $\alpha < 0.05$; ** $\alpha < 0.01$

Significant correlations are in bold, with the level of significance indicated by stars, and standard errors in brackets.

II.4 Discussion

Climate change has become the focus of scientists, politicians, policymakers and the general public since the last decade. The representatives of indigenous peoples have been pushing to engage with climate change agreements since the adoption of the Kyoto Protocol in 1997 (Etchart, 2017). This study, which aims to capture Ivorian local fishers' perceptions and personal experience of climate change, represents an important contribution to the global effort of combating and reducing climate change. Fishers are directly dependent on the aquatic ecosystems for their livelihoods. Thus, understanding their perception and knowledge of climate change is an essential step towards developing and implementing adaptation and mitigation strategies to deal with the effects of climate change on aquatic ecosystems.

The high proportion of awareness of climate change obtained is consistent with a study of Taderera (2010) who argued that the majority of Africa's citizens are aware of change in climate patterns. Many other studies conducted in several parts of Africa found similar results with households (Amos *et al.*, 2015), farmers (Agwu *et al.*, 2018) and fishers (Bah *et al.*, 2018; Utete *et al.*, 2019). Since the twentieth century, increases in temperature and decreases in precipitation have been experienced in Côte d'Ivoire (Bernard, 2014; Soro *et al.*, 2016). In our study, fishers mainly observed an increase in temperature, a decrease in precipitation and an increase in flood occurrence. Ivorian fishers are therefore well informed of the climate trend. Being aware of local perception and knowledge of climate change is essential for formulating climate change education, communication interventions, and for effectively implementing risk reduction strategies (Owusu *et al.*, 2019). Our result, which suggests that most of the Ivorian fishers are well informed about climate change, is a positive feature for global actions against climate change in Côte d'Ivoire. Local fishers should be associated with the process of decision-making concerning climate change adaptation and mitigation strategies. According to previous studies, the demographic background of individuals represents an important factor that influences their awareness and perception of climate change (Agwu *et al.*, 2018; Amos *et al.*, 2015; Combest-Friedman *et al.*, 2012; Owusu *et al.*, 2019). For instance, Owusu *et al.* (2019) have shown that sociodemographic factors such as gender, age and education have a great influence on farmers' knowledge and perception of climate change. The result of the multinomial logit regression model, which highlighted the significant importance of demographic variables such as age, gender, household size ethnic group and education level in

fishers' awareness and perception of climate change, corroborates these findings. Interviewees' awareness of "climate change" was positively influenced by educational level. Our finding is consistent with those of Amos *et al.* (2015) and Nzeadibe *et al.* (2012) which showed an increase of respondents' knowledge of climate with education level. Thus, people with higher educational levels are more likely to get access to information related to climate change than those with low educational levels. The same observations were done by Yu *et al.* (2020), where higher levels of knowledge of individuals allowed them to better assess the threats posed by climate change and reduced the perceived level of uncertainty related to climate change and the impact of pro-environmental behaviours.

The results showed a mean monthly income of fishers of 130 €, with a minimum of 15 €. This average income is very close to the minimum wage in Côte d'Ivoire, which is around 115 €, indicating the high level of poverty in these communities. The low incomes also indicate that these fishers are very vulnerable to any reduction in fisheries resources. Fishers of the Sudanian climate zone in the northern have the lowest monthly mean income (93 €). This low income may be due to the low purchasing power of the local populations in this region, who are the main customers of the fishery catches. The high incomes of fishers in the Guinean climate zone may be because the economic activities of Côte d'Ivoire are concentrated in this part of the country, which increases the fishers' market opportunities and thus their income. The average income of the fishers in this study is comparatively high compared to those of fishers in Lake Victoria, Kenya, which have been estimated at 792 €/year, or about 66 €/month (Odada *et al.*, 2006).

Freshwater fishes represent an important and vital component of the food of many people in sub-Saharan Africa (Smith *et al.*, 2009). Our study suggests that most of the respondents observed significant declines in fish quantity. Climate change, especially changes in temperature and rainfall were acknowledged to contribute to this decline in Ivorian freshwater fish abundance. Additionally, many anthropogenic activities including gold mining, water withdrawal for human needs, use of small-mesh fishing nets, overfishing, industrial waste discharge, pesticides use for agricultural purposes along watersheds, obnoxious fishing practices and increase in human population, were listed by fishers as other stressors contributing in depletion of Ivorian freshwater fish abundance. Since the independence of Côte d'Ivoire, a set of laws and regulations has been adopted for the sustainable management of the fisheries sector (FAO, 2008). The most recent is the law n° 2016–

554 of 26 July 2016 on fisheries and aquaculture, which provides dispositions relating to the regulation and sustainability of aquatic resources, in particular in its articles 8, 9, 10, 11 and 12 (Assemblée nationale, 2016). The dispositions in these articles define the set of measures such as the types of fishing engines allowed, the size of fishing nets allowed, the prohibition of fishing on protected species, the prohibition of the use of any explosive materials, toxic substances or baits likely to weaken, stun, excite or kill aquatic resources or to infect their habitats, etc. However, based on information provided by fishers, there is clear evidence of a lack of application of these measures by fishers' communities. Thus, awareness-raising campaigns on the important values of freshwater ecosystem biodiversity, especially those of fish species, for human livelihoods, and the necessity to preserve these ecosystems for the benefit of future generations are necessary. Similarly, populations living in areas surrounding freshwater habitats should be informed on practices that negatively impact the biodiversity of freshwater ecosystems. In addition, further measures such as a prohibition on fishing during reproduction seasons of fish species, introduction of laws imposing prison sentences to those engaged in obnoxious fishing practices, establishment of buffer zones between watersheds and agriculture farms in order to prevent pesticides used in agriculture to get water bodies, enforcement of mining and agricultural industries to treat their waste before discharging it into waterways, should be taken by the Ivorian government in agreement with local fishery management authorities. These additional measures will contribute to strengthening the existing aquatic resources management policy, then allow the sustainable use of these resources. To reduce the effect of climate change on fish abundance, greenhouse gas emissions and deforestation must be reduced, and reforestation campaigns should be increased all over the country. Another solution for the mitigation of climate change is the protection of watershed forests.

The listed factors threatening Ivorian freshwater fish biodiversity in our study are among the wide spectra of factors threatening Africans' freshwater ecosystems in general. Indeed, according to Smith *et al.* (2009), climate change, water pollution, habitat loss due to deforestation, overfishing, mining, and agriculture represent the greatest threats to freshwater fishes in Africa and specifically in West Africa (Smith *et al.*, 2009). For instance, the impact of climate change was observed in Lake Chad located in West Africa between 1960s and 2001, where the surface area of water was reduced to 5.4% of its initial level (50% caused by climate change), leading to the loss of many aquatic organisms' taxa (Darwall *et al.*, 2011; Peitersen and Beekman, 2006). Also, according to García *et al.* (2010), natural disasters (e.g., droughts) represent the second most serious cause of

decline for around 70% of the freshwater fishes in northern Africa. In Kinshasa and Lagos, pollution from oil exploration, cars in the cities, factories or other urban industries, and from boat traffic are impacting freshwater ecosystems. Pollution from oil exploration, combined with habitat loss, specifically threatens many restricted-range species in the Niger Delta and may pose a threat to species in coastal freshwater of the Republic of Congo, Cabinda, Gabon and Angola (Darwall *et al.*, 2011). Congo freshwater ecosystem was additionally reported to suffer from mercury discharge linked to gold mining activities. In Lower Guinea, freshwater species are particularly threatened by intensive land use and pollution from rubber, banana, and palm oil plantations (Darwall *et al.*, 2011). Another example is the case of eastern slopes of Mount Cameroon, where freshwater fish biodiversity is impacted by habitat loss due to agriculture. In Benin and the Volta region of Africa, overfishing was reported to cause changes in fish community structures and distributions (Helfman, 2007; Smith *et al.*, 2009).

Research studies examining the survival of extremely rare, cryptic or possibly extinct species often rely on local knowledge rather than on direct study of these species. While there is considerable potential for error and bias in the collection and interpretation of traditional ecological knowledge from local informants (McKelvey *et al.*, 2008), this research approach provides a unique source of data with substantial applicability for conservation (Turvey *et al.*, 2010; Drew, 2005). Fish species populations declines have been supported by fishers' perceptions in several studies that have assessed freshwater fish species (Turvey *et al.*, 2010) and marine ones as well (Bender *et al.*, 2013; Lavides *et al.*, 2010; O'Donnell *et al.*, 2010). The study of Bender *et al.* (2013) in the Eastern Brazilian Marine Park corroborated the decline of seven of the reef fish species by fishers. These declines were mostly due to heavy fishing pressure and overfishing along the Brazilian coast. Another example is the study of Turvey *et al.* (2010) in China, which demonstrated the strong awareness of fishers of the major declines in many fish species in the Yangtze River in recent decades. In our study, the species reported by respondents as locally scarce or under threat or with their populations in depletion are all classified in the category of least concern in the IUCN red list. *Heterotis niloticus* is a pelagic species that frequents shallow waters of rivers and lakes for the adults, and marshy places among aquatic vegetation for the young (Diouf *et al.*, 2020a). *Coptodon zillii*, *Parachanna obscura* and *Lates niloticus* are demersal and potamodromous species. *Coptodon zillii* is caught in shallow marginal waters, drowned forest areas and also on sandy shores (Lalèyè, 2020b). *Lates niloticus* inhabits channels, lakes and irrigation canals, and prefers sandy bottoms, but

is also found in rocky to muddy bottoms. Vegetated areas in calm waters provide shelter for its larvae and young (Froese and Pauly, 2003). *Parachanna obscura* is a deep-water inhabitant and migratory freshwater species found mainly in floodplains, swamps, rivers, lakes, ponds and streams (Teugels, 2003). This species breeds throughout the year, but preferably during and just after floods. *Sarotherodon galilaeus* is also demersal and occurs in the shallow coastal waters of lakes and prefers open water, but juveniles and breeding adults can be found offshore (Diallo *et al.*, 2020a). In lakes, it is often associated with beds of submerged vegetation. *Malapterurus electricus* inhabits shallow waters with muddy or sandy bottoms, close to rocky areas, and prefers stagnant or slow-moving water (Diouf *et al.*, 2002b). *Labeo coubie* is a benthopelagic and potamodromous species living in rivers and lakes, and mainly sheltered bays (Diallo *et al.*, 2020a). All of these species breed on seasonal floodplains, overflowed areas or in marginal vegetated areas of the catchment. Thus, any change in the rainy season pattern (late or early arrival, shortening, etc.) or any reduction in rainfall can disrupt their reproduction and spawning. Also, given that fish are often adapted to a certain level of hydrological variability, changes in this variability could have negative effects on fish populations (Ficke *et al.*, 2007). Unusually large floods or seasonal pulses can displace adults and displace or injure juveniles and larvae, and droughts or prolonged dry spells can lead to population declines as well as reductions in abundance and changes in species composition (Ficke *et al.*, 2007; Matthews and Marsh-Matthews, 2003). According to the fishers, there has been a decrease in rainfall and a change in the onset and length of the rainy season as well as an increase in floods occurrence. Thus, this can probably explain why these species were reported as locally threatened by respondents. Freshwater fish are all exotherms, unable to regulate their body temperature by physiological means and having a body temperature virtually identical to that of their environment (Ficke *et al.*, 2007). Consequently, increasing global temperatures can affect them by altering physiological functions such as thermal tolerance, growth, metabolism, food consumption, reproductive success and the capacity to maintain internal homeostasis in the face of a variable external environment (Fry, 1971). Fish populations that experience changing thermal regimes may increase or decrease in abundance, experience range expansions or contractions, or be threatened with extinction (Ficke *et al.*, 2007). The increase in temperature observed by fishers can illustrate the decline of the population of these species. In addition, due to the preference of these species for vegetation or forest areas, agriculture expansion and pesticide use along watersheds may pose a threat to their habitat and populations. Agriculture and pesticide use along watersheds were

listed by the fishers in this study among anthropogenic activities threatening the Ivorian freshwater ecosystem. Most of the species listed are among the main species of the Ivorian fishery (Kassoum, 1996). Overfishing has been reported by fishers as one of the threats to the biodiversity of Ivorian freshwater fish. Thus, it may represent one of the probable causes of the rarity of these species. According to the result of a recent study on the assessment of the conservation status and the vulnerability of the ichthyofauna of the Bandama River in Côte d'Ivoire, species such as *Lates niloticus*, *Labeo coubie*, *Heterotis niloticus* and *Sarotherodon galilaeus*, despite their status as species of least concern, were assessed as vulnerable to fishing pressure (Ouattara *et al.*, 2021). Many other studies carried out on the African continent have reported that these species are locally threatened by many humans' actions and climate change. *Lates niloticus* is reported to suffer from over-exploitation in much of its native range, and to a lesser extent, pollution (Lalèyè *et al.*, 2020c). *Heterotis niloticus* and *Parachanna obscura* are also affected by overfishing in central and western Africa respectively, where they represent commercially important fish species (Diouf *et al.*, 2020a; Lalèyè, 2020a). *Malapterurus electricus*, *Sarotherodon galilaeus*, *Coptodon zillii* and *Labeo coubie* are threatened by dam constructions, water pollution, groundwater extraction and drought in northern Africa, whereas *Malapterurus electricus* and *Sarotherodon galilaeus* are additionally affected by overfishing in eastern Africa (Diallo *et al.*, 2020a; Diallo *et al.*, 2020b; Diouf *et al.*, 2020b; Lalèyè, 2020b).

II.5 Conclusion and perspectives

Côte d'Ivoire is a climatically diverse country with a great diversity of freshwater ecosystems. The results of this study show good awareness among local fishers of climate change and its drivers. The high proportion of climatic awareness in fishers' communities represents a positive prerequisite for the implementation of measures toward climate mitigation and population adaptation. Fish abundance reduction was also reported as a consequence of climate change and several anthropogenic activities. Many fish species were listed by respondents as being locally threatening in Ivorian freshwater ecosystems.

In response to the reduction in fish quantity, the government must ensure the strict application of policies and regulations in force in the fisheries sector, through the establishment of local management and monitoring committees. These should be done by involving fishers' associations (or cooperatives) in the process of decision-making, implementation, and monitoring. This will

improve the effectiveness of actions and contribute to the sustainable management of fisheries resources. In addition, to enable fishing communities to adapt to the decline of fish, they need to be trained to diversify their sources of income. For example, training them in agriculture (livestock, aquaculture, etc.) or other activities such as mechanics, commerce, electricity, etc. This will not only augment their living income (estimated as very low) and strengthen their adaptive capacities, but also reduce excessive pressures on aquatic ecosystems. All these measures should be implemented through fishers' associations or cooperatives. In Côte d'Ivoire, fishers are mainly organized in cooperatives or associations. The roles of these cooperatives or associations are most often to contribute to food security, poverty eradication, promotion of collective action, empowerment of fishers to respond to environmental and socio-economic changes, and sharing of responsibility in the practice of responsible fishing, but also to have a good voice in the social-economic process. However, the movement of cooperatives or associations in the fisheries sector is characterized by a lack of dynamism in Côte d'Ivoire. Those function with difficulty, thus giving the impression that there are no existing fisheries actors. Thus, the government should first revitalise the associations or cooperatives by providing financial support, but also train them on their roles and duties.

The information provided by fishers constitutes basic information on the evolutions and the main factors impacting fish abundance in Côte d'Ivoire. These are useful for directing and approving adaptation and management strategies of fish resources. These results should be supported by further studies that will focus on quantifying the level of decrease in fish quantity, the contribution of each threat in this decline, the level of correlation between these threats, the identification of the most impactful threats, and the assessment of the vulnerability and the already existing local adaptation strategies in Ivorian local fishers' communities. These will give a clear view on which management strategies will be more appropriate for the sustainability of fish resources and how to improve the existing adaptation strategies. Fish species listed by fishers as being threatened are economically among the most important fish species for the livelihood of many African countries, especially in Côte d'Ivoire. The reassessment of the local status of these species using IUCN criteria is needed to guide management and conservation policies. Furthermore, more research studies are needed to assess and quantify the vulnerability of these species to climate change and human activities. The assessment of the distribution, genetic diversity and population dynamics of these species will also be necessary to develop appropriate management and conservation policies.

CHAPTER III:

Local fishers' knowledge on the ecology, economic importance, and threats faced by populations of African snakehead fish, *Parachanna obscura*, within Côte d'Ivoire freshwater ecosystems.

Abstract

Traditionally, population sizes, ecology and threats to species and their habitats have been obtained by empirical scientific studies. However, the knowledge of local and indigenous communities worldwide has been acknowledged as an extremely rich and underused source of information on how the environment, biodiversity and local conditions are changing over time. In this view, the objective of the study was to investigate local fishers' knowledge of local names, habitats, uses, market price, change in population abundance and threats faced by the snakehead fish (*Parachanna obscura*) in Ivorian freshwaters. The study was conducted using face-to-face interviews and a structured questionnaire with 381 fishers during the period October 2020 to February 2021. The results show that this fish species is strongly appreciated, for the good taste of its flesh, with market prices varying between 1.5 and 3 € on average. All respondents confirmed that the species is not yet produced in aquaculture, and mentioned their willingness to support its introduction into aquaculture. Several local names of *P. obscura* fish were recorded, with “Sounôgô-djêguê” (used in 36% of fishers' ethnic groups), “Pino” (21%) and “Édjoué-bile” (21%) being the most popular names used in Ivorian fishers' communities. All respondents agreed that *P. obscura* is a potamodromous fish species living preferably in wetlands, rivers, lakes and streams. A significant decrease in the abundance of this fish was observed by 71% of fishers, perceived mainly due to overfishing, deforestation around watersheds, habitat destruction/modification, obnoxious fishing practices, pesticide use in farms close to watersheds and climate change, especially lack of rainfall. The study demonstrated the importance of local ecological knowledge of fishers in identifying threats to fish populations, habitat types used by the species, and other relevant information, and therefore this ecological knowledge has to be integrated into biomonitoring and conservation policy of aquatic biodiversity. The information obtained from this study are also helpful for future studies on the management and cultivation of this species.

Keywords: *Parachanna obscura*, local names, habitats, climate change, overfishing, habitat modification.

III.1 Introduction

The goods and services resulting from freshwater ecosystems have an estimated global value of up to USD 15 trillion. This sum includes essential products such as food and drinking water in addition to services such as water filtration and flood control (Millennium Ecosystem Assessment, 2005). Fishes form the most important freshwater product globally, and provide the primary source of protein for almost 3.3 billion people worldwide (FAO, 2020). Africa's freshwater fishery harvest is estimated to be around 2.5 million tonnes per year, accounting for nearly 25% of the world's freshwater capture (Kpogue *et al.*, 2012a). It provides essential nutrition for the poorest of communities and is a source of employment and income for many African people (WorldFish Center, 2008; Smith *et al.*, 2009). Despite the importance and enormous contribution of freshwater fish to fish production in Africa, most African countries cannot entirely satisfy their national demand of fish products (Kpogue *et al.*, 2012a), and still depend on imports of fish. Accordingly, the development of aquaculture through the farming of local African freshwater species is needed (Kpogue *et al.*, 2012a).

In Côte d'Ivoire, fishes represent about 50% of animal protein sources (COMHAFAT, 2014). Unfortunately, the country remains highly dependent on imports to satisfy its national demand for fishery products (COMHAFAT, 2014). National fish production is about 50,000 tonnes on average per year, while there is a need for more than 360,000 tonnes, the difference being filled through imports. These imports represent a value of around 289 million euros, resulting in a trade deficit (COMHAFAT, 2014). The country has considerable potential for the development of aquaculture, if their natural resources are considered. One fish species of interest is *Parachanna obscura*, also known as snakehead fish, belonging to Channidae family. The genus *Parachanna* includes two others species, notably *Parachanna africana* and *Parachanna isignis* (Bonou and Teugels, 1985). *Parachanna obscura* is the most popular and widespread African Channidae (Bonou and Teugels, 1985). It is generally distributed in the intertropical convergence zone where the water temperature ranges from 26 ° C to 28 °C, principally in West Africa. Nevertheless, it is also found in the upper course of the White Nile, the Chad lake basin, and the Congo River basin (Teugels, 2003; UA, 2013; Lalèyè, 2020a). It represents a valuable fish resource for African populations due to its high nutritional value and economic potential (Odo *et al.*, 2012). While these fish are rarely used in aquaculture, they represent future potential for increasing Ivorian aquaculture productivity.

However, some preliminary studies and information about biology, reproduction, ecology, and market price are needed before aquaculture of the species could start.

Previous studies carried out in Côte d'Ivoire and other parts of Africa mostly focused on *P. obscura* biology (Odo *et al.*, 2012; Bolaji *et al.*, 2011) and reproduction (Vodounnou *et al.*, 2017; Kpogue *et al.*, 2012b; Agokei and Hart, 2010). However, there is a gap in information related to the goods and services provided by this fish to Ivorian local fishers. Also, regarding the past, current and future trends of climate change and the rate of urbanization, more information is needed on the threats to which *P. obscura* are exposed. Indeed, in Côte d'Ivoire, the urbanization rate increased from 18% to over 50% between 1960 to 2018 (USAID, 2017). The climate has also considerably changed in the country over the twentieth century, and it is expected to continue changing in the future. According to the prediction of Intergovernmental Panel on Climate Change under the RCP4.5 scenario, the temperature will rise by 3°C by 2100, over most of Côte d'Ivoire. The daily precipitation is predicted to drop by 8% during the season from April to July for the next hundred years (Bernard, 2014). Aquatic organisms are very sensitive to any change in their environment (Amoutchi *et al.*, 2021). Freshwater organisms record the highest proportion of species globally categorized as extinct or threatened in the International Union for Conservation of Nature (IUCN) Red List (Costello, 2015; IUCN, 2022). Climate change and human actions such as water pollution, water extraction, overexploitation, habitat loss or transformation and dam construction have been acknowledged to stress Africa's freshwater biodiversity (Darwall *et al.*, 2011). Thus, providing information on *P. obscura* will be helpful for decision making about its introduction in aquaculture and for the management and conservation of its natural populations.

People who have remained in a single location for many generations, sometimes for millennia, possess unique knowledge about their home environments, the species that live there, the changes that have occurred over time, and the close, interdependent relationships between people and other life-forms (Turner *et al.*, 2022). The locally held and mobilized knowledge of these people is variously referred to as traditional ecological knowledge (TEK), indigenous ecological knowledge (IEK), local ecological knowledge (LEK) or experience-based, practical or experiential knowledge (Joa *et al.*, 2018). However, local ecological knowledge (LEK) is part of people's site-specific ecological knowledge, which includes knowledge held and used by traditionally living indigenous people with a historical continuity of resource use as well as by non-indigenous natural resource users, that can be practically applied (Joa *et al.*, 2018). Thus, according to Charnley *et al.* (2007)

LEK is defined as knowledge, practices, and beliefs regarding ecological relationships that are gained through extensive personal observation and interaction with local ecosystems, and shared among local resource users. In contrast to the frequent practice in academia and western science, such knowledge systems represent cumulative lived experience and are not typically divided or reduced to their constituent pieces (Turner *et al.*, 2022). These knowledge systems have several features that can be taken into account in terms of the contributions they have made and will continue to make to the long-term sustainability and wellness of the planet (Houde, 2007). Fishers are people whose livelihoods directly depend on the aquatic ecosystem's services. Consequently, they are the group most impacted by any environmental disturbance in this ecosystem and are also the primary group with the greatest knowledge about the characteristics of the disturbances (Amoutchi *et al.*, 2021). Thus, they are key groups for providing local ecological knowledge regarding habitat, ecosystem services, population dynamics and threats on *P. obscura* populations. In our case, we consider fishers' knowledge as local ecological knowledge, since fishers' communities are made up of traditional or indigenous fishers as well as non-indigenous people with well-rooted and accumulated knowledge. Such knowledge is relevant for the sustainability and conservation of *P. obscura* fishery resources. To this end, the study was designed to investigate the knowledge of local fishers from various ethnic groups on local names, habitats, uses, market price, population dynamics and the threats faced by the snakehead fish *P. obscura* in Ivorian freshwaters, considering the distinct climate zones of the country.

III.2 Material and methods

III.2.1 Study area

The study was carried out in Côte d'Ivoire located in west Africa (Figure 3.1 and Appendix 1). Three among the four Ivorian climate zones were selected for this study: the Guinean, Sudano-Guinean, and Sudanian. Fishers from Bia River, Ayame lake and Faye Lake were randomly selected in Guinean climate zone. These fishers were from Krindjabo, Bianou, Alliekro and Ayame localities. The Guinean climate zone is the sub-equatorial climate characterized by annual precipitation estimated to be more than 1500 millimetres per year, with two rainy seasons and two dry seasons (Bernard, 2014). Within the Sudano-Guinean, fishers from the localities of Koubi, Dibobly and Guiglo working on Kan Lake, Buyo lake and Nzo River respectively, were selected. The Sudano-Guinean climatic zone is characterized by an equatorial transition climate, with annual

precipitation of 1200 to 1500 millimetres. This climate zone has also two rainy and two dry seasons. The Sudanian zone is characterized by a tropical climate with annual precipitation that comprises between 900 and 1200 millimetres. The Sudanian climatic zone has one rainy and one dry season. Fishers from Samorosso village fishing on Bagoue river were selected for the study. The sampling sites were chosen based on known occurrence of the species these regions. Also, the country's main fishing sites were also targeted.

III.2.2 Sampling procedure and data collection

The sampling procedure and method used for selecting fishers' have been fully described in chapter II (section II.2.2). Concerning the data collection, 381 fishers were randomly selected within the different sites. Because of various local languages of local people, in each of the communities, we engaged the services of a translator who is usually a member of such community, with some level of formal education. Both men and women were interviewed, with 141, 119, and 48 men compared to 30, 37, and 6 women respectively in Guinean, Sudano-Guinean, and Sudanian zones. Women were principally engaged in *P. obscura* fish trading activities. The interviewed fishers included those from indigenous and non-indigenous ethnic groups involved in fishing activities of the locations where the study was conducted. Most of non-indigenous fishers relied solely on fisheries as their main source of income, whereas indigenous fishers had diversified sources (e.g., agriculture, livestock, retail shopping, etc) of incomes. The interview was done face-to-face using a structured questionnaire (Appendix 2) during the period from October 2020 to February 2021. The respondents were distributed into 14 ethnic groups including both Ivorian and foreign (majority from Mali, a neighbour country) ethnic groups. The set of information about the selected fishers' socio-demographic background is summarised in Table II. I (Chapter II). The questionnaire was designed to assess the fishers' knowledge of the local names, habitats (where the species is caught or found), market price, uses and production. Fishers' perceptions of decrease in *P. obscura* fish abundance or quantity over the last decade were also assessed. Furthermore, the threats faced by the snakehead fish populations in Ivorian aquatic ecosystems were additionally addressed by the questionnaire. The data collection and the procedure of fishers' selection are summarized in figure 3. 2.

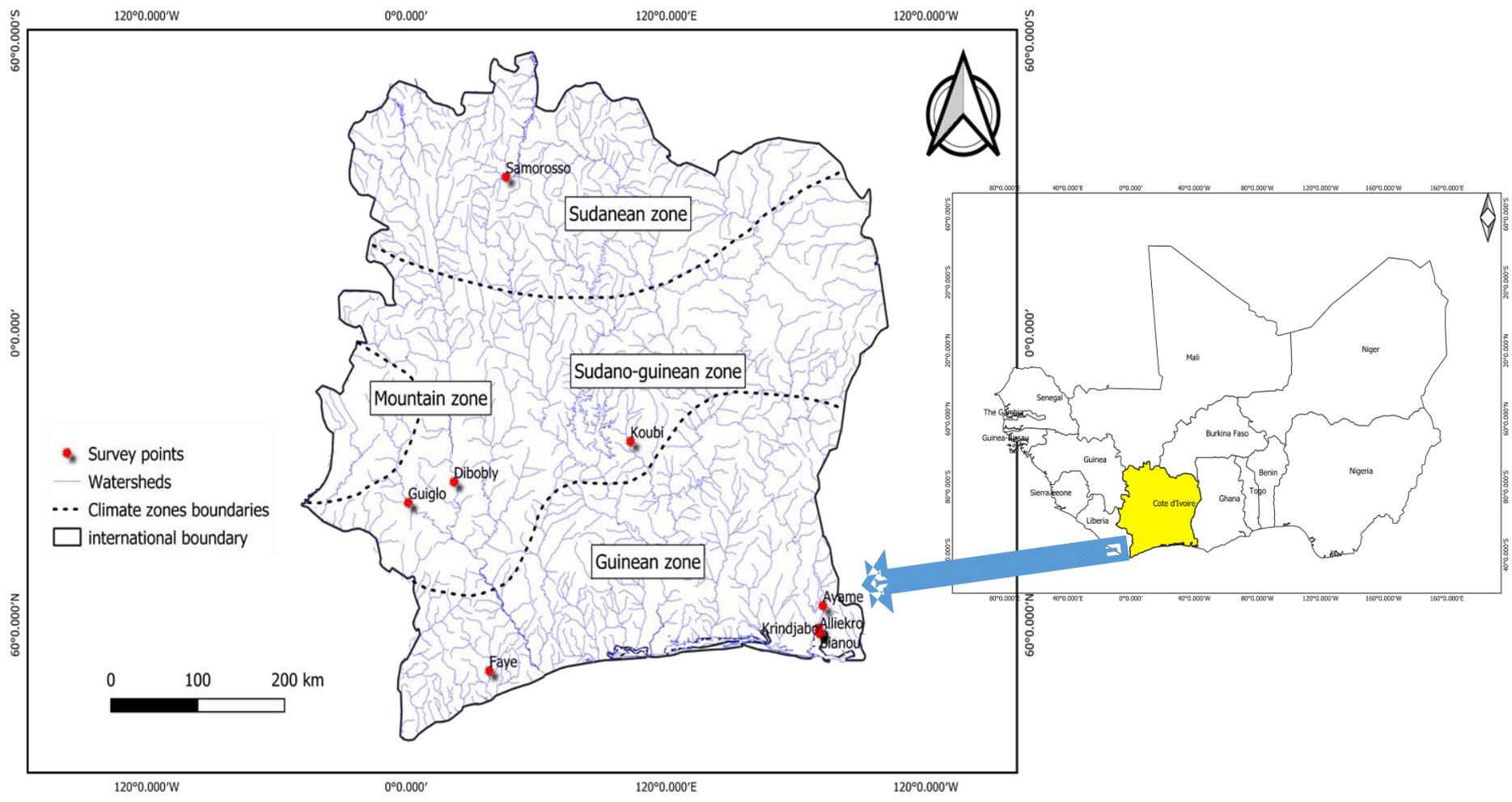


Figure 3. 1: Map of Côte d’Ivoire, showing the main climate zones and the locations where the study were conducted, and its position in West Africa.

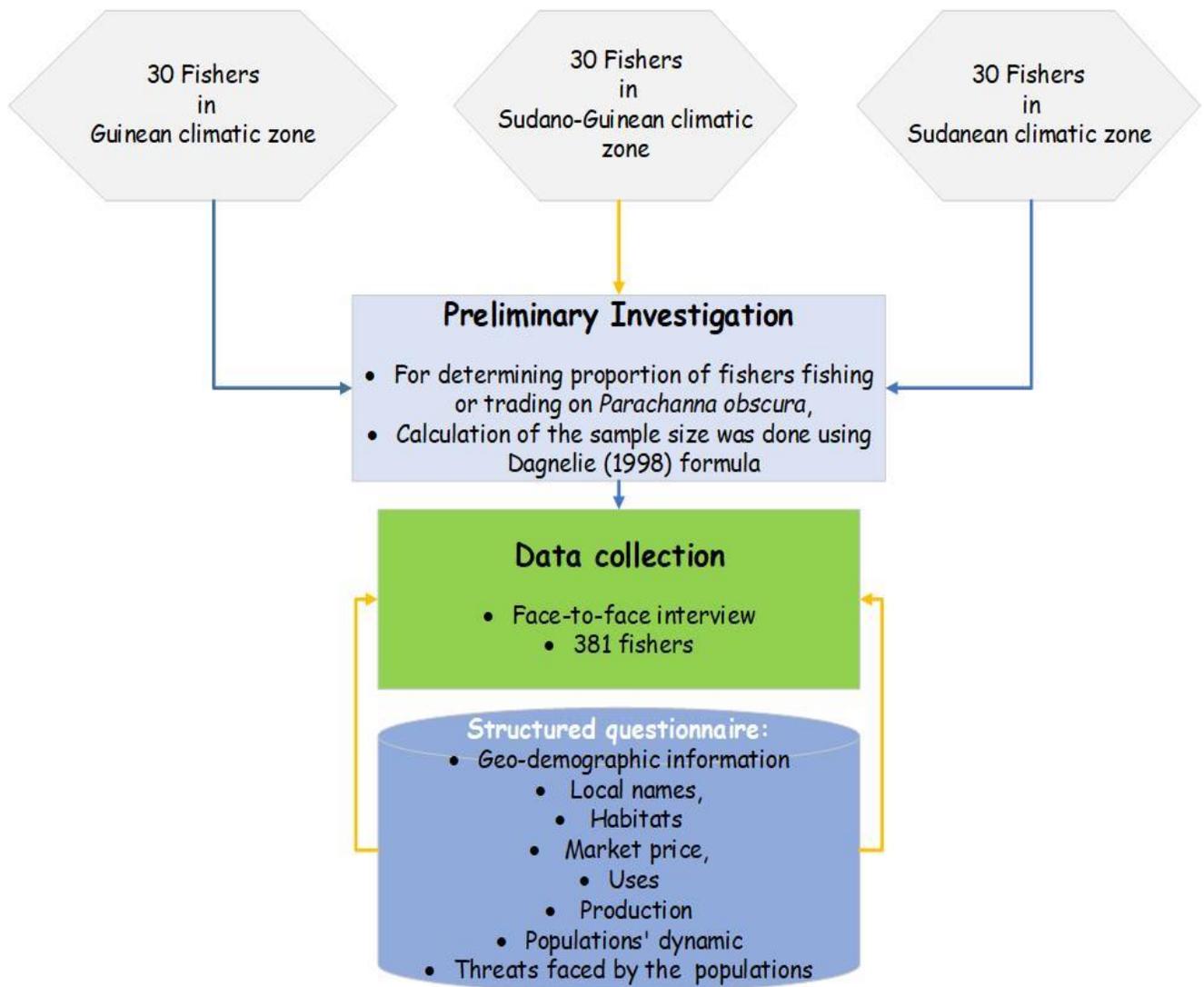


Figure 3. 2: Framework summarising the sampling procedure and data collection

III.2.3 Data analysis

Descriptive statistics (frequency, percentage) were applied to analyze fishers' demographic information and their knowledge of market price, uses, production, and threats faced by *P. obscura* populations. A binary logistic regression model was used to test the relationship between demographic variables (climate zone, fishing watersheds, age, and education) and fishers' perception of a decrease in *P. obscura* abundance. The binary logistic regression model is an extension of simple linear regression, used to predict the probability of an observation falling into one of two categories of a dichotomous dependent variable as a function of one or more independent variables (or predictors), which may be continuous or categorical. In this study, all the independent variables were categorical. We considered socio-demographic and geographic variables of fishers as the independent (predictors) variables and perception of decrease in *P. obscura* abundance variable, as dependent variables. The perception variable included the following categories: 0= no decrease and 1= decrease. The significance was evaluated against the reference category, which was the first category of each independent variables. Guinean zone, age group of 60 years and over, Agni ethnic group, Bia River, and university level, were respectively considered as reference groups of the following independent variables: climate zone, age, ethnic group, watershed, education level, and sex. Z-test was applied to test the significant differences among the threats listed by fishers as affecting snakehead fish in each climate zone and to compare the proportions of each habitat type of the species between climate zones. Alpha (α) lesser than 0.05 was considered statistically significant. SPSS version 2.2 software was used for the descriptive statistics, while the binary logistic regression model and Z-test were done in R 3.6.3 software (R Core Team, 2021).

III.3 Results

III.3.1 Local names for *P. obscura*

Fourteen (14) ethnic groups involved in Ivorian fishery belonging to several socio-linguistics groups were surveyed. For *P. obscura* fish known as "Poisson dormant" (meaning sleeping fish) in Côte d'Ivoire, various names were recorded according to the socio-linguistic group and the related ethnic groups. A total of seven local names were recorded (Table III. I). The most popular name is "Sounôgô-djêguê" (used in 35.7% of fishers' ethnic groups) used by the ethnic

groups originating from the northern part of Côte d'Ivoire (Dioula, Sénoufo, Tagbana) and some Malian ethnic groups, notably Bambara and Keke involved in Ivorian fishery. Another popular name of *P. obscura* fish is “Édjoué-bilé” (used in 21.4% of interviewed fishers' ethnic groups) used by almost the majority of Akan group ethnics. “Pino” is also one of popular name of the snakehead fish used in Bozo, Bambara and Songhaï ethnics groups (21.4% of ethnic groups). The fish is called “Ablo”, “Blinguidé”, “Poupougboon” and “Guossa” in Baoulé, Samogor, Guéré and Guossa ethnic groups, respectively.

III.3.2 Habitats of *P. obscura*

Major freshwater ecosystems were listed by the local fishers as favoured habitats of *P. obscura*. Wetland (38%) and rivers (26%) were the most often mentioned, in general. Guinean and Sudano-Guinean zones fishers mostly mentioned wetland as favourite habitat of the species whereas fishers in Sudanian zone mentioned rivers as the dominant habitat (Figure 3. 3). The proportion of each habitat type of *P. obscura* mentioned in the interviews differed significantly ($p < 0.05$) between fishers from the three climate zones (Table III. II).

III.3.3 Use of *P. obscura*

Most respondents (N=377; 99%) consume snakehead fish. The majority (87% or 327) of those consuming *P. obscura* do so because of the good taste of its flesh, whereas 11% (41 respondents) consume it for its high nutritional value, 1.3% (5 respondents) for cultural reasons and the remaining respondents (1.1%) did not know why they consume it (Figure II-4). In addition to consumption, 1.6% of respondents, belonging to Baoulé and Guéré ethnics groups, responded that *P. obscura* fish is used in traditional medicine to treat deafness. Also, one respondent within Songhai ethnic group said that this fish is used in magic for luck attraction.

Table III. I: Fishers' knowledge regarding local names of the snakehead fish *P. obscura* according to the socio-linguistic and ethnic groups.

Socio-linguistic group	Ethnic group	Local names	Number of respondents	
Akan	Abron	Édjoué-bile	1	
	Agni	Édjoué-bile	75	
	Appolo	Édjoué-bile	4	
	Baoulé	Ablo	65	
Gore	Guéré	Poupougboon	57	
Mandee	Sénoufo	Sounôgô-djêguê	14	
	Tagbana	Sounôgô-djêguê	1	
Malinké	Dioula	Sounôgô-djêguê	8	
	Samogor	Blinguidé	57	
Foreign ethnic group (from Mali)	Bozo	Pino	63	
	Bambara	Sounôgô-djêguê /Pino	17	
	Keke	Sounôgô-djêguê	3	
	Koroboro	Guossa	7	
	Songhaï	Pino	9	
Total	5	14	7	381

III.3.4 Market price

The majority of the 381 respondents mentioned that *P. obscura* is a valuable fish mostly sold up to 3 € per kg. However, the price per kilogramme varied significantly according to the localities and the climate zone. In the Guinean and Sudanian climates zones, the price of *P. obscura* is cheapest (varies from 1.5 to 3 €), while the price of *P. obscura* per kg in the Sudano-Guinean climate zone is considered expensive, principally varying between 3.1 to 4.5 €. Table III. III summarise the fishers' perceptions about the market price per kg of *P. obscura* in Côte d'Ivoire.

III.3.5 Respondents' willingness for introducing *P. obscura* in Aquaculture

All (100%) of the respondents mentioned that *P. obscura* is not yet produced in aquaculture in Côte d'Ivoire. According to their opinion, *P. obscura* should be introduced into aquaculture. They justified their interest by the sweet taste and high nutritional value of the fish. Some even said “*because of the sweet taste of P. obscura fish, I prefer to keep them for household consumption whenever I catch them, instead of selling them*”.

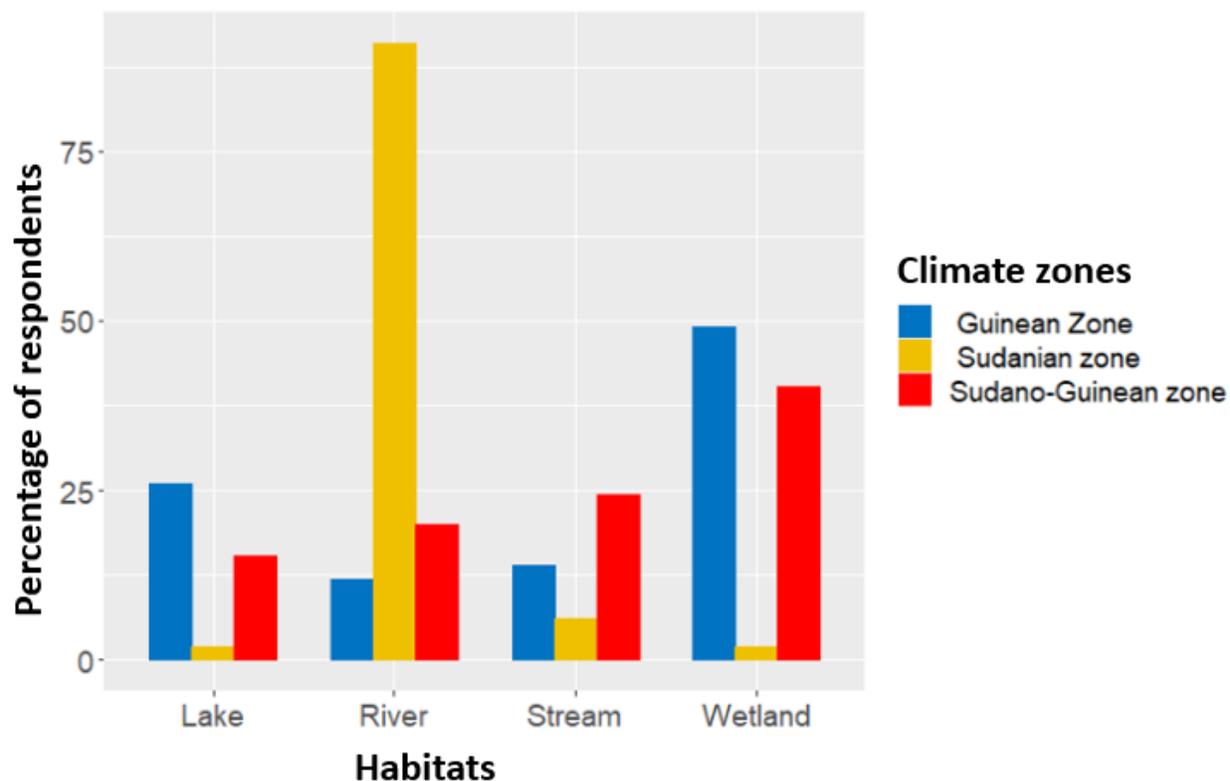


Figure 3. 3: Perception of fishers about the types of habitats where *P. obscura* fish is caught or found according to their climate zone.

Table III. II: Comparison of proportions of perceptions of fishers about each type of habitat of the snakehead fish among three climate zones, based on z-test.

Habitat	χ^2	df	p-value
Wetland	38.1	2	p<0.001*
Lake	17.1	2	p<0.001*
River	138.0	2	p<0.001*
Stream	12.0	2	0.002*

*= p<0.05

Significant difference (p<0.05) in bold, with the level of significance indicated by asterisks.

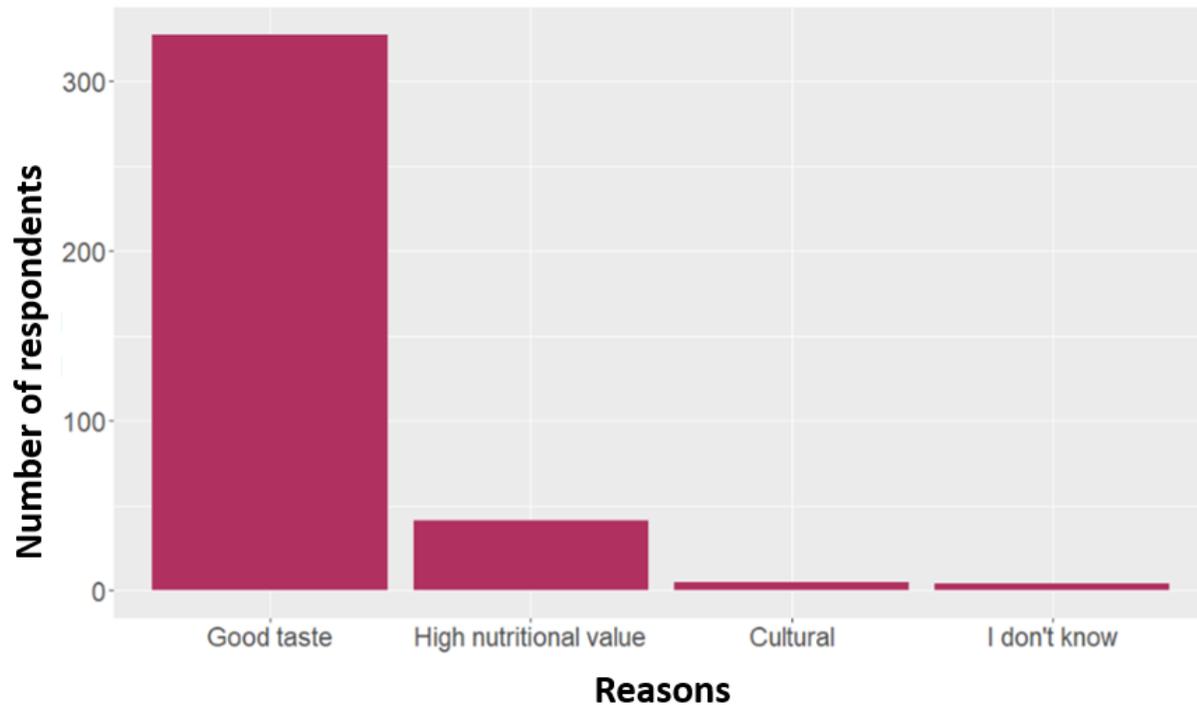


Figure 3. 4: Reasons for the consumption of *P. obscura* by the 377 fishers who consume this fish.

Table III. III: Fishers' perception (N=381) about the market price of the snakehead fish of *P. obscura*.

Climate zone	Market price (€ per kg)	Percentage of respondents (%)
Guinean Zone	Less than 1.5	49
	Between 1.5 and 3	48
	more than 4.5	1
	I have never sold	2
	Total	100
Sudano-Guinean zone	less than 1.5	36
	Between 1.5 and 3	9
	Between 3.1 and 4.5	52
	more than 4.5	3
	Total	100
Sudanian zone	Between 1.5 and 3	100
	Total	100

III.3.6 Threats faced by *P. obscura* populations within Ivorian's aquatic ecosystem

From the 381 respondents, 71% reported a significant decrease in *P. obscura* abundance in Côte d'Ivoire over the last decade, whereas 29% did not observe any change. Of the total percentage of the respondents who observed a decrease in *P. obscura* abundance, respondents of the Guinean zone principally pointed out deforestation around watersheds (17.8%), obnoxious fishing practices (chemical products used for fishing, 17.8%), habitat destruction/modification (11.9%), and overfishing (12.9%) as the practices that are causing these decreases. The Sudano-Guinean zone respondents reported that pesticide use in farms close to watersheds (36.8%), overfishing (21.6%) and water reduction in watersheds due to lack of rainfall (20%) were the main causes of these decreases in the species' abundance. Habitat destruction/modification (84.4%) was reported by respondents from the Sudanian zone as the main threat affecting the decline in snakehead fish's abundance (Figure 3. 5 and Table III. IV). Statistically significant differences ($p < 0.05$) were observed among proportions of the threats cited by fishers within each climate zone (Table III. IV).

Respondents' fishing watershed, climate zone and ethnic group (Koroboro and Songhai ethnic group only), education and gender, were significantly associated with fishers' perception of decrease in *P. obscura* fish abundance (Table III. V). Perception of decrease in *P. obscura* fish abundance was higher (positive coefficients) among fishers in Buyo and Kan lakes, while it was lower (negative coefficients) among those in Ayame and Faye lakes. Perception of decrease in the amount of the snakehead fish was stronger in Koroboro and Songhai ethnic groups fishers, and lower in those of Senoufo ethnic. This perception was also stronger in females and lower in fishers from Sudano-Guinean zone.

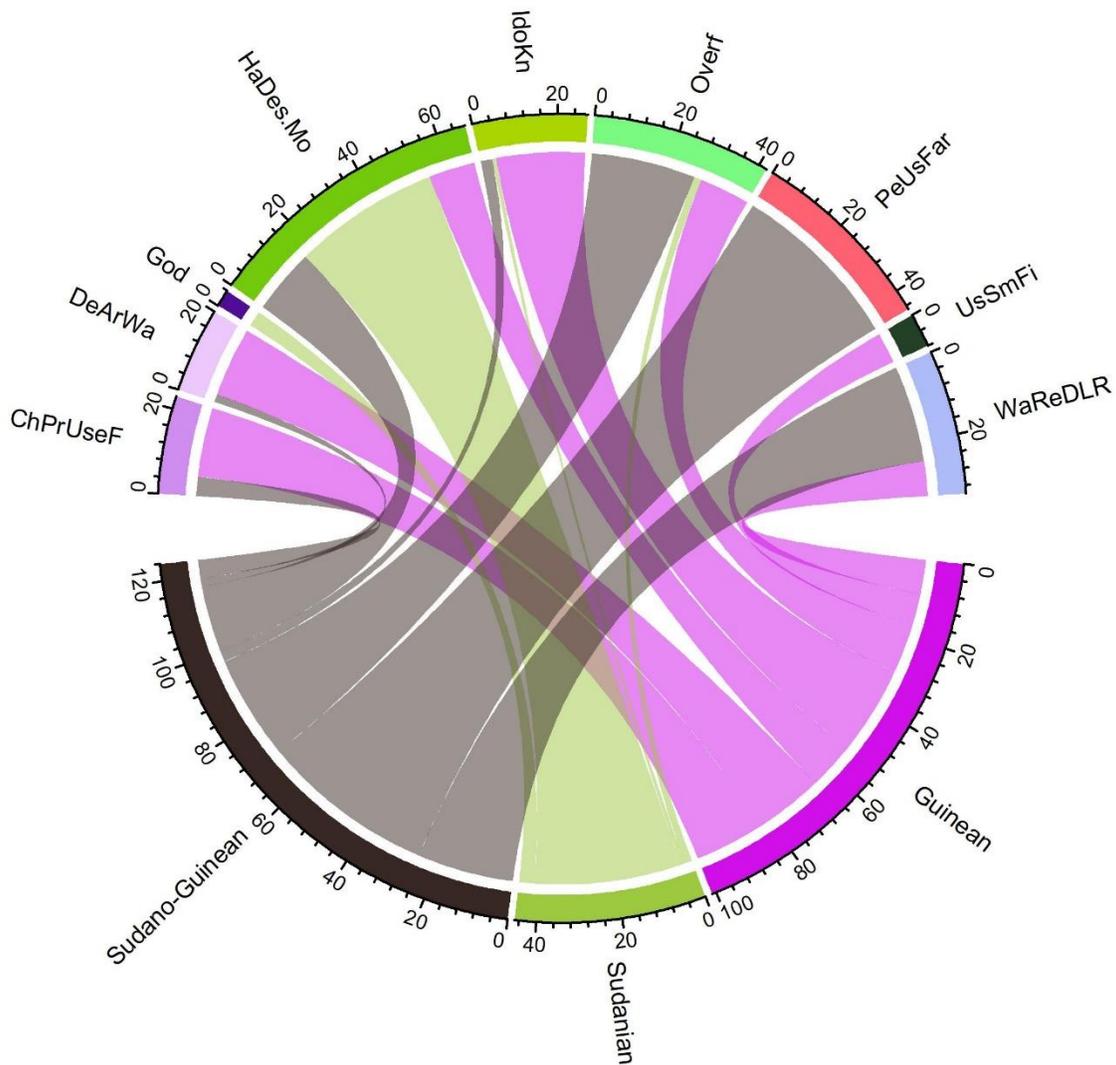


Figure 3. 5: Chord diagram showing fishers’ perceptions regarding the threats faced by *P. obscura* fish populations within Ivorian’s freshwater according to the 271 fishers who reported a decrease in the species populations.

ChPrUseF= obnoxious fishing practices (Chemical products use for fishing), DeArWa = Deforestation around watersheds, HaDes/Mo = Habitat destruction/modification, IdoKn = I don't know, Overf = Overfishing, PeUsFar = Pesticides use in farms close to watersheds, UsSmFi = Use of small-mesh fishing nets, WaReDLR= Water reduction in watersheds due to lack of rainfall, Guinean= Guinean climate zone, Sudanian= Sudanian climate zone, and Sudano-Guinean= Sudano-Guinean zone.

Table III. IV : Comparison the proportions of threats faced by the populations of snakehead *P. obscura* in Ivorian freshwater ecosystems considering each climatic zone, based on Z-test.

Climate zone	Threat	Percentage (%)	χ^2	p-value
Guinean Zone (N=101)	Deforestation around watersheds	17.8	14.37	0.03*
	Habitat destruction/modification	11.9		
	Chemical products use for fishing	17.8		
	Overfishing	12.9		
	Use of small-mesh fishing nets	7.9		
	Water reduction in watersheds due to lack of rainfall	8.9		
	No knowledge	22.8		
	Total	100		
Sudano-Guinean zone (N=125)			350.7	p <0.001*
	Deforestation around watersheds	1.6		
	Habitat destruction/modification	13.7		
	Chemical products use for fishing	4.0		
	Overfishing	21.6		
	Water reduction in watersheds due to lack of rainfall	20		
	Pesticides use in farms close to watersheds	36.8		
	No knowledge	2.4		
	Total	100		
Sudanian zone (N=45)			113.63	p <0.001*
	God	8.9		
	Habitat destruction/modification	84.4		
	Overfishing	4.4		
	No knowledge	2.2		
	Total	100		
Total respondent is N=271				*p<0.05

Table III. V: Relation between geographic and socio-demographic factors, and fishers' perception about decrease in abundance of the snakehead fish *P. obscura*, revealed binary logistic regression.

Explanatory variable	Category	Observed decrease in <i>P. obscura</i> fish quantity
		Coef ^{Sig} (SE)
Climate zone	Guinean (Ref. group)	
	Sudanian	-0.26 (1.72)
	Sudano-Guinean	-2.16* (1.08)
Watershed	Bia river (Ref. group)	-
	Lake Ayame	-1.65* (0.68)
	Lake Buyo	2.21* (0.80)
	Lake faye	-3.59* (1.02)
	Lake Kan	4.13* (1.53)
	Bagoue	NA
	River Nzo	NA
	Ethnic group	Agni (Ref. group)
Abron		14.50 (2,399.55)
Appolo		-17.51 (1,199.57)
Bambara		0.96 (0.94)
Baoule		-2.30 (1.35)
Bozo		0.54 (1.02)
Dioula		-0.05 (0.92)
Guere		1.80 (1.00)
Keke		16.27 (1,384.50)
Koroboro		3.65* (1.49)
Samorgor		0.17 (1.69)
Senoufo		-2.05* (0.99)
Songhaï		3.93* (1.48)
Tagbana		10.87 (2,399.55)
Age	≥ 60 (Ref. group)	-
	[20-29]	0.12 (0.78)
	[30-39]	0.02 (0.65)
	[40-49]	0.28 (0.64)
	[50-59]	-0.12 (0.71)
Education level	University (Ref. group)	-
	No formal education	-1.98 (1.48)
	Primary	-2.07 (1.48)
	Junior high school	-3.07* (1.47)
	Senior high school	-2.23 (1.57)
Gender	Male (Ref. group)	
	Female	0.87* (0.46)
Log Likelihood		-168.49
Akaike Inf. Crit.		394.99

*p<0.05

Significant correlations (p<0.05) are in bold, with the level of significance indicated by asterisks, and standard errors (SE) in brackets.

III.4 Discussion

Effective and sustainable research for wildlife conservation depends upon having long-term information that can keep pace with the unprecedented global changes we are seeing today. Traditionally, population sizes, ecology and threats to species and their habitats have been obtained through empirical studies. However, the knowledge of local and indigenous communities worldwide has been acknowledged as an extremely rich and underused resource of information on how the environment, biodiversity and local conditions are changing over time (Baird and Flaherty, 2005; Sobral *et al.*, 2017; Turner *et al.*, 2022). Thus, the objective of this study was to assess the knowledge of local fishers from various ethnic groups on local names, habitats, uses, market price, population dynamics and the threats faced by the snakehead fish *P. obscura* in the Ivorian freshwaters, considering the climate zone. Results showed that several local names are used in fishing communities to refer to *P. obscura*. Fishers cited major freshwater ecosystems as habitat of the fish. Respondents also considered *P. obscura* to be a valuable fish species for their livelihoods with a market price ranging from less than 1.5 to 4.5 € depending on the zones. Most respondents expressed a willingness to support aquaculture of the species. Substantial decreases in the abundance of individuals of this fish population were observed by the respondents, caused by many anthropogenic pressures.

Worldwide, species are known by their local or vernacular names, which are usually given by indigenous people in their languages. Local names are the result of a human's long-standing interaction with their surrounding environment. Most often, the local names are given based on some salient characteristics which can be appearance, shape, size, habitat, smell, taste, colour, utility or other characters of the species (Singh, 2008). They are essential for improving the exchange of information between academic and non-academic fields. Several local names of *P. obscura* fish were relieved by fishers of the various ethnic groups surveyed, meaning that these fish play an important cultural role in these communities. Indeed, according to the theory of ethno-taxonomic diversity, the species identified by several traditional names are likely to be culturally important (Gaoué *et al.*, 2017). Ethnic groups where the same local name is used for *P. obscura*, belong to the same socio-linguistic group or live in most cases in a close area. Thus, the similarity of local name facilitates communication about species between communities.

Parachanna obscura is a demersal, potamodromous fish species that inhabits marginal vegetation and floodplains (Lalèyè, 2020a). It lives in the creeks of swamps, ponds, streams, rivers, lakes, marshes and floodplains. *Parachanna obscura* prefers calm and muddy areas and marginal vegetation stands in flowing water (Teugels *et al.*, 1992; Kpogue *et al.*, 2012a). The different *P. obscura* habitats enumerated by the fishers in this study agree with the above habitat types, confirming the reliability of the local peoples' knowledge on the ecology of this species. The highest proportion of respondents said that wetlands represent the favourite habitats of this fish. That emphasises the preference of the species for the muddy and vegetated area, and calm water (Kpogue *et al.*, 2012b). The clear identification of the African snakehead fish habitat types by local fishers show the importance for incorporating local knowledge in study of ecology of fish, especially from developing countries where there is often a lack of data and resources. For example, the study of Begossi *et al.* (2016) in Brazil showed that fishers were able to provide information on the biology and ecology of species such as *Rhinobatos percellens*, *Sphoeroides dorsalis*, *Mycteroperca acutirostris* and *Dasyatis guttata*, for which there was scarce or no information on diet and habitat. Also, Le Fur *et al.* (2011) showed that fishers in West Africa were able to identify the migration periods of mature adults to spawning grounds and the recruitment periods of juveniles of many fish species.

Parachanna obscura is a favourite fish for food and constitutes an extremely important part of the staple food for African people because of the taste, few bones, remarkable growth and high economic value (O'Bryen and Lee, 2007). The present study showed that the majority of the respondents consume *P. obscura*, mostly for the good taste of its flesh and high nutritional value. The study also revealed that *P. obscura* is valuable, with a considerable market price, more or less similar to the price of other common species such as *Oreochromis niloticus*, *Oreochromis aureus*, *Chrysichthys nigrodigitatus*, *Heterotis niloticus*, *Heterobranchus longifilis*, *Clarias gariepinus*, etc, sold on the Ivorian fish markets between 2.2 and 4.5 € per kg (FAO, 2021). Therefore, it is a source of income for Ivorian fishers that are involved in its fishing or trading. The variation in the market price of *P. obscura* across the climatic zones indicates the variability in the appreciation and availability of the fish. The highest market price recorded in the Sudano-Guinean climate demonstrated that this species is particularly valued in this zone, increasing demand, reducing the availability and hence increasing the price. The low price recorded in the Sudanian zone is more likely to be related to the low purchasing power of consumers in this

zone. *Parachanna obscura* occupies a prominent place in the diet of African local people, but its natural production cannot meet local demands (O'Bryen and Lee, 2007; Anonymous, 2010). Therefore, its introduction to aquaculture is needed to satisfy the national demand. According to the result of this study, *P. obscura* is not yet produced in Ivorian aquaculture. However, respondents clearly expressed their willingness to engage in production in Ivorian aquaculture. Some fishers express a preference for eating the fish rather than selling it, which they justified by the good taste of the fish. Thus, policymakers and researchers should start exploring possibilities and conditions to realise *P. obscura* aquaculture. The introduction of *P. obscura* in aquaculture will be useful to fill the country's national demand for fishery products. It will also reduce human pressures on its wild populations.

Regarding the other uses of the fish, some fishers reported that the fish is used in traditional medicine for treating deafness, and some used it in magic for luck attraction. According to the World Health Organisation (WHO), 80% of the world's more than six billion people depend mainly on medicines of animal and plant origin (Alves and Rosa, 2005). A wide range of natural pharmacopoeia consisting of wild plants and animals is available to traditional human populations. Wildlife and plant ingredients are not only used in traditional medicines, but are also increasingly valued as raw materials in the preparation of modern medicines and herbal preparations (Kang, 2003). Thus, attention has to be paid by government for conserving nature populations of *P. obscura* in order to sustain its use in traditional medicine.

From the result of the present study, fishers observed a significant reduction in the abundance of *P. obscura* (according to their catches). Overfishing was mentioned by fishers from all the climate zones as one of the major causes of the decline in wild populations of the species. Earlier, it was noted that some populations of this fish have declined in western Africa, possibly due to overfishing (Lalèyè, 2020a). In addition to overfishing, climate change, especially lack of rainfall, and human actions such as deforestation around watersheds, habitat destruction/modification, obnoxious fishing practices, the use of small-mesh fishing nets and pesticide use in farms close to watersheds, are the other main causes mentioned by fishers for the decline in *P. obscura* fish populations in this study. Poor harvesting methods using poison, fire and dynamite, together with the use of poor quality or illegal nets have been reported affecting this fish species in Africa (UA, 2013). The greatest number of threats were principally perceived

by fishers in the Guinean and Sudano-Guinean climate zones. Indeed, Guinean and Sudano-Guinean region of the country concentrates most of the economic activities, which depend mainly on agriculture, including traditional export crops such as cocoa and coffee, and other export crops such as palm oil, rubber, pineapple, etc. The growing of such crop is greatly associated with deforestation of large land surface and intensive use of pesticides. Lost of forest cover destroys several fish species' shelters and draw changes in water temperature (Brummett *et al.*, 2009; Fugère *et al.*, 2018). Additionally, deforestation alters surface runoff and increases river sediment loads, which may lead to aquatic habitat change (Brummett *et al.*, 2009). The watersheds in which the fishers of these regions fish are among the main continental fishing grounds of the Côte d'Ivoire (Kassoum, 1996), therefore, subject to intensive threats as reported by respondents. The preference of this species for wetlands and floodplains, which are often surrounded by vegetation areas explains why deforestation around watersheds and use of pesticide have led to population declines of this species, according to respondents. *Parachanna obscura* breeds preferably during and just after the floods (Teugels, 2003). Thus, lack of rainfall is likely a cause disturbing the reproduction cycle of the fish, leading to a decline in their abundance. This explains why fishers have mentioned the lack of rainfall as one of the main causes of its decline. The factors threatening *P. obscura* fish according to our results are among the factors threatening West Africa freshwater ecosystems and organisms in general. Indeed, climate change, water pollution, habitat loss due to deforestation, overfishing, mining, and agriculture represent the greatest threats to freshwater fishes in Africa and specifically in West Africa (Smith *et al.*, 2009). Also, the study of Amoucthi *et al.* (2021), based on local fishers' ecological knowledge, showed that Côte d'Ivoire freshwater ecosystems are impacted by climate change, mining activities, water withdrawal for human needs, overfishing, industrial waste discharge, and many other pressures. Thus, our study demonstrated the importance of local ecological knowledge of fishers in identifying threats to fish populations, and thus the need to integrate local knowledge into biomonitoring and conservation of aquatic biodiversity. The study of Veneroni and Fernandes (2021) in Europe also showed how fishers help to accurately identify significant declines in the abundance of sole (*Solea solea*), common cuttlefish (*Sepia officinalis*) and mantis shrimp (*Squilla mantis*).

The results showed that perception of decrease in *P. obscura* fish abundance were significantly associated with socio-demographical variables such as respondents' fishing watershed, climate

zone and ethnic group. According to many other studies, socio-demographic background of respondents are factors likely to influence individuals' local ecological knowledge (Avakoudjo *et al.*, 2019; Sobral *et al.*, 2017). For example, Sobral *et al.* (2017) showed that age influenced the knowledge of local communities on climate indicators and population structure of *Caryocarcariaceum*. Our results did not show any influence of age on fishers' knowledge. We found that fishers' perception of decrease in the amount of the snakehead fish was stronger in Koroboro and Songhai ethnic groups fishers. These people are non-indigenous with fisheries as main source of income, therefore continuously in contact with their fishing aquatic ecosystem. Thus, are most likely to observe any change.

III.4 Conclusion and recommendations

This study provided important insights about the knowledge of local fishers involved in Ivorian fishery on *P. obscura*. The local names of *P. obscura* recorded in this study will be helpful for researchers in carrying out studies on the species in the respective indigenous communities and will facilitate communication and the exchange of information about the species. The result of the study showed that the fish is very appreciated by the local communities because of its taste and nutritional value. The species is a valuable source of income for local fishers. Its introduction to Ivorian aquaculture will be necessary to satisfy the national demand of fishery products. This study additionally highlighted a decline in *P. obscura* fish abundance is perceived to be caused by anthropogenic pressures.

Given the considerable decline in this fish abundance, rules and regulations should be established by local authorities and water resources managers for mitigating the threat caused by humans. For instance, the prohibition of deforestation of vegetation surrounding watersheds for preventing the destruction of the species habitat is of major importance. Campaigns with local populations to increase awareness about the negative impacts of poor and obnoxious fishing practices on populations of the species as well as on the entire aquatic organisms are needed. Overall, the present study demonstrates the major importance of local ecological knowledge on the sustainable use of natural resources, which has to be taken into account before exploitation is expanded. Local fishers' knowledge must therefore be taken into account in further studies for example on ecology and biology of fish and in the planning of conservation policy.

As perceptive, an extension of this study within the other communities or regions of Africa where the species occurs will be necessary for a broad database on its local names. Additionally, since this study captured only the perspective and opinion of fishers and did not include those of consumers, and hence further investigations will be needed to fill this gap. Furthermore, the assessments of the distribution of the fish are needed for the monitoring of the species populations and also for establishing an efficient conservation policy.

CHAPTER IV:

Morphological variations of *Parachanna obscura* fish populations along climate and habitat gradients.

Abstract

Intraspecific morphological variation may reflect phenotypic plasticity or adaptive divergence. While adaptive shape divergence may occur more likely among isolated populations with reduced gene flow, phenotypic plasticity may reflect morphological responses to heterogeneous environments even in spatially connected populations. We applied this concept to examine morphological variations among seven wild populations of snakehead fish (*Parachanna obscura*) along climate and habitat gradients in Côte d'Ivoire, West Africa. Morphological variations were studied by multivariate Canonical Variate Analysis (CVA) as based on geometric morphometrics of 15 fish body landmarks. Correlations between shape variations among populations and climate and habitat characteristics, and between morphological and geographic distances were calculated. We found significant morphological variations among the seven populations, but only modest effects of climate variables (temperature, precipitation, relative humidity) and physico-chemical parameters of the water bodies (redox potential) on fish shape. Spatial distance and isolation among populations increased morphological distances, but this trend was likewise relatively weak. The variations in fish shape were concentrated on landmarks related to swimming and feeding, hence suggesting correspondence between morphology and environmental conditions. However, without extended genetic analyses and common-garden experiments, a mechanistic understanding of the factors causing shape variation of *P. obscura* could not yet be achieved.

Keywords: phenotypic plasticity, environment, geographical distance, geometric morphometrics

IV.1 Introduction

In Africa, many researchers have reported that freshwater organisms, especially fish populations, are strongly affected by numerous threats including climate change and anthropogenic perturbations such as dam construction, water extraction, habitat modification, water pollution and overexploitation (Darwall *et al.*, 2011). For example, in Côte d'Ivoire, climate has significantly changed over the twentieth century, and the trend is expected to continue in the future. Experts on Intergovernmental Panel on Climate Change predicted an increase in temperature by 3°C by 2100, and a decrease of precipitation by 8% during the next hundred years, under the RCP4.5 scenario in Côte d'Ivoire (Bernard, 2014). It is predicted that by 2050s, hydrologic conditions that are significantly different from the existing conditions will be experienced by more than 80% of Africa's freshwater fish species (Darwall *et al.*, 2011), which is likely to have a significant impact on fish diversity.

One of the African freshwater fish species with great economical value is *Parachanna obscura* (family Channidae), commonly known as African snakehead fish. It is widespread in Africa, distributed in the intertropical convergence zone where the water temperature ranges from 26 °C to 28 °C. Some studies have indicated a decline in the populations of *P. obscura*, mainly due to overfishing and other anthropogenic threats coupled with the effect of the ongoing climate change (Lalèyè, 2020a; Amoutchi *et al.*, 2021). However, studies have shown that Channidae can withstand stressful conditions, for example, low oxygen concentrations, notably by the possession of a cavity above the gill chamber, which functions as an accessory respiratory organ (Lee and Ng 1991; Kpogue *et al.*, 2012; Herborg *et al.*, 2007; Courtenay and Williams, 2004). In addition to these specific organs developed during phylogeny, variation in body morphology along climate and habitat gradients may also contribute to the persistence of populations. For example, many fish species exhibit wide morphological plasticity to variations in temperature (Lema *et al.*, 2019, Del Rio *et al.*, 2019; Munday *et al.*, 2008).

Intraspecific morphological variation is often produced and maintained by divergent selective regimes, for example in response to abiotic and biotic factors that differ among the habitats of populations. Under these conditions, morphological variation can either reflect phenotypic plasticity of a common gene pool or may reflect even adaptive processes resulting in strong genetic divergence among populations (Lazzarotto *et al.*, 2017). While adaptive morphological

variation based on genetic divergence develops and is maintained more likely among spatially isolated populations with reduced gene flow (Rundle and Nosil, 2005), phenotypic plasticity is predicted to be most advantageous in a heterogeneous environment when future conditions can reliably be predicted (Sultan and Spencer, 2002).

Côte d'Ivoire is a West Africa country characterised by a diversified climate and water network system. The climate divides the country along the latitude into three principal climatic zones such as Guinean in the south, Sudano-Guinean in the middle and Sudanian in the northern, with a fourth zone being the particular climate of the mountain zone (Amoutchi *et al.*, 2021). Guinean zone is characterised by sub-equatorial climate, the Sudano-Guinean zone by an equatorial transition climate, and Sudanian zone by characterised by a tropical climate. Concerning the water systems, the country is characterized by a vast and complex system including many lakes, wetlands, rivers and streams. Four major river basins including Comoé, Sassandra, Cavally, and Bandama, are found in the country, with several tributaries (Girard *et al.*, 1970). Many coastal rivers are also found. Thus, if morphological variation among *P. obscura* populations is caused by responses to differing climatic factors and local environmental conditions, and magnified by spatial isolation among populations, we would expect a strong morphological variation of this species within Côte d'Ivoire.

Morphological variations in fish have traditionally been evaluated using linear morphometry (e.g., measurement of lengths, and widths). A more sophisticated, yet readily accessible method is landmark-based geometric morphometrics, in which data can be collected in the form of spatial arrangements of landmarks along a biological structure (Loy *et al.*, 2000; Park *et al.*, 2015). This powerful technique can capture differences in shape that are not easily observed through linear morphometry. Geometric morphometrics has already successfully been applied in studies of morphological differentiation of fish populations or species (Jacquemin and Pyron 2016; Xiong 2018; Norte *et al.*, 2019; Mouludi *et al.*, 2019).

In our study, we used geometric morphometrics to examine morphological variation among seven wild populations of *P. obscura* along the climate and habitat gradients in Côte d'Ivoire. We tested whether shape variation correlates to differences of climate and habitat characteristics, and examined whether geographical distance among populations correlates with morphological distance. We expected the variations to be localised primarily in fish body parts associated with

ecological functions, for example in fins and caudal peduncle involved in swimming and manoeuvring, thus reflecting phenotypic plasticity. Strong correlation between morphological and spatial distance might be indicative of a stronger effect of spatial isolation on morphological divergence.

IV.2 Material and methods

IV.2.1 Field sampling and data collection

This study was conducted on several Ivorian inland watersheds (Figure 4. 1, Table IV.I and Appendix 3). Bia river (KRIN), Sassandra river (SBR) and San-Pedro Lake (SANP) were sampled in the southern region, characterised by a sub-equatorial climate (Guinean climate zone) comprising two rainy and dry seasons, with annual precipitation estimated to be more than 1500 mm (Bernard, 2014). Kan Lake (KAN) is located centrally, while Buyo Lake (SAS) and Nzo River (NZO) were sampled in the centre-western part of Côte d'Ivoire. These areas are characterised by equatorial transition climate (Sudano-Guinean climate zone) with two rainy and dry seasons, and 1200 to 1500 mm precipitation per year. Finally, Bagoue river (BAG) was sampled in the northern part, characterised by a tropical climate (Sudanean climate zone), where annual precipitation is between 900 and 1200 mm per year, and one rainy season and one dry season are recorded.

A total of seven *P. obscura* populations comprising 167 fish were collected (Table IV. I). *Parachanna obscura* fishermen from each sampling site were employed for fish sample collection using traps and fish nets. Following fish capture, the left side of each specimen was photographed using Nikon (D5600) camera (calibrated against a graduated ruler to standardize measurements) device for geometric morphometric analysis. Each specimen's length and weight were also measured to the nearest 0.1 cm and 0.1 g, using an ichthyometer and an electronic scale respectively. Then, specimens were fixed in 10% formaldehyde solution and transported to laboratory for further analysis.

Physico-chemical parameters of each site including water temperature (°C), pH, total dissolved solids (ppm), electrical conductivity ($\mu\text{S}/\text{cm}$) and redox potential (mV) were measured *in situ* with a handheld multi-parameter water quality monitoring device (WQM-243/PHTK-243, TEKCOPLUS, Hong Kong, China). Water depth (cm) and water transparency (cm) were also

measured (Appendix 4). The canopy cover of vegetation (%) along the shoreline was estimated visually. Measurements were done over the dry (twice) and rainy (twice) seasons at each site, and values were later averaged (Appendix 4). The latitude and longitude of each site were measured using a handheld global positioning system. Field data collection was done from September 2020 to December 2021. Additional climate data (mean air temperature, relative humidity and mean precipitation) were obtained for each sampling site from NASA POWER Data Access (<https://power.larc.nasa.gov/data-access-viewer/>) by entering latitude and longitude of sampling sites (Appendix 4).

IV.2.2 Morphological data collection

We digitized 15 landmarks (LMs) on 2D pictures to obtain the x-y coordinates of all points using TpsDig2 v31 (Rohlf 2015) (Figure 4. 2).

IV.2.3 Data analysis

- **Morphological variation**

To perform geometric morphometric analysis, landmarks were converted to shape coordinates by the generalised least square Procrustes superimposition (GPA; Rohlf and Slice 1990). This method transforms landmark configuration by preserving all information about shape differences among specimens but removes non-shape variability in raw coordinates such as location, orientation, scale and rotation, and then standardises each specimen to unit centroid size (CS). Centroid size represents a dimensionless size measure computed as the square root of the summed squared Euclidean distances from each landmark to the specimen centroid (Bravi et al. 2013). The shape data obtained were further size-corrected using a regression of shape (Procrustes coordinates) on size (log centroid size) for each population separately. The obtained regression residuals were used as standardised shape data in further analyses on shape variations. Canonical variate analysis (CVA), a multivariate statistical method used to distinguish variation among multiple pre-defined groups (populations) of specimens, was applied to quantify inter-population shape variations. CVA results are statistically reported as Mahalanobis distance (Md), which represents a measure of distance among populations relative to the within-sample variation. The statistical significances among Mahalanobis distances were determined by bootstrapping the Md matrix (permutation test with 10,000 runs). All the subsequent analyses

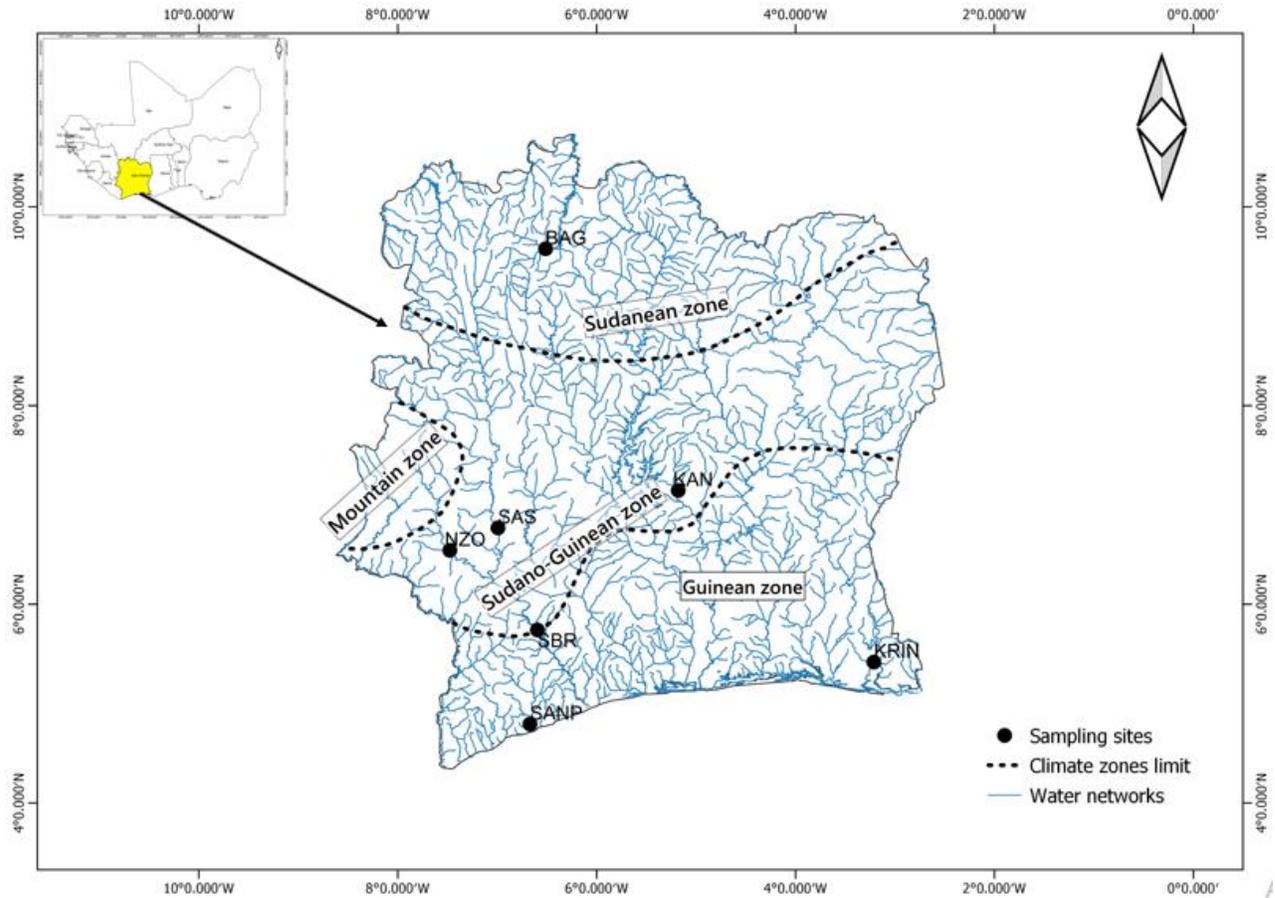


Figure 4. 1: Map of the study area, showing locations of populations from which *P. obscura* specimens were collected, and position of Côte d'Ivoire in West Africa.

KRIN: Bia River sample, SBR: Sassandra river sample, SANP: San-Pedro Lake sample, KAN: Kan Lake sample, SAS: Buyo Lake sample, NZO: Nzo River sample and BAG: Bagoué river sample.

Table IV. I: Sample size, standard length (SL, cm) and weight (g) of seven populations of *P. obscura* used in the study.

River basin	Watershed	Population	Sample Size (N)	Standard length (SL)		Weight
				Range (cm)	Mean±SE	Mean±SE
Niger river	Bague river	BAG	22	14.5-37.8	24.5±6.2	208±164
Bandama	Kan Lake	KAN	18	19.4-37.6	27.7±5.5	269±155
Coastal river Bia	Bia river	KRIN	12	16.2-35.1	20.9±4.7	131±136
Sassandra	Nzo river	NZO	40	16.5-28.5	21.4±3.4	138±73.8
Coastal river San-Pedro	San-Pedro Lake	SANP	26	18.4-32.8	25.5±4.9	254±139
Sassandra	Buyo Lake	SAS	32	14.7-25.5	20.3±2.9	108±39
Sassandra	Sassandra river	SBR	17	22.9-31	27.6±2.5	297±81

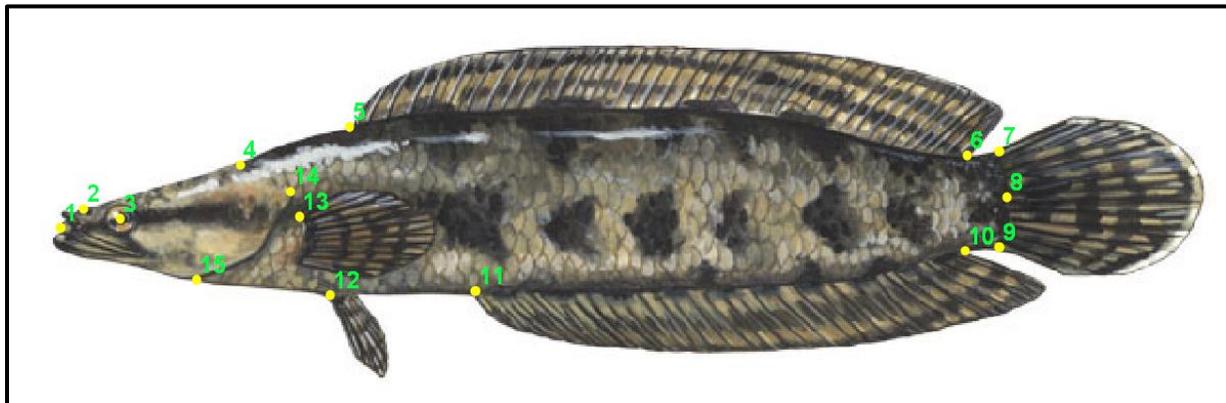


Figure 4. 2: Defined landmark points for collection of *P. obscura* body shape data.

Landmarks are: 1- anterior-most point of the snout tip on the upper jaw, 2- anterior-point of nasal bones 3- centre of the eye, 4- superior margin of head, 5- anterior and 6- posterior insertion point of the dorsal-fin base, 7- posterior-dorsal end of the caudal peduncle at its connection to the caudal fin, 8- posterior end of the medial region of the caudal peduncle, (9) postero-ventral end of the caudal peduncle at its connection to the caudal fin, 10- insertion and 11- origin point of the anal-fin base, 12- most anterior point of pelvic fin, 13- most anterior point of pectoral fin, 14- posterior edge of the opercle and 15- ventral end of the gill slit.

were performed in MorphoJ version 1.07a software. Probabilities <0.05 were considered significant.

- **Influence of geographical isolation or distance on morphological variations**

To test the effect of geographic distance on the morphological variation among *P. obscura* populations, Mantel correlation between the pairwise morphological distances determined through Mahalanobis methods in CVA analysis (Table IV.II) and the natural logarithm (ln) of the pairwise Euclidean geographic distances (km) was calculated. The geographical distance matrix was calculated by QGIS 3.22.6 using the global positioning system (GPS) coordinates of the sampling locations. Mantel correlation was run in vegan package (Oksanen *et al.*, 2022) in R 3.6.3 software, with 1000 permutations.

- **Climate and habitat variability**

To assess the environmental heterogeneity among collection sites of *P. obscura* populations, principal component analysis (PCA) on all physico-chemical, climatic and habitat variables (Table IV.II) was applied. The PCA was calculated by R.4.1.2 software using factoextra' package (Kassambara and Mundt, 2020).

- **Influence of climate and habitat predictors on *P. obscura* morphology**

For testing the link between fish body shape, and climate and habitat variables, Pearson correlations were calculated between the first two principal components explaining the highest percentage of variability in climate and habitat variables among sampling sites, and the population centroids of body shape from CVA. Pearson correlation was computed in stats package in R4.1.2 (R Core Team, 2021).

IV.3 Results

IV.3.1 Morphological variation among *P. obscura* populations

Average length and weight of specimens varied among populations (Table IV. I). Fishes of KAN and SBR were largest, while NZO, KRIN and SAS populations were composed of smaller specimens.

Canonical variate analysis indicated significant ($p<0.05$) Mahalanobis distances (Md) among all population pairs (Table IV. II), with the highest Md values observed between KRIN, KAN and

the other populations. The first two CVA factors contributed 38.4% (CV1) and 21.9% (CV2) of the total variation. CV1 reflected variation in caudal body part (landmarks 6, 7, 8, 9 and 10), dorsal fin length (landmark 5), and upper body depth (Figure 4. 3). CV2 described variation in the anterior region of the body, notably in the snout orientation (landmarks 1 and 2), lower body depth (landmark 11), the shape of the upper region of the head (landmark 4), eyes position (landmark 3), and the positions of the pectoral fin and posterior edge of opercula (landmarks 13, 14). Overall, however, the morphological variation between individuals and populations was relatively weak, and in no region of the fish body was particularly strongly accentuated.

Despite the statistically significant differentiation among populations, individuals of KAN and BAG were strongly scattered in the CVA plot and hence their population ellipses overlapped substantially with those of other populations (Figure 4. 4). Apart from these two populations, the other five populations were grouped distinctly from each other on the scatterplot. NZO and SANP were the most distinct groups, with only few individuals overlapping with other groups. Individuals of KAN and KRIN populations with negative CV1 and CV2 values, had a deeper and slightly shorter caudal peduncle and dorsal fin, less deep body, a posterior edge of their operculum and pectoral fin in a downwardly sloping position, the snout slightly sloping upwards, and eyes positioned in the bottom part of the head towards the snout, in contrast to individuals from NZO. Individuals of SANP with negative CV2 and positive CV1 values were characterised by a slightly longer caudal peduncle narrowing at the insertion bases of the dorsal and anal fins, a slightly longer dorsal fin, a posterior edge of their operculum and pectoral fin in a downwardly sloping position, the snout slightly sloping upwards, and eyes positioned in the bottom part of the head towards the snout. These individuals were morphologically opposed to individuals of the SAS population. Finally, SBR individuals, with negative CV2 values and central CV1 values, had a posterior edge of their operculum and pectoral fin in a downwardly sloping position, and the snout slightly sloping upwards with eyes positioned in the bottom part of head towards the snout. Individuals of BAG population were morphologically strongly diverse and hence their positions scattered throughout the diagram.

Table IV. II: Mahalanobis distances (lower diagonal) and significance (upper diagonal) of pairwise comparisons by the canonical variate analysis performed between populations of the *P. obscura*.

	BAG	KAN	KRIN	NZO	SANP	SAS	KAN
BAG		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
KAN	3.3		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
KRIN	3.2	4.1		<0.0001	<0.0001	<0.0001	<0.0001
NZO	2.9	4.2	4.8		<0.0001	<0.0001	<0.0001
SANP	3.5	4.5	5.1	3.3		<0.0001	<0.0001
SAS	2.3	3.4	3.5	3.1	4.0		<0.0001
SBR	3.1	4.0	4.2	3.4	3.1	3.2	

Results were obtained from 10,000 permutation runs. KRIN: Bia River sample, SBR: Sassandra river sample, SANP: San-Pedro Lake sample, KAN: Kan Lake sample, SAS: Buyo Lake sample, NZO: Nzo River sample and BAG: Bagoue river sample.

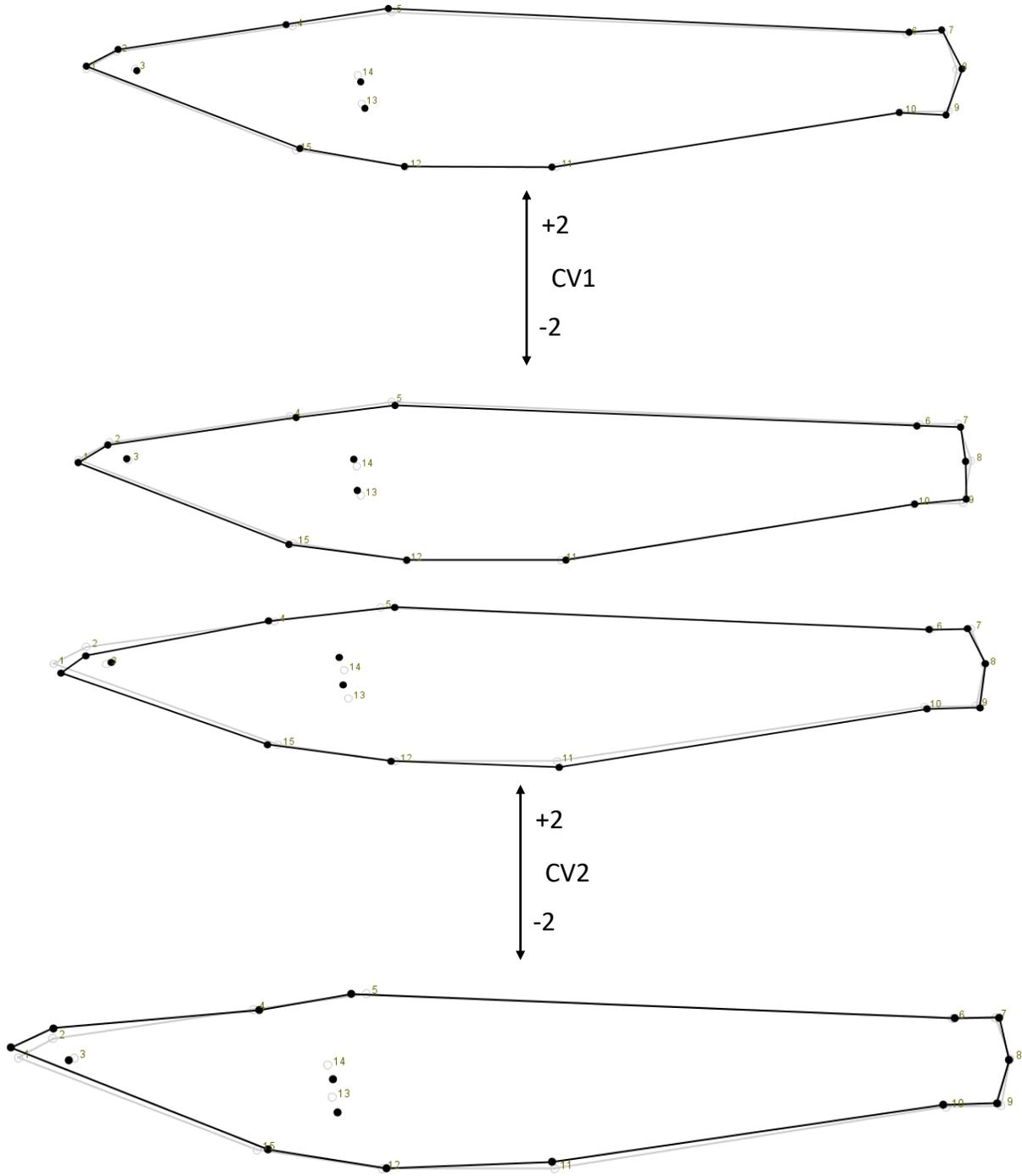


Figure 4. 3: *Parachanna obscura* shape variations corresponding to wireframe deformation along the first two CVA axes (CV1, CV2).

Bleu light shape lines are the mean shapes of all specimens and black lines are shape modifications along the two main CVA axes. The black dots numbered in red reflect the 15 landmarks measured.

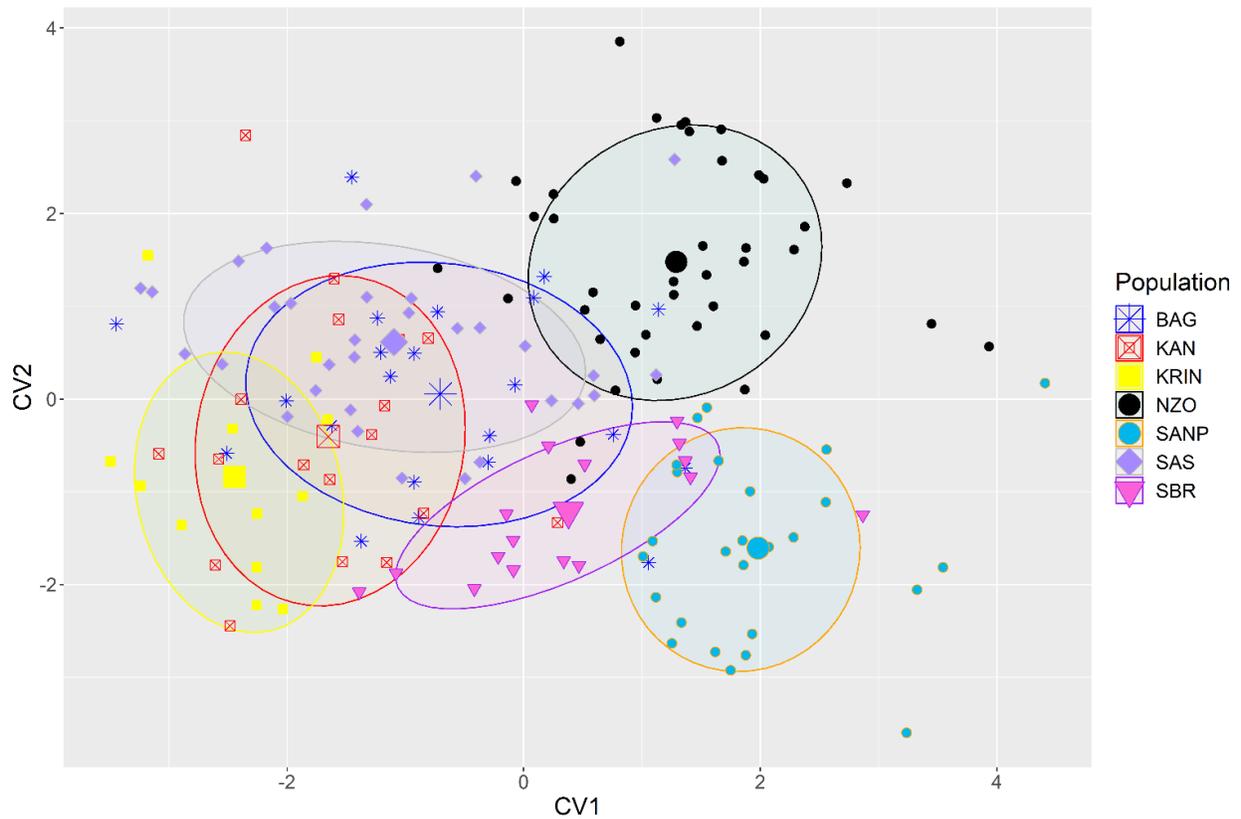


Figure 4. 4: Scatter plot obtained of first two factors of the canonical variate analysis on 15 geometric morphometrics characters (landmarks).

Individuals of different populations are represented by a different set of symbols. Populations are presented as an ellipse (containing 80% of the individuals in the population in question), and their centroid (mean) as a large central symbol. KRIN: Bia River sample, SBR: Sassandra river sample, SANP: San-Pedro Lake sample, KAN: Kan Lake sample, SAS: Buyo Lake sample, NZO: Nzo River sample and BAG: Bagoue river sample.

IV.3.2 Influence of geographical distance on morphological variations

There was no significant correlation between pairwise morphological distance and geographical distance among the seven populations (Mantel test, $P=0.22$) (Figure 4. 5). However, the positive slope reflects that the highest morphological distances were found among populations that were also geographically most distant.

IV.3.3 Climatic and habitat characteristics of collection sites of *P. obscura* populations

PCA of 11 climate and habitat variables extracted two principal components explaining 76.1% of the total variation (Figure 4. 6). PC1 (43.9% of total variation) mainly reflected the variation in climatic variables such as relative humidity (RH), mean air temperature (T_Mean), and mean precipitation (precipit), as well as the habitat variables like water temperature and redox potential (ORP). T_Mean, ORP and water temperature were negatively correlated with PC1, while all other variables were positively correlated with PC1 (Table IV. III). PC2, with a loading value of 32.2%, mainly reflected the variation of habitat variables, including water depth (Depth), electrical conductivity (cond), total dissolved solids (TDS), transparency (Transp) and canopy. Except transparency and water depth which were positively correlated with PC2, all other variables were negatively correlated with PC2. The habitat of KRIN population was characterised by high canopy, low water transparency, acidic pH, and shallow water depth. The habitats of NZO, SAS and SBR populations were characterised by high water transparency, neutral or basic pH, low water and air temperature, a short canopy, moderately high precipitation and humidity, and deeper water. The collection sites for BAG and KAN populations had higher air and water temperatures, high redox potential, and low precipitation and relative humidity. The SANP population collection site had the highest values for chemical parameters such as electrical conductivity and total dissolved solids. Precipitation and humidity were also higher at this site.

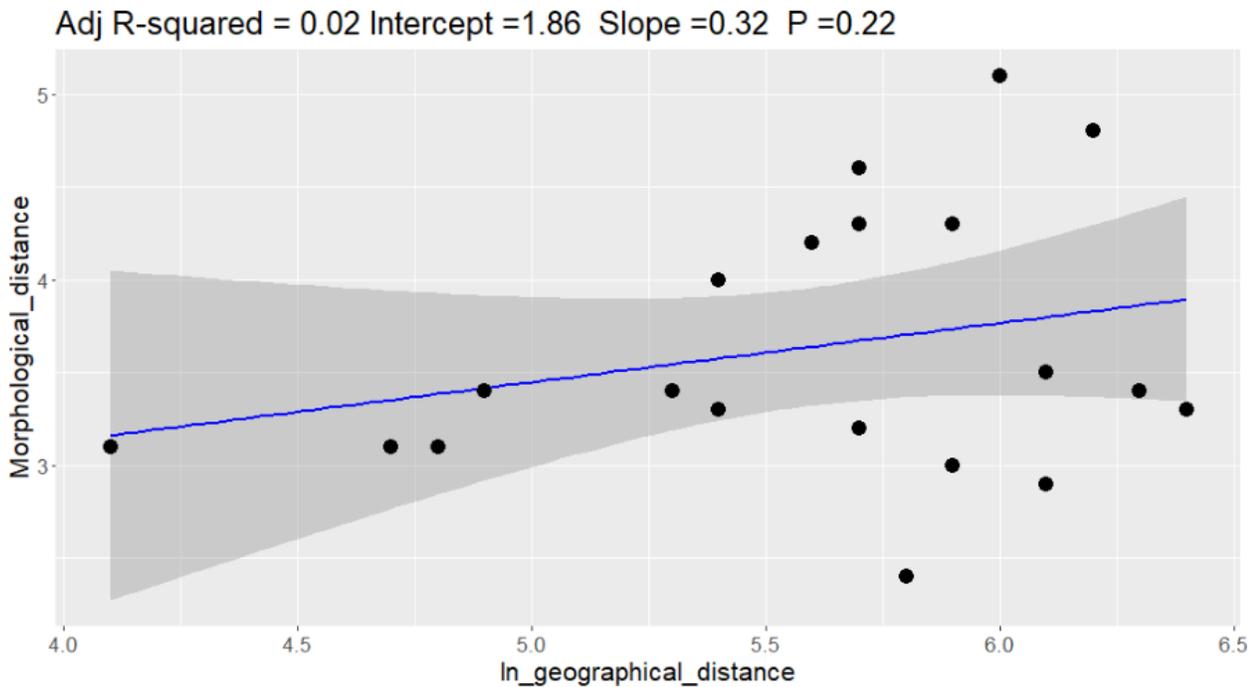


Figure 4. 5: Estimation of pairwise morphological distances between populations plotted against natural logarithm (ln) of pairwise Euclidean geographical distance (km).

P was obtained based on Mantel test.

Table IV. III: Loadings of the 11 climate and habitat variables on the first two principal components explaining 76.1% of total variation and with Eigenvalues greater than 1.

Variables	PC1	PC2
T_Mean	-0.8	-0.4
RH	0.8	0.0
Precipit	0.9	-0.2
T_water	-0.8	0.0
Depth	0.5	0.8
Ph	0.5	0.2
Cond	0.6	-0.8
TDS	0.6	-0.8
ORP	-0.8	0.4
Transp	0.3	0.7
Canopy	-0.4	-0.9

T_Mean= mean air temperature (°C), RH= relative humidity (%), precipit= mean precipitation (mm/day), T_water= water temperature (°C), Depth= Water depth (cm), Cond= electrical conductivity (µS/cm), TDS= total dissolved solids (ppm), ORP= redox potential (mV), Transp= transparency (cm), Canopy= canopy coverage of what vegetation (%).

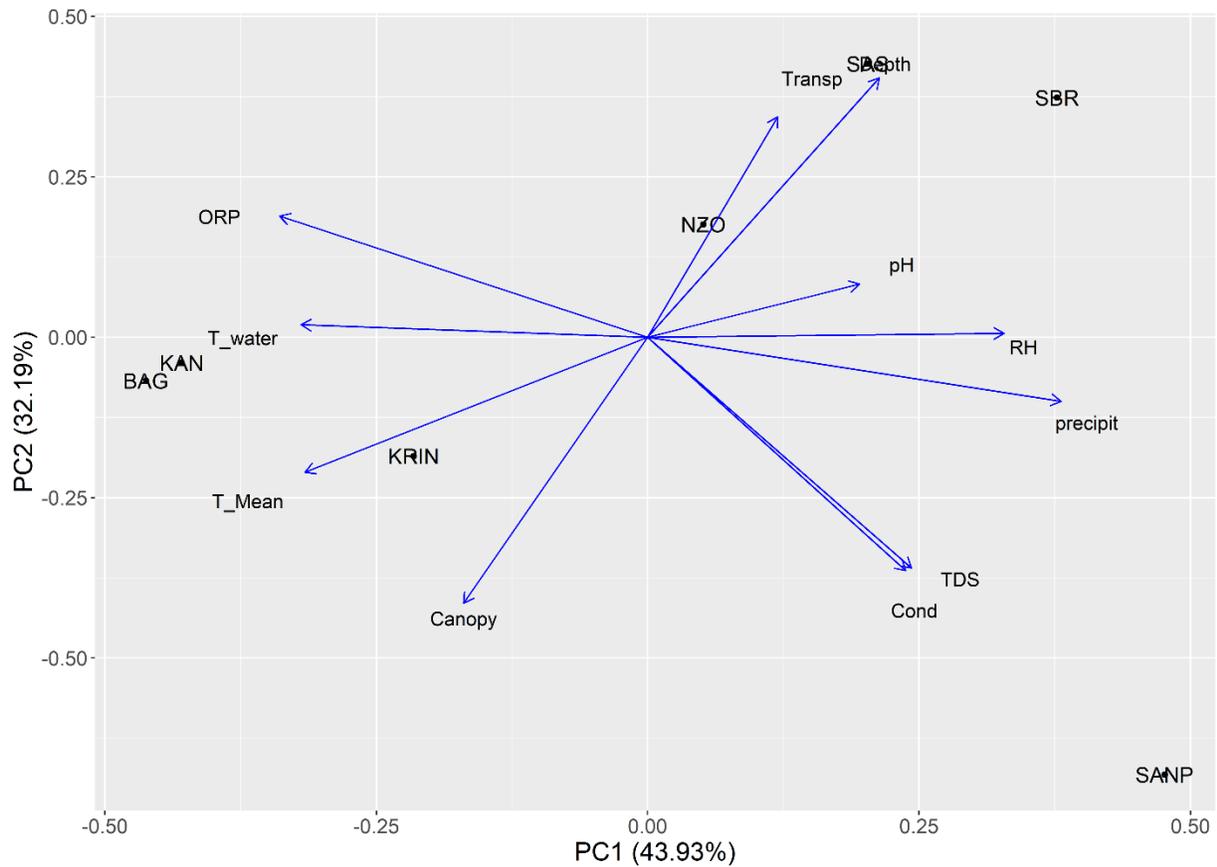


Figure 4. 6: Scatterplot of the projection of the populations, and habitat and climate variables (arrows) on the first two principal components explaining 76.1% of the total variation in climate and habitat variables.

T_Mean= mean air temperature (°C), T_max= maximum air temperature (°C), T_min= minimum air temperature (°C), RH= relative humidity (%), precipit= mean precipitation (mm/day), T_water= water temperature (°C), Depth= Water depth (cm), Cond= electrical conductivity (µS/cm), TDS= total dissolved solids (ppm), ORP= redox potential (mV), Transp= transparency (cm), Canopy= canopy (%).

IV.3.4 Correlation between morphological variation and climate and habitat variables

Overall, there was only a weak correspondence between morphological variation and environmental conditions among populations (Figure 4. 7). The highest correlation coefficient ($r=0.68$, $P=0.090$, $n=7$) was obtained between CV1 and PC1. With declining temperature (water and air), increasing precipitation and humidity (high PC1), the caudal peduncle is elongated and narrows at the insertion bases of the dorsal and anal fins, the dorsal fin becomes longer, the body becomes deeper in its anterior part, and the posterior edge of the operculum and pectoral fin shift towards a downwardly sloping position (high CV1). All other combinations of PC and CV axes were less strongly correlated.

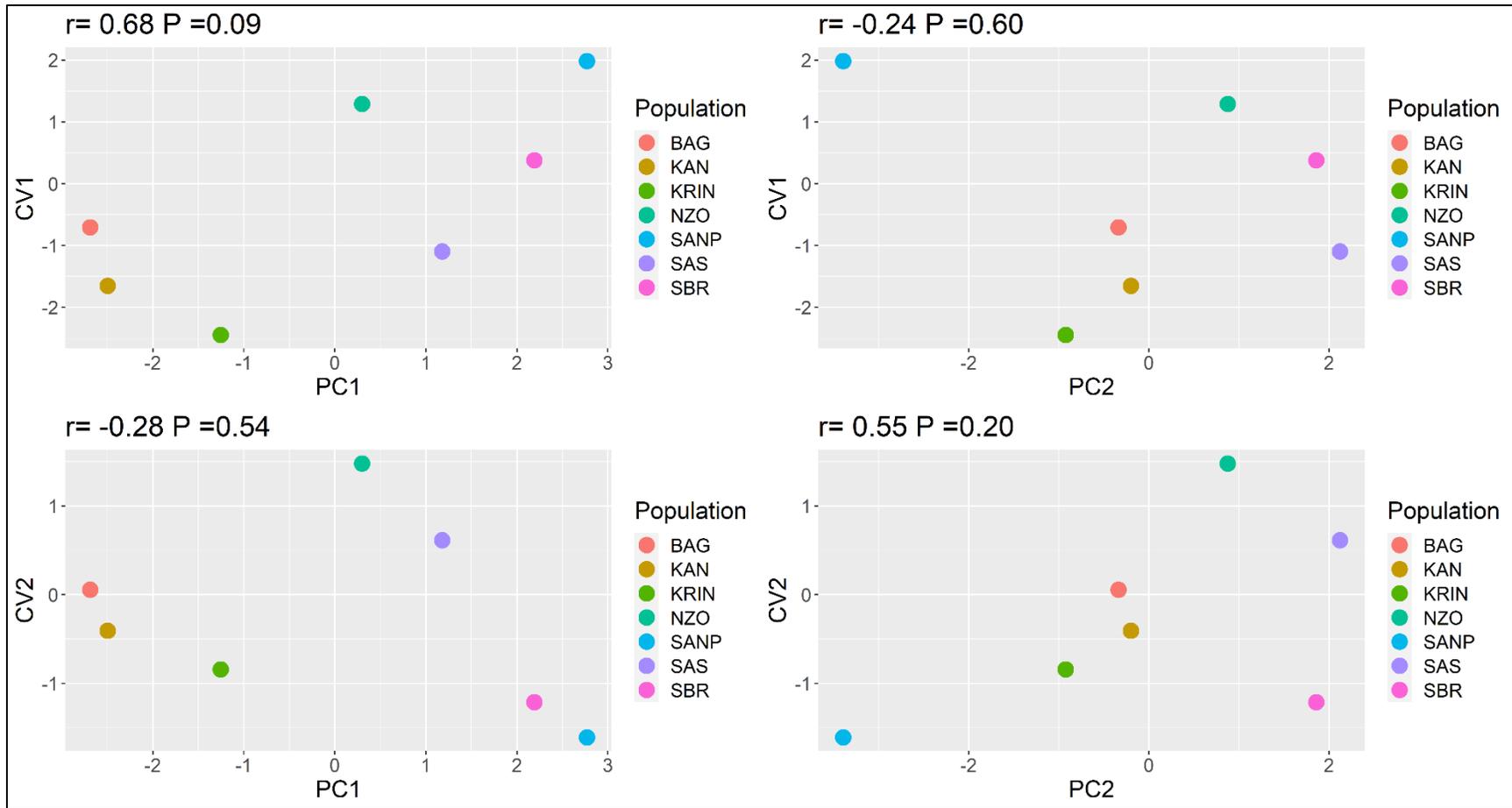


Figure 4. 7: Pearson correlation plots between the first two CVA axes (CV1 and CV2), representing morphological variation among populations, and the first two PCA axes (PC1 and PC2), which represent variation in habitat and climate variables between sites.

Upper left plot - CV1 and PC1, upper right plot - CV1 and PC2, lower left plot - CV2 and PC1, and lower right plot - CV2 and PC2. The correlation coefficient (r) and probability (p) are shown on each plot.

IV.4 Discussion

We analysed intra-specific morphological variation of *P. obscura* populations along climate and habitat gradients in freshwater habitats of Côte d'Ivoire. Significant morphological variation was observed among all populations, although the within-population variability was also high, and was particularly strongly expressed in the population with the lowest number of studied individuals (KRIN). The morphological variations were principally documented in head, caudal peduncle, and pectoral and pelvic fins. Other studies on fish species such as *Gobiocypris rarus* (Shao *et al.*, 2007), *Hemigrammus coeruleus* (Lazzarotto *et al.*, 2017), *Nothobranchius orthonotus* (Bravi *et al.*, 2013; Vrtílek and Reichard, 2016), *Channa punctatus* (Kashyap *et al.*, 2016) or other Cyprinidae family fish (Jacquemin and Pyron, 2016), corroborate our findings that intra-specific morphological variation in fishes can be strongly significant. However, we did not find potential causes of intra-specific variability. The isolation by distance test showed no significant correlation between morphological variations and geographical distance. Furthermore, there was only a weak correspondence between morphological variation and differences of environmental conditions among populations. Accordingly, we did not find significant evidence for environmental-driven phenotypic plasticity or for effects of spatial isolation on expression of intraspecific morphological variation in this species.

Our results (from CVA) showed that most shape variations were localised in head (shape, eye and snout positions), caudal peduncle, and pectoral and pelvic fins. The study by Mouludi *et al.* (2019) on two populations of *Channa gachua*, another species belonging to the Channidae family, also showed body shape differences in the position of the snout and caudal peduncle length. Similar morphological variations mostly localised in fins and head region were observed among populations of *Lavinia symmetricus* (Brown *et al.*, 1992). Variation in eye diameter and head length was observed among population of *Trachurus trachurus* through linear morphometrics methods (Bektas and Belduz, 2009). A study on *Phycis phycis* populations also showed that morphological variation was mainly found in fins regions as well as in the position of the posterior limit of the operculum (Vieira *et al.*, 2016). These regions of fish body are mainly associated with functions such as fish locomotion (pelvic and pectoral fins and caudal peduncle) and feeding (eyes and snout), vital functions that are essential for the survival of the species. Fin and caudal peduncle dimensions are related to swimming ability, which includes speed and maneuverability (Sampaio *et*

al., 2013, Li *et al.*, 2021). Thus, variation in these regions of *P. obscura* fish body may help the fish in coping with environmental variability between different locations.

However, in our study, no significant associations were found between fish shape and climate and habitat variables. Many fish species can change their shape, for example in response to temperature, dissolved oxygen, radiation, water depth, food availability, current or hydrology, or correlated with their feeding mode, predation risk and habitat use (Swain *et al.*, 2005; Clabaut *et al.*, 2007; Spoljaric and Reimchen, 2011; Antonucci *et al.*, 2012; Bravi *et al.*, 2013; Scharnweber *et al.*, 2013; Jacquemin and Pyron, 2016). Jacquemin and Pyron (2016) demonstrated changes in morphology of Cyprinid fishes related to hydrology, where more fusiform individuals with downward turned and extended caudal peduncle dominated during periods of lower discharge. Scharnweber *et al.* (2013) demonstrated that *Rutilus rutilus* cyprinids from lakes with high predation pressure were characterized by a more streamlined body and caudally inserted dorsal fin, attributes that facilitate escape from predators. Phenotypic plasticity of body morphology is regarded as a key strategy for populations living in changing environments, although morphological variation may even play a role in adaptive diversification (Svanbäck, 2004). We did not find significant evidence for phenotypic plasticity in the African snakehead fish in response to variations in environmental conditions. However, there was a relatively high correlation coefficient obtained between CV1 and PC1 ($r=0.68$), which supports that morphological variation between snakehead fish populations may in part be affected by environmental variation.

Thus, air and water temperature, and precipitation, were among variables (explained by PC1) which had the highest correlation coefficient with morphological variation. Under increasing temperatures, ectothermic organisms such as fish may experience several consequences of higher energy demands, including reduced food intake and lower conversion efficiency (Morgan *et al.*, 2001), altered mitochondrial respiratory capacity (Salin *et al.*, 2016), and altered developmental and growth rates (Del Rio *et al.*, 2019; Munday *et al.*, 2008), which together may result in slower growth rates of fish and smaller bodies (Gardner *et al.*, 2011; Lema *et al.*, 2019). In our study, KAN and KRIN populations from sites with high water and air temperatures had small bodies with deeper and slightly shorter caudal peduncles and dorsal fins, supporting these explanations. Thus, shape variations observed may reflect probable morphological plasticity of *P. obscura* to gradients of temperature. Considering the precipitation, it modifies the flow regime, and hence differences in

fish morphology often reflect a compromise between stable and unstable locomotion abilities in response to water currents (Langerhans and Reznick, 2010). Stable swimming allows fish to stay in place against the current and is found in fish living in open habitats with high-flow water regimes. Steady locomotion activities are often achieved by aerodynamic body shapes, narrow caudal peduncle regions and high caudal fin aspect ratios (Langerhans and Reznick, 2010). Unstable swimming is frequently associated with deep bodies in the caudal region, median fins and large caudal fins with low aspect ratios, and is found in fish living in habitats with low-flow regime waters (Domenici *et al.*, 2008; Langerhans and Reznick, 2010; Bruckerhoff and Magoulick, 2017). Therefore, our finding which showed that fish from areas with high precipitation (NZO and SANP) were characterized by relatively elongated caudal peduncle narrowed at the insertion bases of the dorsal and anal fins, while those from low precipitation areas (KAN and KRIN) had a deeper and slightly shorter caudal peduncle, is in agreement with these explanations. Evidence of phenotypic variations in swimming organs, in response to flow regime, was also shown for many other fish species such as *Melanotaenia australis* (Kelley *et al.*, 2017) and *Cyprinella venusta* (Franssen *et al.*, 2013).

Geographical isolation of populations can lead to morphometric variations between populations, and this morphometrical variation can provide a basis for population differentiation (Bookstein, 1991). Spatial isolation by unconnected river systems or by connectivity barriers within river systems may prevent gene flow among populations, and hence adaptive morphological diversification may have contributed to shaping the morphological variation among populations. In contrast, connectivity of river systems facilitates the movement of organisms, nutrient transfer and energy flow across the landscape (Opperman *et al.*, 2010), and is used by fish for reproductive migrations, recruitment and recolonisation, and access to floodplains (Pettit *et al.*, 2017). Spatial connectivity also allows genetic connectivity among populations and would facilitate weak genetic divergence, such that morphological variation would reflect primarily phenotypic plasticity. In our study, no significant association was observed between spatial and morphological distances, despite the fact that we found significant morphological variations (as indicated by Mahalanobis distances) among the populations obtained from hydraulically unconnected sites. Furthermore, we found even differentiation among populations from the same basin (SBR and SAS, both from Sassandra River), likely caused by a dam constructed on Sassandra River. Indeed, the SBR population was collected from downside of the Sassandra River downstream the dam while the SAS population was collected

from the upstream side of the river in the artificial Lake Buyo which is the reservoir impounded by the dam. Finally, fishes of the NZO population that were collected from Nzo River, a tributary of Lake Buyo, were also morphologically different to SBR and SAS populations. A significant effect of spatial isolation on genetic differentiation of snakehead fish populations including those studied here (Amoutchi et al. 2023) supports that spatial arrangement of rivers and potential connectivity among fish populations can be important. Larger sample sizes and a spatially refined sampling scheme be needed to detect the spatial effects on the morphometry of the snakehead fish.

IV.5 Conclusion

The current study demonstrates significant morphological variation among seven *P. obscura* populations from sites that strongly differed in climate and habitat variables. However, the correlations between fish shape and climate and habitat variables were weak, and spatial isolation likewise did not contribute substantially to the differences of fish shape among populations. The differences in shape as obtained by geometric morphometrics may aid the fish in surviving in a variety of environments. It may also contribute to enhanced fitness under the various threats of freshwater ecosystems in Africa, such as climate change, gold mining, water withdrawal for human needs, overexploitation, industrial waste discharge, pesticide use for agricultural purposes along watersheds, and obnoxious fishing practices. However, a functional and mechanistic understanding of the adaptive value of shape variations between populations would require common garden experiments and extended analyses of functional genomics, data that are currently not yet available.

CHAPTER V:

Population genetics of the African snakehead fish *Parachanna obscura* along West Africa's water networks

Abstract

An essential factor for aquatic conservation is genetic diversity or population divergence, which in natural populations reflects the interplay between geographical isolation with restricted gene flow and local evolution of populations. The long geological history of Africa may induce stronger among-population divergence and lower within-population divergence in fish populations of African watersheds. As an example, we studied population structure of the African snakehead fish *Parachanna obscura*. Our study aimed: (1) to develop a set of highly polymorphic microsatellite markers suitable for the analysis of genetic diversity among *P. obscura*, and (2) to study the genetic diversity and structure of *P. obscura* populations from the West Africa region and mostly from Côte d'Ivoire, with respect to the effects of climate region and geographical distance on the genetic differentiation. A total of 259 specimens from 15 locations of *P. obscura* were collected over the West Africa region reflecting a high variability of pairwise geographical distances and variability of hydrological connectivity of the area. We developed a set of 21 polymorphic microsatellite markers for studying population genetics of the fish. The results showed relatively low intra-genetic diversity for all the 15 locations, certainly attributable to the confinement of fish in segregated catchments, resulting in limited gene flow. We also found evidence for local adaptation processes, suggested by five out of 21 microsatellite loci being under putative selection, according to BAYESCAN analysis. In turn, there was strong genetic differentiation ($F_{ST} > 0.5$) among fish from most locations, reflecting the allopatric development in watersheds without hydraulic connectivity. Neighbour-joining dendrogram, Principal Coordinate Analysis and analysis of ancestral groups by STRUCTURE suggested that the 15 locations can be divided into three clusters, mainly matching the dominant climate zones and the segregation of the watersheds in the region. The distinct genetic structure of the fish from the 15 locations obtained in this study suggests that conservation and sustainable management actions of this fish resource should avoid genetic mixing of potentially locally adapted populations.

Keywords: snakehead fish, genetic diversity, genetic differentiation, hydrological networks, paleogeographic history.

V.1 Introduction

Tropical regions host the world's richest freshwater fish faunas. According to estimates, there are over 3000 species of freshwater fish in Africa, which is comparable to the number of species in Asia (over 3600) and South America (over 4200) (Lévêque *et al.*, 2008). Complex climatic and geological events have caused a long history of geographical isolation followed by diversification for some and extinction for other populations, ultimately resulting in the diversified fauna of the African freshwater ecosystems (Darwall *et al.*, 2011, Amoutchi *et al.*, 2021). Since the division of Gondwanaland in the early Cretaceous, many African rivers went through complex geological histories involving changes in the structure of their catchments and river beds (Goudie, 2005). The evolution of Africa's fauna and landscapes has been influenced by the cycles between the Pleistocene and Pliocene dry and rainy eras (deMenocal, 2014; Maslin *et al.*, 2014; Steenberge *et al.*, 2020). Along with fluctuations of water levels in the African Great Lakes, these climate cycles have caused alternating expansions and contractions of savannah and forest-like habitats (Malinsky and Salzburger, 2016). According to Tedesco *et al.* (2005), these climatic shifts led to migration, extinction, and allopatric divergence, which resulted in the current diverse fish faunas. In addition, the long geological history of Africa also affects the interplay between the contemporary distribution of populations and their genetic diversity, with longer periods of spatial segregation and allopatric development than those typically found for the much younger post-glacial landscapes of the Palearctic or Nearctic.

An essential factor for aquatic conservation is genetic diversity or population divergence, which in natural populations reflects population history and the evolutionary potential of a species (Jaisuk and Senanan, 2018). Within a fish species, population subdivision results from the interaction of distinct genetic changes within isolated populations and restricted gene flow among them (Hedrick, 2011). Conspecific populations typically diverge from one another in the absence of gene flow due to mutation, natural selection and genetic drift (Freeland, 2005). In addition, the degree to which landscape shapes patterns of genetic variation among populations is determined by life-history features linked to migration and fish dispersal capabilities (Pilger *et al.*, 2017). Geographical factors favouring population division include geographical distance between locations (Crookes and Shaw, 2016; Beneteau *et al.*, 2009), the presence of barriers (Neville *et al.*, 2006; Yamamoto *et al.*, 2004),

the complexity of a river network (Pilger *et al.*, 2017) and habitat fragmentation (Sterling *et al.*, 2012).

The freshwater ecosystem in Côte d'Ivoire in Africa is characterised by a large and complex system consisting of four major river basins: Sassandra, Cavally, Bandana and Comoé ranging in length from 650 to 1,160 km and rising in geographically wide-ranging areas beyond the Côte d'Ivoire. In addition to these systems, there are many coastal rivers such as the Tabou, San Pedro, Niouniourou, Boubo, Agneby, Bia and Me Rivers as well as two tributaries of the Niger River and many lakes (Girard *et al.*, 1970). These habitats are endowed with numerous economically important fish species.

Among the economically important fish, *Parachanna obscura* Gunther, is the most popular and widespread African fish species from the Channidae family. It is commonly known as African snakehead fish and has great economical and commercial values for local African communities. This species is benthopelagic and a strict freshwater habitant. It is generally distributed in the intertropical convergence zone where the water temperature ranges from 26 ° C to 28 °C principally in West Africa. Nevertheless, it is also found in the upper course of the White Nile, the Lake Chad basin and the Congo River basin (UA, 2013). Given the complexity and geological history of the region, the resulting patterns of genetic variation merit investigation in *P. obscura*. For example, Bezault *et al.* (2011) suggested that paleo-geographic history, climatic events of Africa, and geographic barriers, have induced strong genetic differentiation among *Oreochromis niloticus* populations from different parts of Africa. Strong genetic differentiation was also detected among African freshwater river and lake populations of *Lates niloticus*, reflecting the complexity of freshwater systems originating from the geological history of the continent (Basiita *et al.*, 2018). Furthermore, the long-time isolation of populations can favour adaptations to local environmental conditions with the occurrence of particular alleles. The adaptive capacity of populations depends on microevolution, e.g., the selection of local genotypes better adapted to changing environmental conditions (Canale and Henry, 2010; Hoffmann and Sgro, 2011). These adaptation processes will likewise influence the amount and distribution of genetic diversity among populations (Pauls *et al.*, 2013). Thus, assessment of the genetic diversity of *P. obscura* is necessary for understanding the evolutionary patterns of this species, and its capacity to cope with future environmental conditions,

as well as for planning conservation policy for sustainable management of this species as fisheries resource.

Previous studies on *P. obscura* have mostly focused on biology (Odo *et al.*, 2012; Bolaji *et al.*, 2011), reproduction (Vodounnou *et al.*, 2017; Agokei and Hart, 2010), aquaculture potential (Azrita *et al.*, 2015), and phylogenetic range of the fish (Conte-grand *et al.*, 2017; Li *et al.*, 2003; Adamson *et al.*, 2012). However, there is no information about the genetic diversity among populations of this species. Since no previous studies have been conducted on the genetic diversity of *P. obscura*, genetic markers, for example microsatellites, were not available. Accordingly, the objectives of our study were: (1) to develop a set of highly polymorphic microsatellite markers suitable for the analysis of genetic diversity among *P. obscura* fish, and (2) to study the genetic diversity and structure of *P. obscura* fish from 15 locations from the West Africa region and mostly from Côte d'Ivoire. According to the geological history of the region with potentially long periods of geographical isolation, we expected low genetic diversity and high genetic differentiation for this species. Furthermore, we expected that the genetic differentiation was affected by geographical isolation caused by the interplay between connectivity barriers, landscape structure and geographical distances among locations.

V.2 Materials and methods

V.2.1 Study area and collection of samples

A total of 259 specimens of *P. obscura* from 15 locations were collected over the West Africa region from Côte d'Ivoire (14 locations), and Benin republic (one location) (see Figure 5. 1 and Table V.I and Appendix 3). The sampling sites were selected to represent a high variability of pairwise geographical distances. In Côte d'Ivoire, individuals were sampled from Bia River (KRINA, and KRINB, locations about 7 km distant from each other), Wayadji stream (SIK), Sassandra river (SBR), San-Pedro Lake (SANP) and Abengourou lake (ABIN). This region is characterised by a sub-equatorial climate (Guinean climate zone) including two rainy and dry seasons, with an estimated annual precipitation of more than 1500 mm (Bernard, 2014). Specimens were also collected from Kan Lake (KAN), Baho (BAHO) and Glo (GLO) streams, Buyo Lake (SASA and SASB, sampling distance of about 26 km), and Nzo River (NZOA and NZOB, with sampling distance of about 13 km), in the centre and centre-western Côte d'Ivoire, characterised by an equatorial transition climate (Sudano-guinean climate zone), with two rainy and dry seasons, and

an annual precipitation of 1200 to 1500 mm per year. Finally, individuals were collected in Bagoue river (BAG), situated in the north Côte d'Ivoire, characterised by a tropical climate (Sudanean climate zone) with a very hot and dry season from November to March and a rainy season from April to October. Specimens sampled from Benin republic were collected in Nokoue lake (BIN), located in the southern part characterized by a sub-equatorial climate with two rainy and dry seasons.

Parachanna obscura fishermen from each sampling site were employed for fish sample collection using traps and fish nets. The intended sample size per location was 25-30 individuals; however, for several sites this number could not be obtained. For molecular analyses, approximately 1 cm of pectoral fin was clipped from each individual and stored in individual Eppendorf tubes containing 95% ethanol. The rest of the entire specimens were fixed in 10% formaldehyde solution and transported to laboratory for further analysis. The molecular analysis was performed in the genetic laboratory of the Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin.

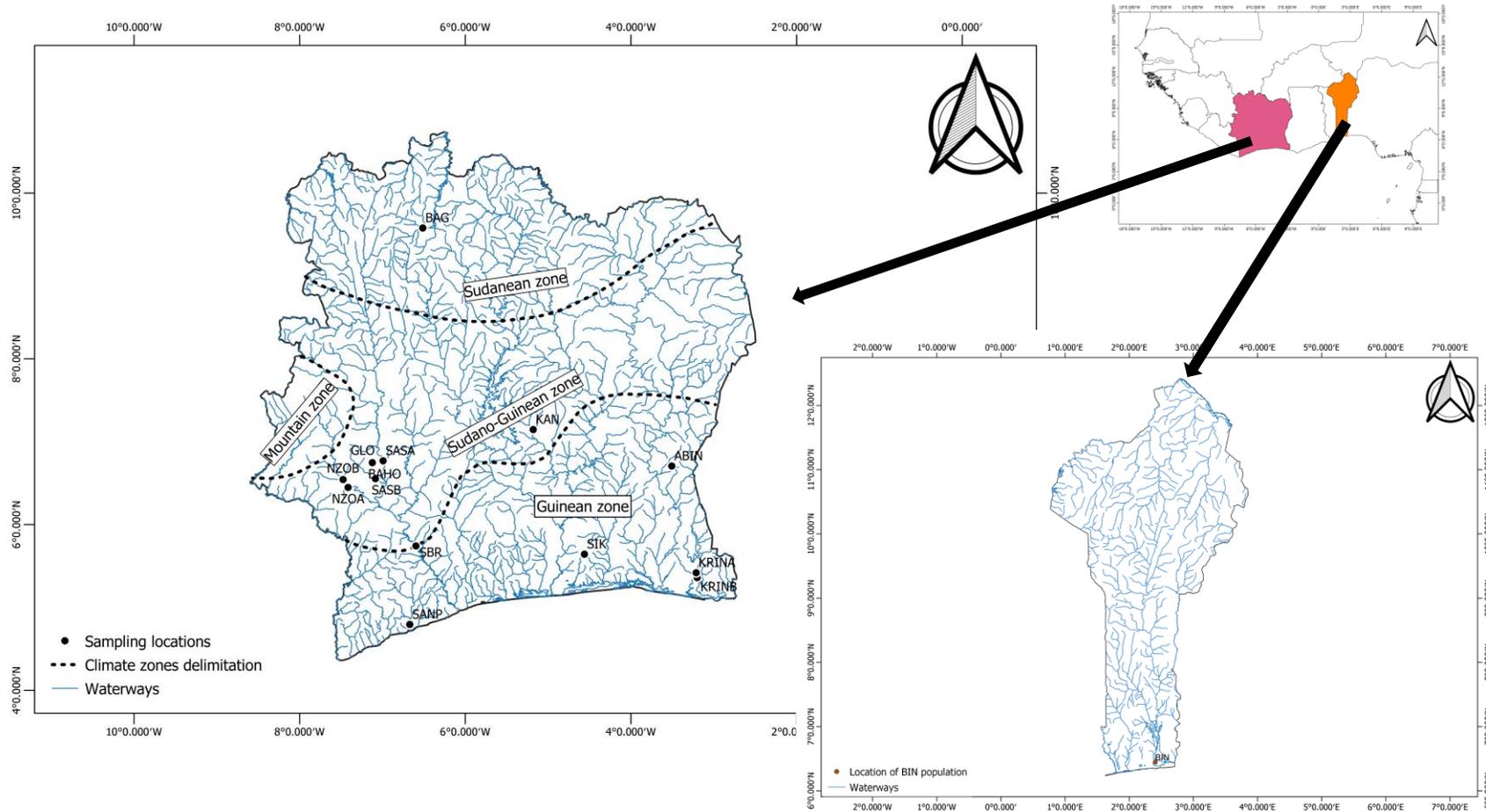


Figure 5. 1: Map of the study area, showing sampling locations from which *P. obscura* specimens were collected, in Côte d'Ivoire (left) and in Benin republic (right down), and position of these countries in West Africa.

ABIN: Abengourou Lake, KRINA: Bia river, KRINB: Bia river, SANP: San-Pedro Lake, SBR: Sassandra river, SIK: Wayadji stream, BAHO: Baho stream, GLO: Glo stream, KAN: Kan Lake, NZOA: Nzo river, NZOB: Nzo river, SASA: Buyo Lake, SASB: Buyo Lake, BAG: Bagoue river and BIN: Nokoue lake

Table V. I: Samples sizes, basins, country and climate of locations of 15 samples of *P. obscura* (with total sample size of 259 individuals).

River basin	Water body	Location	Sample Size (N)	Country	Climate
Comoe	Abengourou Lake	ABIN	6	Côte d'Ivoire	Sub-equatorial
Coastal river Bia	Bia river	KRINA	38	Côte d'Ivoire	Sub-equatorial
Coastal river Bia	Bia river	KRINB	13	Côte d'Ivoire	Sub-equatorial
Coastal river San-Pedro	San-Pedro Lake	SANP	26	Côte d'Ivoire	Sub-equatorial
Sassandra	Sassandra river	SBR	17	Côte d'Ivoire	Sub-equatorial
Coastal river Agneby	Wayadji stream	SIK	5	Côte d'Ivoire	Sub-equatorial
Sassandra	Baho stream	BAHO	7	Côte d'Ivoire	Equatorial transition climate
Sassandra	Glo stream	GLO	6	Côte d'Ivoire	Equatorial transition climate
Bandama	Kan Lake	KAN	18	Côte d'Ivoire	Equatorial transition climate
Sassandra	Nzo river	NZOA	12	Côte d'Ivoire	Equatorial transition climate
Sassandra	Nzo river	NZOB	40	Côte d'Ivoire	Equatorial transition climate
Sassandra	Buyo Lake	SASA	16	Côte d'Ivoire	Equatorial transition climate
Sassandra	Buyo Lake	SASB	17	Côte d'Ivoire	Equatorial transition climate
Niger river	Bagoue river	BAG	22	Côte d'Ivoire	Tropical climate
Fed by Ouémé and Sô Rivers	Nokoue lake	BIN	16	Benin	Sub-equatorial

V.2.2 Molecular genetics analyses

Genomic DNA from fin clippings was isolated using the DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer protocol. The development of microsatellite markers suitable for the analysis of population genetics of *P. obscura* was conducted by the commercial company GenoScreen (Lille, France). Their procedure consisted of two steps: (1) GenoSat library preparation using 5 µg DNA from an equimolar pool of 10 DNA samples followed by high throughput DNA sequencing run on Nano 2x250 v2 - MiSeq Illumina and bioinformatic analysis and primer design. (2) Biological validation of 142 primer pairs on eight *P. obscura* DNA samples from different populations including PCR amplification and analysis of the obtained profiles on QIAxcel (Qiagen). GenoScreen usually considers as validated those primer pairs with a specific PCR product at the expected size for at least 5 samples. This was the case for 120 (or 84.5%) of the tested 142 primer pairs. Based on the delivered list of validated primers with comments for each pair and migration profiles generated by QIAxcel ScreenGel 1.6.0, the number of potentially suitable primer pairs was further reduced by excluding those with weak, very weak or no visible PCR product for one or more samples and focusing on those indicating polymorphism on the migration profiles. This screening resulted in 29 primer pairs selected for testing on a larger number of individuals using the PCR protocol described below. However, only 21 primer pairs (Table V. II) turned out to be suitable for routine genotyping based on the observed polymorphism.

Each forward primer of the 21 loci was synthesised with either DY751 or Cyanine 5 or BMN-6 fluorescent dyes attached to its 5' end. A set of eight multiplex reactions were conducted (Table V. III). PCR amplification was conducted using Qiagen Multiplex PCR kits, following the recommendations of the manufacturer. PCR amplification was carried out in 11.3 µl reaction volumes, containing 10 µl PCR mix and 1.3 µl DNA (~ 20 ng/µl). The composition of the PCR mix of each of the multiplex reactions is described in Table V.III. The primer concentration was 10 pmol/µL. The thermocycling profile started with an initial denaturation step at 95°C for 15 min, followed by 35 cycles of 30 seconds at 94°C, 55°C and 72°C and ended with a final extension step of 30 min at 60°C. Denatured fragments were resolved on an automated DNA sequencer (Beckmann Coulter CEQ 8000) using 0.83 µl of PCR product and a mixture of 30 µl formamide (SLS; Sciex, Darmstadt, Germany) and 0.5 µl size standard-400 (Sciex). Genotypes were identified using the GenomeLab™ GeXP Genetic Analysis System version 10.2 (Beckman Coulter) fragment analysis module.

V.2.3 Statistical data analyses

The majority of the analyses and graphical output were created using R 4.1.2 (R Core Team, 2021). Allele polymorphism at each of the 21 microsatellite loci and the intra-population genetic diversity metrics, such as number of alleles per location and allelic richness A_R , were quantified by PopGenReport 3.0 package (Adamack *et al.*, 2014). Potential existence of individuals with missing genotypes among the loci was evaluated using poppr 2.9.3 (Kamvar *et al.*, 2014) package in R. Null allele frequencies per locus were calculated in the genepop 1.1.7 package (Rousset, 2008). The inbreeding coefficient (F_{IS}), representing the probability that the two alleles at one locus of an inbred individual are identical alleles per descent (Gazal *et al.*, 2014), was estimated in genepop_in_R. The significance of this coefficient was evaluated based on 95% confidence intervals calculated using bootstrapping ($N=100$) in hierfstat 0.5-11 package in R (Jerome and Thibaut, 2022). Deviations from Hardy-Weinberg equilibrium (HWE) at the location level were tested by the exact (probability) test using genepop v1.1.7 in R. Probabilities of HWE deviations (Guo and Thompson, 1992) per locus per location were corrected by the false discovery rate for multiple tests (Benjamini and Hochberg, 1995), supplemented by U-tests on excess homozygotes. We conducted an Analysis of Molecular Variance (AMOVA)(Excoffier *et al.*,1992) using the R-package pegas 1.1 (Paradis, 2010) to compare within- and between-location variance for the 15 locations.

Through the genepop v1.1.7 package in R, genetic differentiation was estimated by F-statistics between locations (F_{ST}) (Weir and Cockerham, 1984), with the significance of differentiation assessed by exact conditional contingency table tests for genotypic differentiation. Using the poppr v2.9.3 package in R, a neighbourhood tree (Saitou and Nei, 1987) based on Prevosti's pairwise genetic distance (Prevosti,1974) was constructed to identify genetic relationships between *P. obscura* locations. The 259 individual genotypes were also subjected to a principal coordinate analysis (PCoA), which is a multidimensional metric scaling, in order to visualize the distribution of individuals and location centroids in reduced space. This analysis was carried out in ade4 v1.7-19 (Thioulouse *et al.*, 2018), while adegraphics v 1.0-16 (Siberchicot *et al.*, 2017) was used to visualize the resulting graphs.

Bayesian approaches as implemented in the standalone program STRUCTURE v2.3.4 (Pritchard *et al.*, 2000) were used to estimate and visualize the genetic structure among samples from the 15 locations. After a burn-in period of 100,000 iterations, the number of Markov-chain Monte Carlo iterations was set to 100,000 using admixture model's default

parameters and locations' correlated allele frequencies. Ten runs were performed for each K (ancestral groups or clusters) between 1 and 15. The greatest mean estimate of the posterior probability based on the ad hoc ΔK statistics was used to determine the optimum K (Evanno *et al.*, 2005).

Mantel correlation tests were performed between the pairwise genetic distance matrices calculated as $F_{ST}/(1 - F_{ST})$ values and the natural logarithm (ln) of the pairwise straight-line geographic distances (km) to assess the effect of geographic isolation or distance on the genetic structure among *P. obscura* sample locations. The genetic distance matrix was calculated in the genepop package of R, while the geographical distance matrix was calculated with QGIS 3.22.6 using the global positioning system (GPS) coordinates of the sampling locations. Mantel correlation tests with 1000 permutations were performed by the vegan v 2.6-2 package (Oksanen *et al.*, 2022) in R.

To examine non-neutral evolutionary forces acting on the microsatellite loci, a scanning analysis was realized using the BAYESCAN v2.1 software (Foll and Gaggiotti, 2008) to detect candidate loci under selection. BAYESCAN was run with a sample size of 5,000, a number of pilots runs of 20, length of pilot runs of 5,000, a burn-in of 50,000, and the false discovery rate (FDR) threshold of 0.05.

Table V. II: Microsatellite markers developed and used for the population genetic study of *P. obscura*.

Locus name	Forward sequence	Reverse sequence	Dye	Repeat motif	Expected size
Para018	CGTCCAGGAGTGGTCTTCAG	ACCTCATGATGGTGCTCTGG	BMN-6	(AC)13	206
Para023	AAACTGAACACAGGGCATGC	AGAGGTCTTGACATGATGTGGA	Cyanine 5	(AC)12	296
Para025	GGTGTGTCACCTTGTGACCC	AGCTGTGCAAATTACCTAGAAGC	Cyanine 5	(AG)12	198
Para026	CTGTTTGGTGTAGCACTAAAGGT	TTGATATCTGAACGGCTCCTTT	BMN-6	(AC)12	190
Para027	CCCGTGCAGTAAATGGATGAAG	GGATTCAAGGCTAGACTGAAAGA	Cyanine 5	(AC)12	178
Para036	AGCATGGTAATGAGCAGCTAA	TGTTTCAGAGCTAAGACGTGGT	BMN-6	(AC)11	227
Para037	CAGGTACAAATTGGTGGCCC	TACCCTGAAATGAGGCGCAG	DY-751	(AC)11	222
Para038	AAGCCACAGAACCAAAGCCA	GGACAAGTATCAGTGGCCGA	Cyanine 5	(AC)11	205
Para039	TCGTGTTAGGCGAGCATTCA	CTCGTAGCGTGAAGGGCTTT	DY-751	(AG)11	198
Para040	ACAAGCAAGTTTACATGCAGCA	ATGGAGGCAGATGATCCGCT	DY-751	(AAG)11	192
Para041	GGCACCGAAATGTCAGCAAC	ACAACAAACACTGAGCTCACTT	DY-751	(AAT)11	128
Para042	GGGAGGCGTACCAGCAAATA	CTGTTGCCACAGTTCCTTCA	BMN-6	(AC)11	126
Para049	GAGCATGTGGAGTAGGTGGG	ATTGAGGTGCTTTGGCCACT	BMN-6	(AG)10	213
Para059	GTCCCAGTACAACAGCGAGA	TCAGAGAAACCAGTGGACTGT	DY-751	(AC)10	140
Para104	TGTCAGCTTTCCAAGTACTGCA	TAATACCTCAGCTGCACCGG	Cyanine 5	(ACC)8	211
Para107	GTGGGCTCTGCACTAGTTGT	AGCCCAGACTAGAAGGAGCT	Cyanine 5	(AC)8	206
Para110	GGCGACACAAACATCTGAGC	TACCTGCGACCGGATGAGAT	DY-751	(AC)8	198
Para128	AATGACATAGACCGCTGGCC	AGCTGGGACAAGCCAAGATG	DY-751	(AC)8	144
Para134	ACAACAACACTGCACACGCTTG	GGAGCGTGAATGCCTGTTCA	BMN-6	(AC)8	139
Para136	TGCTTAATCCTCTGCTGACGG	CTGTGTTGTTCCCACTTACGT	BMN-6	(AGAT)8	137
Para137	GCCCTCTGAGCGTGATCTTT	CCCATCTGTGACACTATGGTCT	DY-751	(AAC)8	120

Table V. III: Composition of the PCR mix of the eight multiplex reactions performed for studying the population genetics of *P. obscura*.

Multiplex	Product	Volume	Multiplex	Product	Volume
Multiplex 1	Master mix	5 μ l	Multiplex 5	Master mix	5 μ l
	dH2O	4.32 μ l		dH2O	4.63 μ l
	Para136-F	0.13 μ l		Para059-F	0.065 μ l
	Para136-R	0.13 μ l		Para059-R	0.065 μ l
	Para025-F	0.07 μ l		Para027-F	0.04 μ l
	Para025-R	0.07 μ l		Para027-R	0.04 μ l
	Para137-F	0.14 μ l		Para036-F	0.08 μ l
	Para137-R	0.14 μ l		Para036-R	0.08 μ l
Multiplex 2	Master mix	5 μ l	Multiplex 6	Master mix	5 μ l
	dH2O	4.55 μ l		dH2O	4.62 μ l
	Para042-F	0.09 μ l		Para049-F	0.07 μ l
	Para042-R	0.09 μ l		Para049-R	0.07 μ l
	Para038-F	0.035 μ l		Para026-F	0.12 μ l
	Para038-R	0.035 μ l		Para026-R	0.12 μ l
	Para039-F	0.10 μ l			
	Para039-R	0.10 μ l			
Multiplex 3	Master mix	5 μ l	Multiplex 7	Master mix	5 μ l
	dH2O	4.59 μ l		dH2O	4.67 μ l
	Para128-F	0.095 μ l		Para041-F	0.12 μ l
	Para128-R	0.095 μ l		Para041-R	0.12 μ l
	Para107-F	0.040 μ l		Para104-F	0.045 μ l
	Para107-R	0.040 μ l		Para104-R	0.045 μ l
	Para134-F	0.070 μ l			
	Para134-R	0.070 μ l			
Multiplex 4	Master mix	5 μ l	Multiplex 8	Master mix	5 μ l
	dH2O	4.49 μ l		dH2O	4.68
	Para023-F	0.05 μ l		Para037-F	0.060 μ l
	Para023-R	0.05 μ l		Para037-R	0.060 μ l
	Para018-F	0.11 μ l		Para040-F	0.10 μ l
	Para018-R	0.11 μ l		Para040-R	0.10 μ l
	Para110-F	0.095 μ l			
	Para110-R	0.095 μ l			

V.3 Results

V.3.1 Genetic structure within populations

In total, 0.3% missing genotypes were obtained among all microsatellites for the 259 individuals from the 15 locations (Appendix 5). Loci Para041 (1.9%) and Para023 (1.5%) had the highest proportions of missing genotypes. Among locations, ABIN (1.6%) and SIK (1.0%) recorded the highest proportions of missing loci. No individual with more than two missing loci was found. Therefore, all individuals and loci were used for further analyses.

A total of 87 alleles were observed across the 21 microsatellite loci. All microsatellite markers developed in this study were variable. The allele number (N_A) per locus ranged from two found at Para038, Para128, Para136 and Para137 loci to 12 found at Para027 locus (Table V. IV). Among the loci genotyped, Para027 was the most variable one ($H_E = 0.67$, $H_O = 0.42$), while the lowest variability was detected at locus Para042 ($H_E = 0.21$, $H_O = 0.03$). Following maximum likelihood estimates, relatively high null allele frequencies were estimated for loci Para038 (16%) and Para059 (59%). However, since no difference was observed in the estimates of genetic differentiation among locations after removing these loci (pairwise F_{ST} values; Appendix 6), we included all 21 loci in the analyses.

The genetic diversity was low in most of the locations (Table V. V). However, KRINA ($N_A = 57$, $H_O = 0.35$, $H_S = 0.33$, $\bar{A}_R = 1.9$), KRINB ($N_A = 55$, $H_O = 0.33$, $H_S = 0.34$, $\bar{A}_R = 2.0$) and BIN ($N_A = 57$, $H_O = 0.302$, $H_S = 0.30$, $\bar{A}_R = 1.9$) had a higher genetic diversity than the other locations. The estimated inbreeding coefficient (F_{IS}) value was low for all locations, and the confidence intervals showed that the F_{IS} coefficients were non-significant for all locations. Except for SASA (Para 107), SASB (Para027) and KRINA (Para104) locations where deviations from HWE at single loci were found (Table V. VI), most of the samples did not deviate from HWE for all 21 analysed microsatellite loci after correction by the false discovery rate for multiple tests.

Table V. IV: Allelic variability across the 21 microsatellites developed and used for this studying the population genetics of *P. obscura*.

Locus	H _O	H _S	N _A
Para018	0.15	0.53	6
Para023	0.15	0.39	4
Para025	0.04	0.50	3
Para026	0.05	0.55	5
Para027	0.42	0.67	12
Para036	0.10	0.25	3
Para037	0.17	0.51	5
Para038	0.11	0.19	2
Para039	0.06	0.21	3
Para040	0.12	0.29	6
Para041	0.13	0.41	3
Para042	0.03	0.21	3
Para049	0.19	0.44	3
Para059	0.18	0.44	3
Para104	0.31	0.50	4
Para107	0.21	0.36	5
Para110	0.25	0.66	7
Para128	0.10	0.47	2
Para134	0.07	0.28	4
Para136	0.15	0.43	2
Para137	0.12	0.39	2

N_A: observed number of alleles, H_O: observed heterozygosity, H_S: expected heterozygosity.

Table V. V: Genetic diversity of *Parachanna obscura* fish from 15 sampling locations at 21 microsatellite loci.

Location	N _A	H _O	H _S	\bar{A}_R	F _{IS}	95% CI for F _{IS}
ABIN	33	0.16	0.18	1.4	0.09	[-0.17; 0.33]
BAG	27	0.02	0.023	1.1	-0.04	[-0.06; 0.00]
BAHO	23	0.02	0.03	1.1	0.28	[0.00; 0.37]
BIN	57	0.30	0.30	1.9	-0.01	[-0.15; 0.14]
GLO	22	0.02	0.02	1.0	-0.25	[-0.25; -0.25]
KAN	28	0.09	0.10	1.2	0.09	[-0.05; 0.22]
KRINA	57	0.35	0.33	1.9	-0.06	[-0.14 - 0.01]
KRINB	55	0.33	0.34	2.0	0.01	[-0.08; 0.13]
NZOA	23	0.04	0.04	1.1	0.07	[-0.22; 0.29]
NZOB	25	0.04	0.04	1.1	0.09	[0; 0.11]
SANP	35	0.27	0.26	1.6	-0.05	[-0.22; 0.12]
SASA	25	0.04	0.05	1.1	0.19	[-0.09; 1]
SASB	25	0.02	0.03	1.1	0.40	[-0.03; 0.54]
SBR	24	0.06	0.05	1.1	-0.16	[-0.19; -0.13]
SIK	34	0.30	0.26	1.6	-0.14	[-0.41 ; 0.13]

N_A: observed number of alleles, H_O: observed heterozygosity, H_S: expected heterozygosity, \bar{A}_R : mean allelic richness and F_{IS}: inbreeding coefficient and 95% CI: 95% confidence interval.

Table V. VI: P-values of deviations from Hardy-Weinberg equilibrium population after correction by the false discovery rate for multiple tests.

	BAG	ABIN	KRINB	GLO	SASA	BAHO	SASB	NZOA	NZOB	KAN	SANP	SBR	KRINA	SIK	BIN	N HWE per loci
Para137	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para136	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para025	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para042	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para039	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para038	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para128	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para107	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para134	1	1	1	1	0.01	1	1	1	1	1	1	1	1	1	1	1
Para023	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para018	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para110	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para059	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para027	1	1	1	1	1	1	0.02	1	1	1	1	1	1	1	1	1
Para036	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para049	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para026	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para041	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para104	1	1	1	1	1	1	1	1	1	1	1	1	<0.0001	1	1	1
Para037	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Para040	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
N HWE per population	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0

V.3.2 Genetic structure between populations

The pairwise F_{ST} was high and significantly differentiated all location pairs of *P. obscura*, except the few locations from the same watershed only few kilometres apart (Table V.VII). BAG was most genetically differentiated, with the highest pairwise F_{ST} values (all above 0.7) recorded relative to the other location pairs. Estimation of the pairwise F_{ST} were extremely low (close to zero) between SASA, SASB, NZOA, NZOB and BAHO from Sassandra river basin, and between KRINA and KRINB from Bia River.

The result of AMOVA showed significantly ($P < 0.05$) high genetic variation among locations (66.7%) and within individuals (33.5%), while no significant variance was detected among individuals within locations (-0.2%) (Table V.VIII).

The neighbor-joining dendrogram obtained based on Prevosti's genetic distance separated the locations into three major clusters (Figure 5.2). The locations SIK, KRINA, KRINB, SANP, KAN and BIN fish representing cluster I are located in southern regions characterized by sub-equatorial climate, except KAN from the central Côte d'Ivoire. The second cluster (II) included SASA, SASB, NZOA, NZOB, GLO, SBR and BAHO locations fish from Centre-western region of Côte d'Ivoire with an equatorial transition climate. The third cluster (III) was composed of BAG (Bagoue river) and ABIN (Abengougou lake) from northern (with a tropical climate) and south-eastern Côte d'Ivoire (with sub-equatorial climate), respectively. Principal coordinate analysis (PCoA) of individuals confirmed the classification of locations obtained from the dendrogram (Figure 5.3). The first five axes explained around 77.4% of the total predicted variation with 36.9%, 21.7%, 7.5%, 5.8% and 5.3% of predicted variation, respectively. The projection of the 259 specimens over the first two axes is shown in Figure 5.3. PCoA-Axis 1 principally separated samples of cluster II (negative PCoA-values) and samples of cluster I (positive PCoA-values). PCoA-Axis 2 isolated cluster III locations BAG and ABIN with negative PCoA-values from the other locations.

A complex spatial genetic structure of *P. obscura* samples was revealed by the correlation between pairwise genetic distances ($F_{ST} / (1 - F_{ST})$) and the natural logarithm of the pairwise Euclidean geographical distance between the 15 locations. Although there was a significant positive trend between genetic and geographical distances, there were strong deviations from the linear pattern at 5.5 and 6.5 ln geographical distances, caused by the strong genetic distances between BAG and SASA, SASB, NZOA, NZOB, BAHO and BAHO locations (Slope=0.96, Adj $R^2=0.052$; Mantel test $P=0.04$) (Figure 5.4).

Table V. VII: Matrix of pairwise F_{ST} between the 15 *P. obscura* locations (lower diagonal), and their P-values as obtained by G-tests (upper diagonal).

	ABIN	BAG	BAHO	BIN	GLO	KAN	KRINA	KRINB	NZOA	NZOB	SANP	SASA	SASB	SBR
ABIN		<0.0001												
BAG	0.90		<0.0001											
BAHO	0.81	0.95		<0.0001	0.0255	<0.0001	<0.0001	<0.0001	0.388	0.469	<0.0001	0.755	1	0.006
BIN	0.67	0.82	0.72		<0.0001									
GLO	0.80	0.96	0.66	0.73		<0.0001	<0.0001	<0.0001	0.0005	<0.0001	<0.0001	<0.0001	0.0009	<0.0001
KAN	0.79	0.93	0.85	0.63	0.85		<0.0001							
KRINA	0.56	0.72	0.52	0.38	0.53	0.42		0.277	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
KRINB	0.56	0.80	0.55	0.41	0.54	0.50	0.01		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
NZOA	0.83	0.95	0.04	0.74	0.61	0.85	0.54	0.59		0.999	<0.0001	0.608	0.244	0.054
NZOB	0.88	0.94	0.07	0.83	0.59	0.88	0.64	0.72	-0.03		<0.0001	0.223	0.027	0.037
SANP	0.58	0.78	0.51	0.54	0.56	0.53	0.34	0.34	0.53	0.63		<0.0001	<0.0001	<0.0001
SASA	0.83	0.94	-0.02	0.76	0.55	0.85	0.56	0.61	0.01	0.05	0.54		0.478	0.018
SASB	0.85	0.95	-0.07	0.78	0.61	0.87	0.57	0.63	0.07	0.11	0.57	0.00		<0.0001
SBR	0.84	0.94	0.22	0.76	0.61	0.85	0.56	0.61	0.08	0.09	0.53	0.11	0.25	
SIK	0.56	0.89	0.68	0.59	0.65	0.68	0.47	0.45	0.71	0.80	0.46	0.72	0.76	0.70

Significant pairwise differentiations are indicated in bold.

Table V. VIII: Analysis of molecular variance for 259 *Parachanna obscura* individuals originating from 15 locations sampled in Côte d'Ivoire and Benin for this study.

	Df	Sum Sq	Mean Sq	Sigma	% of variation	P
Variance between populations	14	2958.9	211.3	6.2	66.7	0.01
Variance between samples within populations	244	747.6	3.1	-0.02	-0.2	0.59
Variance within samples	259	805.0	3.1	3.1	33.5	0.01
Total variance	517	4511.5	8.7	9.3	100	

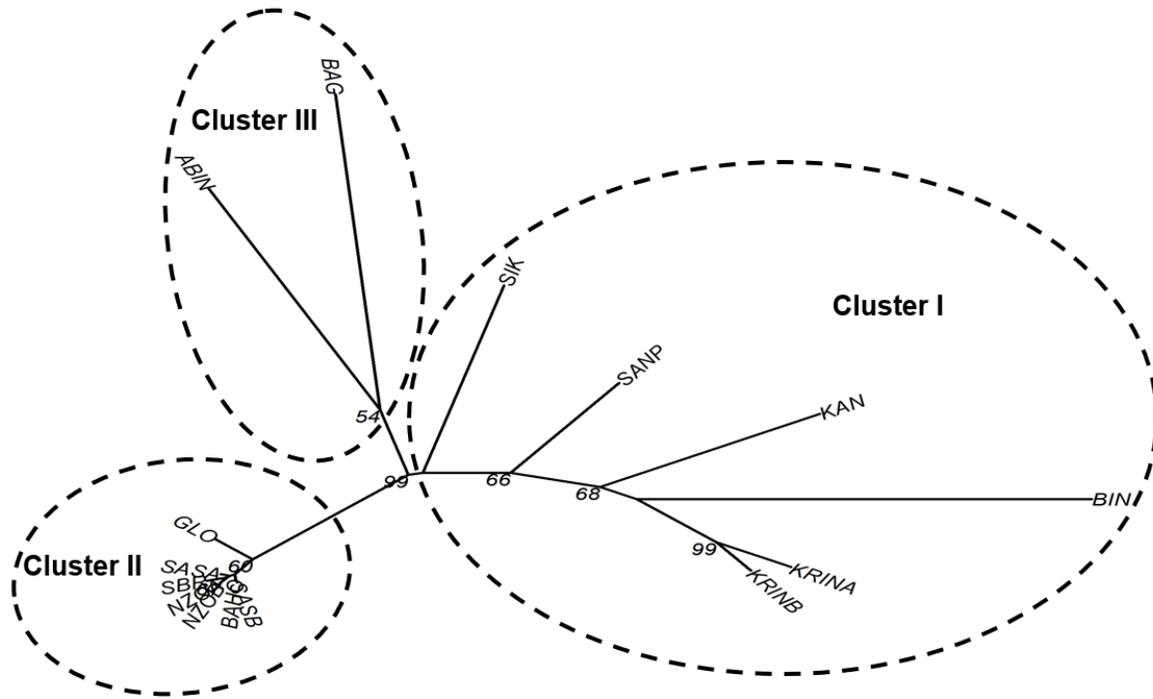


Figure 5. 2: Neighbor-joining dendrogram *P. obscurafish* from 15 sampling locations in Côte d'Ivoire and Benin, based on Prevosti's genetic distance.

Only bootstrap values >50% are shown.

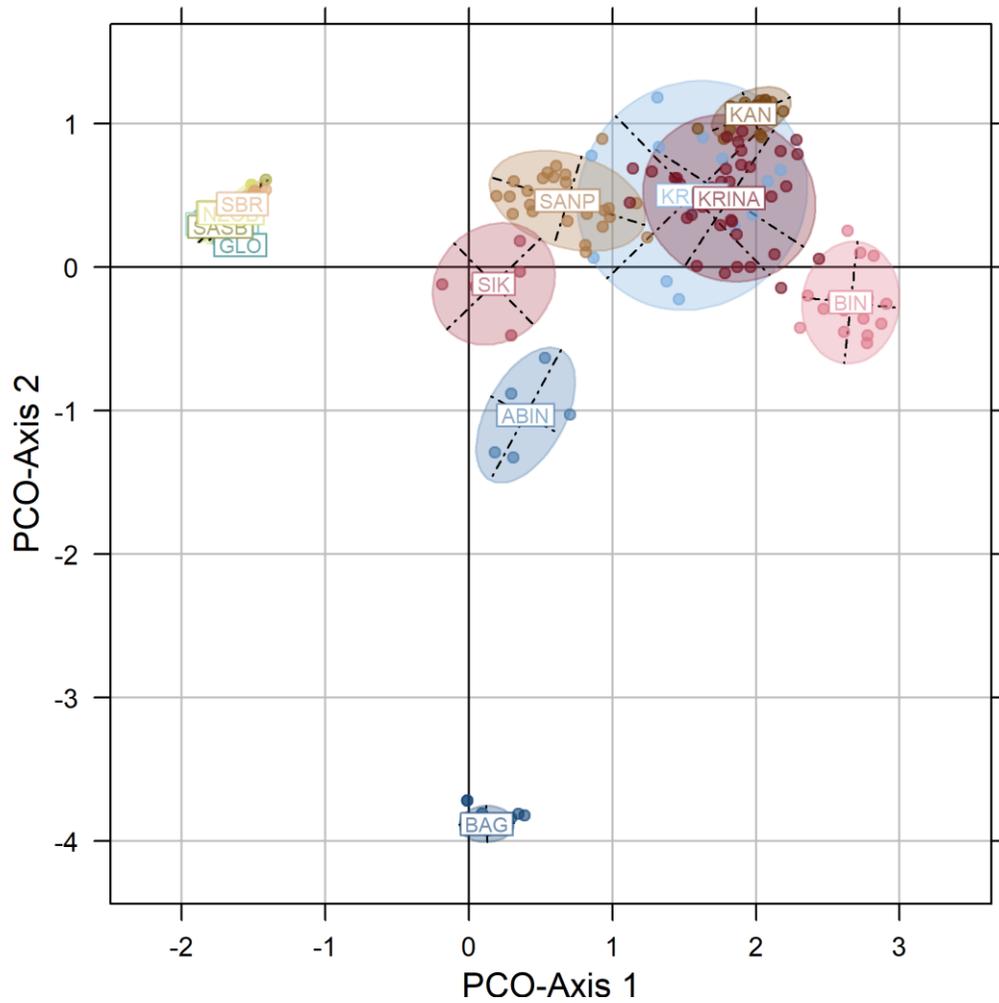


Figure 5. 3: Axes 1 and 2 of the principal component analysis (PCoA) of 259 *P. obscura* individuals (dots) and inertia ellipses representing 15 sampling locations.

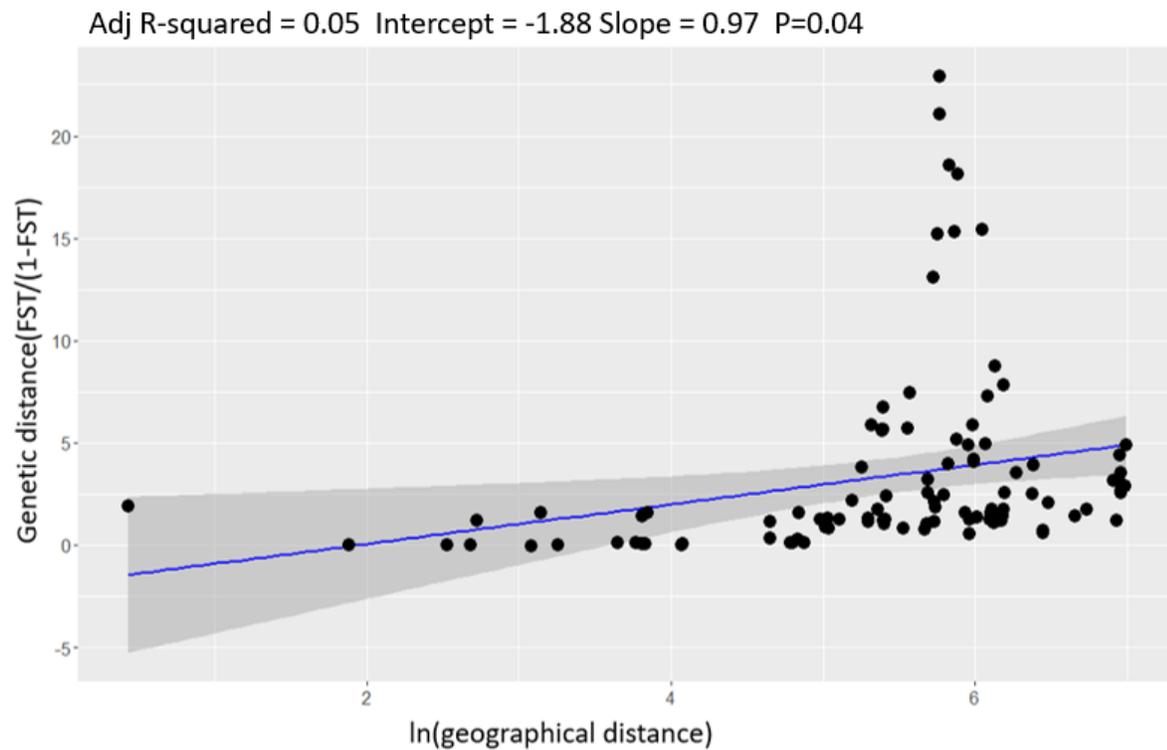


Figure 5.4: Multi-locus estimates of pairwise genetic distances ($F_{ST} / (1-F_{ST})$) between fish from 15 sampling locations plotted against natural logarithm (ln) of pairwise Euclidean geographical distance (km).

P was obtained based on Mantel test.

The fish from the 15 locations could be divided into three ancestral genetic groups (Figure 5.5), following the peak value $\Delta K \sim 100$ (Figure 5.5a) (Evanno *et al.*, 2005). However, a second small peak of ΔK (~ 18) was recorded at $K=9$, suggesting that nine ancestral groups would be an alternative split worth to be explored. With $K=3$, the STRUCTURE clustering diagram corresponded to differentiation among locations into three clusters as proposed previously in the distance-based and Principal coordinate analysis. However, individuals of SANP and SIK locations displayed a more complex genetic structure with shared membership of ancestral origins from clusters I and II. Also, ABIN defined as belonging to cluster III, shared memberships with clusters I and II. Considering $K=9$, the STRUCTURE clustering diagram showed that the locations of the previously defined cluster II were clearly differentiated from the other locations, with two admixed ancestral genetic groups (yellow and orange). The other locations were unique with dominance of one ancestral group in each location, except KRINA and KRINB which belong to the same ancestral group.

V.3.3 Detection of loci potentially under selection

The BAYESCAN analysis indicated five among the 21 loci with a q-value of less than 5%, suggesting that they are under selection (Figure 5.6). Of these five loci, Para027 with lowest F_{ST} and negative alpha (coefficient indicating the strength and direction of selection) was putatively under balancing selection, while the other four loci (with highest F_{ST} and positive alpha) were under putatively directional selection (see Appendix 7). However, the F_{ST} estimates showed high values for all loci (>0.4), also for those with $q>0.05$ (Figure 5.6).

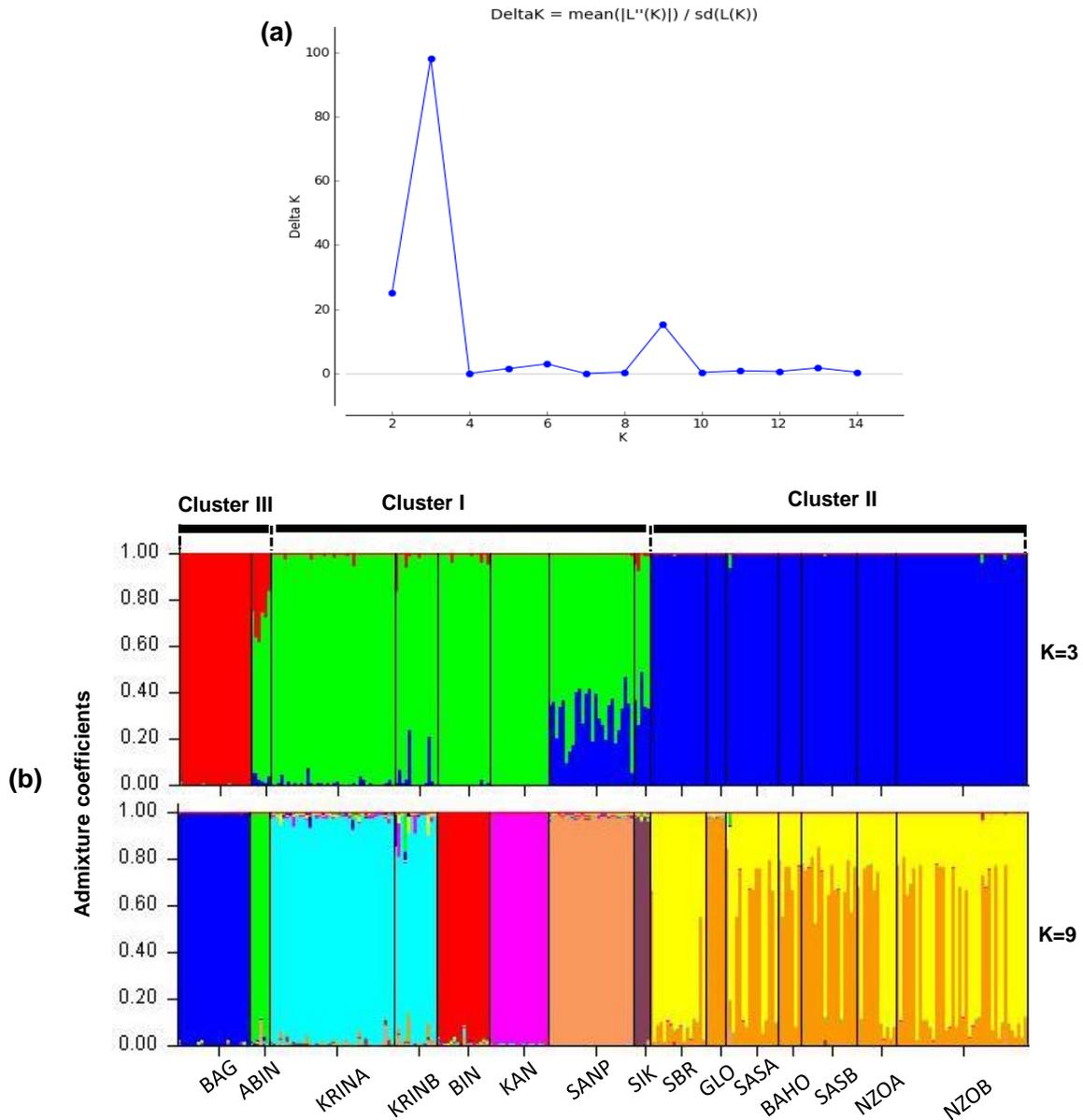


Figure 5. 5: Admixture analysis by STRUCTURE of *P. obscura* fish obtained from 15 sampling locations. (a) Line plot of successive ΔK from $K = 2-14$. (b) Bar plots of genetic clusters for $K = 3$ and $K = 9$ ancestral groups.

Each color corresponds to a unique ancestral group. Markov-chain Monte Carlo iterations were set at 100,000 after a burn-in period of 100,000.

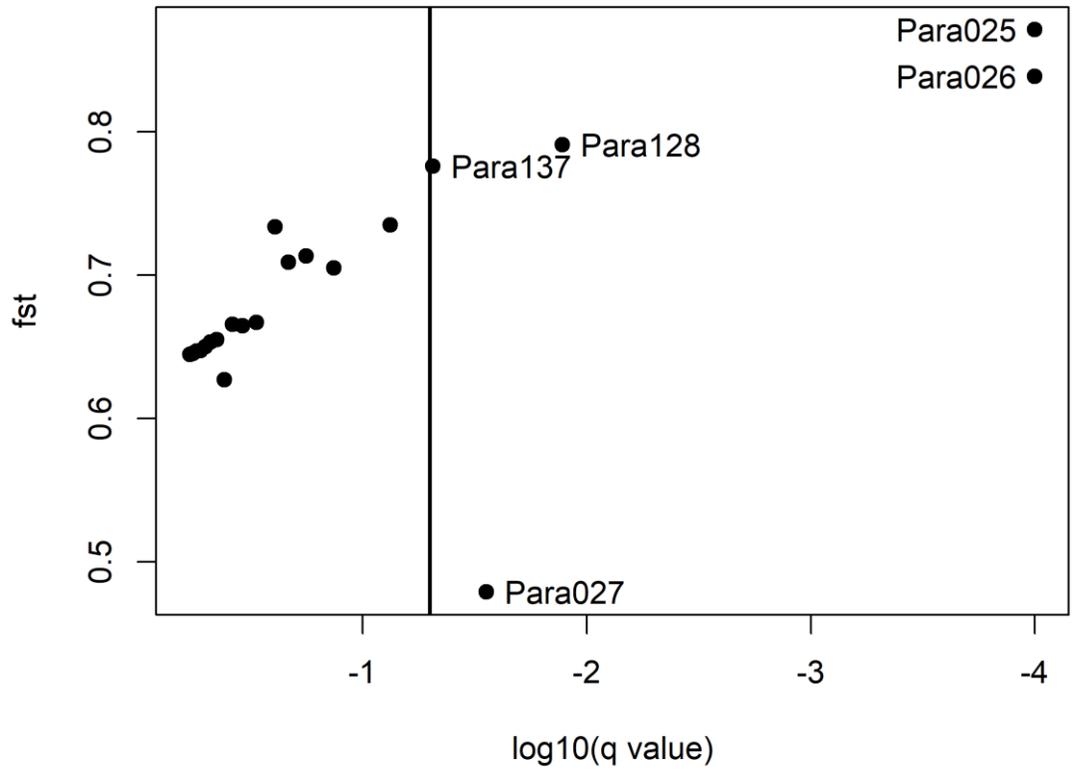


Figure 5. 6: Plot representing the BAYESCAN results for search of candidate loci under putative selection.

q-value: minimum false discovery rate (FDR) at which a locus may become significant; F_{ST} : coefficient to measure the difference in allele frequencies between the common gene pool and those of each population, calculated as posterior mean using model averaging. The vertical line represents the FDR threshold of 0.05. Points to the right of the vertical line represent loci under selection.

V.4 Discussion

We characterised the genetic structure and diversity of *P. obscura* fish from 14 locations in Côte d'Ivoire and one location in Benin, using the set of polymorphic microsatellite markers developed in the current study. Among the 120 produced and validated markers, a group of 21 polymorphic microsatellites were deemed suitable for the analysis of genetic differentiation among the sampling locations. However, some of these markers had a slightly increased frequency of null alleles. Microsatellite null alleles have been documented in studies of population genetics and PCR primer characterisation (Dakin and Avise, 2004), and have been discovered in a wide variety of taxa. Examples include insects (Meglecz *et al.*, 2004; Chapuis *et al.*, 2005), molluscs (Li *et al.*, 2003; Astanei *et al.*, 2005) and fishes (Jaisuk and Senanan, 2018; Robert *et al.*, 2019). It is generally not advised to include null allele loci in population genetics because they may affect estimates of population differentiation (Chapuis and Estoup, 2007). However, we did not exclude any locus from our study because it has been demonstrated that the influence of null alleles in studies of population genetics may be minimal compared to other parameters such as the number of loci (Carlsson, 2008). Moreover, for our data, the estimation of the population differentiation (F_{ST}) using only 19 microsatellites showed no difference in the value compared to the original data including null alleles. Jaisuk and Senanan (2018) also found no change in populations differentiation of *Garra cambodgiensis* after removing alleles with high null alleles frequencies.

The estimated within-population genetic diversity was low for all the 15 locations. In contrast to our result, high genetic diversity was obtained in other fish species occurring in Africa and other parts of the world using microsatellite loci. Angienda *et al.* (2011) reported a relatively high genetic diversity for *Oreochromis esculentus* ($H_O= 0.795- 0.81$, $H_S= 0.745- 0.77$, $\bar{A}_R = 7.13-8.13$) and *Oreochromis niloticus* ($H_O=0.70-0.78$, $H_S= 0.71-0.79$, $\bar{A}_R =7-8.38$) populations in eastern Africa. Mehner *et al.* (2021) found high genetic diversity in the European *Coregonus cisco* populations ($A_R =3.4-6.3$). Many studies on the genetic diversity of other species from the Channidae family such as *Channa striata* (Adamson *et al.*, 2012; Tan *et al.*, 2016; Robert *et al.*, 2019) and *Channa marulia* (Pathak *et al.*, 2018) showed relatively high genetic diversity. The low within-population genetic diversity observed in our study is likely a result of limited gene flow among populations. Also, the very low genetic diversity observed in SASA, SASB, NZOA,

NZOB, and GLO, all originating from the same basin (Sassandra river basin), may be due to the Wahlund effect, which occurs when genotypic proportions are computed from heterogeneous samples where individuals belonging to genetically differentiated entities (subpopulations) are pooled (De Meeûs, 2018), resulting in an excess of homozygotes. This assumption is supported by the STRUCTURE results ($K=9$) with the mix from two ancestral groups in these samples, as well as the positive F_{IS} obtained for these samples. Furthermore, confinements of populations in segregated catchments have probably facilitated local adaptation, thus further reducing genetic diversity. Microsatellite markers are normally neutral to selection. However, adaptive micro-evolutionary mechanisms may reduce genetic diversity both at selected loci under adaptation and in those parts of the genome that are hitchhiking with them (Via and West, 2008; Via, 2009). Genetic hitchhiking is a process that allele frequencies change without being under natural selection, because these genes are located on the same DNA chain near to another gene that is undergoing a selective sweep. The hitchhiking process may affect larger regions of the genome in particular in small populations (Charlesworth *et al.*, 1997). As a result, genetic diversity of populations may decrease fast in response to environmental changes, lowering the population's ability to respond to future selection pressures. We found high F_{ST} for all loci and five loci suggested to be under selection in the BAYESCAN analysis, indicating that micro-evolutionary mechanisms may have contributed to the reduction of the genetic diversity.

The estimation of the pairwise genetic differentiation (F_{ST}) showed highly significant differences among most of the locations of *P. obscura* except among locations from connected river networks. This result suggests that the fish from most of the different locations belong to distinct populations, except those collected from interconnected water networks, which may form one unique population together. In our study, SASA, SASB, NZOA, NZOB and BAHO are samples from interconnected rivers (Nzo River, Baho and Glo streams) and therefore had low values of pairwise genetic differentiation (F_{ST} close to zero). Nzo River, Baho and Glo streams are tributaries of Buyo lake, which is an artificial lake created by dam construction on Sassandra river. Thus, fish from these five locations can be considered as belonging to one population. KRINA and KRINB are both from Bia River, with samplings only a few km apart, and therefore likewise can be considered to belong to the same population.

Aquatic species, and freshwater fishes in particular, frequently display strong population structures probably as a result of their confinement to the network structure of aquatic systems in the landscape (Pérez-Espona *et al.*, 2008; Loxterman *et al.*, 2011). The pattern of genetic differentiation obtained in our study suggests an allopatric evolution of populations of *P. obscura*. The freshwater systems of the area where populations were collected are heterogeneous and complex, characterized by geographical barriers and lack of connectivity, which has favoured the isolation of populations and prevented gene flow. Isolation of fish populations based on height of watershed boundaries and relatively frequent occurrence of movement barriers within watersheds, have generally been demonstrated to generate significant genetic differentiation (Taylor *et al.*, 2003; Pfrender *et al.*, 2004; Gomez-Uchida *et al.*, 2009; Faulks *et al.*, 2010, Loxterman and Keeley, 2012). The results are in line with the hypothesis developed by Meffe and Vrijenhoek (1988) for explaining population genetic patterns for aquatic organisms inhabiting stream networks. Indeed, these authors predict that genetic isolation will occur among stream networks that do not have hydrological connections, resulting in an imbalance between drift and gene flow (where gene flow is effectively zero). A study on *Channa argus*, another Channidae species, revealed significant genetic differentiation among populations related to the structure of the river system (Yan *et al.*, 2018). Loxterman and Keeley (2012) also demonstrated that watershed boundaries have probably driven the genetic isolation obtained among Cutthroat trout (*Oncorhynchus clarkii*) populations from western North America.

The high values of the genetic differentiation obtained between locations from unconnected water networks (F_{ST} higher than 0.5 in most cases) and the high genetic variation obtained among locations (66.7%) from AMOVA in our study, suggest that the populations have been isolated for a long period of time, probably matching with the paleogeographic history of the formation of the hydrological systems on the African continent. Indeed, various paleogeographic (such as the disruption of fluvial drainages) and paleoclimatic (such as wet-dry cycles) events have had a significant impact on the African ichthyofauna from the Miocene to the Pleistocene by altering the connectivity between the various hydrographic systems (Lévêque, 1997; Drake *et al.*, 2011; Bezault *et al.*, 2011). A study of Bezault *et al.* (2011) demonstrated that paleo-geographic events have resulted in high genetic differentiation among *Oreochromis niloticus* populations across Africa. Using mitochondrial DNA based markers, Mwanja *et al.* (2013) found different lineages of *Lates* sp, which may have developed during geographical isolation during the Pleistocene and

have remained largely allopatric without gene flow since that time, on the African continent. The effect of paleo-historical lake level variations on genetic diversity of African cichlids has also been demonstrated (Egger *et al.*, 2007).

Although there was a significant and positive trend between genetic and geographical distances, some location pairs strongly deviated from the expected linear pattern. This pattern suggests that genetic diversity may additionally be shaped by insurmountable barriers resulting from landscape characteristics between the different sampling locations that prevent any exchange of genetic material among populations from non-connected water bodies. The population most strongly differentiated from all others was from Bagoue river (BAG), situated in the north Côte d'Ivoire, characterised by a tropical climate. As seen on the map, the watersheds of Bagoue River are completely disconnected from the watersheds of the other populations analysed, making geographical separation very likely. This separation is likely induced by the geography of the area, which is characterized by a mountain ridge south of Bagoue River that prevents the river flowing to the south, as most of the other rivers in the southern part. Similar observations were taken on salmonid fishes for which it has been suggested that landscape characteristics such as the complexity of the drainage network and differences in channel gradients between habitats are likely to limit dispersal between their populations (Angers *et al.*, 1999; Hebert *et al.*, 2000; Castric *et al.*, 2001; Guy *et al.*, 2008).

The classification of *P. obscura* populations into three clusters from both the neighbor-joining dendrogram and the principal coordinate analysis suggested that the genetic diversity of the populations may have probably been shaped by isolation due to geographical barriers and micro-evolutionary adaptive mechanisms, with climate-related environmental conditions as a potential driver. Indeed, the location of the populations in these clusters partly matched the climatic zones of Ivory coast and Benin republic. In the first cluster, five populations are combined, which originate from regions with a sub-equatorial climate. Only fish from the KAN location were collected in an area characterised by an equatorial transition climate. The second cluster was composed of samples from an equatorial transition climate, except the SBR. SBR is linked to other populations of this cluster by habitat connectivity which facilitate gene flow. The third cluster included two populations, with BAG located in the tropical climate regions and ABIN located in sub-equatorial climate regions. The population structure characterised by the ancestral

groups inferred by admixture coefficients in STRUCTURE has given the same classification (K=3) but showed that ABIN shared a higher admixture with those populations from the sub-equatorial climate areas, which form cluster I. Therefore, it is more likely that ABIN location also belongs to cluster I. The partly match between clusters and climate zones suggests that regional climate conditions may have contributed to the patterns of genetic diversity of *P. obscura* in West Africa. However, more appropriate types of markers (e.g., SNP data obtained through RAD-seq) should be applied in future for confirming this hypothesis of regional climate as driver of the pattern of genetic diversity in *P. obscura*. In contrast, the population structure at higher resolution with classification into nine ancestral groups (K=9) reflects the geographical configuration of the network of watersheds with populations from the same watersheds belonging to the same cluster. Hence, hydraulic connectivity or isolation has shaped gene flow among the habitats, facilitating differing evolution of the populations.

V.5 conclusion

Using the collection of polymorphic microsatellite markers developed in the present work, we characterized for the first time, the genetic diversity and structure of *P. obscura* populations from West Africa, representing an important baseline for further exploration of the population dynamics in this species. Understanding the genetic diversity of wild populations can help establishing aquaculture breeding programs as well as conservation initiatives to preserve fish stocks and their unique genetic identities. Low genetic diversity and high populations differentiation were observed.

The low genetic diversity of *P. obscura* demonstrated that particular attention has to be paid for conservation and sustainable management of this fish resource. Regarding the high genetic differentiation between populations attributable to habitat heterogeneity and local adaptation, *in situ* conservation will be required in order to maintain genetic integrity. These populations may serve as reservoirs or stocks for future selection programmes in aquaculture as well as improving population fitness and ability to respond to future environmental disturbance.

**GENERAL CONCLUSION,
RECOMMENDATIONS AND
PERSPECTIVES**

This thesis aimed to contribute to the development of appropriate strategies to ensure the conservation and sustainable management of fisheries resources, in general, and *Parachanna obscura* in particular, under changing climatic conditions and expanding human activities, for future use in aquaculture in West Africa. We first evaluated fishers' perceptions of climate change, human activities expansion, and their impact on freshwater fish biodiversity. The result revealed that majority of the interviewed fishers were well aware of climate change and its drivers. Fishers further listed climate change and many anthropogenic activities as impacting freshwater fish biodiversity in their fishing water with a consequence of a decline in fish quantity over the past years. We additionally investigate local indigenous knowledge of the goods and services of *P. obscura*, and local threats to populations of the fish in Côte d'Ivoire freshwater ecosystems. The results demonstrated that according to fishers, *P. obscura* is valuable fish species with socio-economic and nutritional importance and considerable market prices. However a substantial decrease in *P. obscura* abundance was observed by fishers, the decrease being attributed to climate change and anthropogenic pressures. This result showed the necessity for protecting and implementing good management policies for the sustainability of the fish resources in wild. All findings above confirm that local fishers are well grounded with very important socio-economic and ecological knowledge of their immediate environment useful for the scientist, confirming, therefore, our first hypothesis.

We also assess the morphological variation among populations of *P. obscura*, relying on the hypothesis that the heterogeneity and variability of the climate and freshwater systems of Côte d'Ivoire, have favoured high morphological variation, resulting from genetic variation caused by isolation, or phenotypic plasticity to local environmental conditions. The result showed a significant morphological variation in *P. obscura* populations according to climate and habitats heterogeneity. However, weak correspondence was obtained between fish shape and climate and habitat variables, and spatial isolation similarly did not contribute significantly to the differences in fish shape among populations. This finding demonstrates that our hypothesis was verified in part.

We finally characterize the genetic diversity, and population structure of *P. obscura*, with the hypothesis that there is strong genetic differentiation among *P. obscura* populations as a result of heterogeneity in climate and freshwater systems, as well as the history of African freshwater hydrology. The result demonstrated low and high within and inter-populations genetic diversity,

respectively, with the structuration of the gene pool according to the climate zones and habitat heterogeneity (connectivity of river networks).

The high level of awareness among fishers of climate change and anthropogenic threats to freshwater fish biodiversity is positive for the implementation of sustainable fisheries resource management policies and the mitigation of the effects of climate change and anthropogenic pressures on fisheries resources. Particular attention should be paid to fish species reported as locally threatened for the sustainable use and conservation of these fisheries resources. Actions are needed to be undertaken by governments for ensuring the strict application of policies and regulations in force in the fisheries sector, through the establishment of local management and monitoring committees. These actions should be inclusive of local fishers' communities to ensure effectiveness, efficiency and sustainability.

For *P. obscura*, the results of this study regarding economic importance, threats to its populations, morphological variation, genetic diversity and population structure provided a substantial basis for making decisions regarding its domestication, the management and conservation of its natural populations. The output of morphological study can help to select the individuals whose characteristics are targeted in the domestication process. The morphological variation observed can also contribute to the adaptation of fish populations to a variety of environmental disturbances. The different population groups obtained from the genetic diversity analysis can be used as reservoirs or stocks for future breeding programmes in aquaculture, as well as to improve the fitness of populations and their ability to respond to future environmental disturbances. The genetic diversity model has shown that *in situ* conservation will be the best conservation strategy as it will preserve the genetic integrity of populations already adapted to local environmental conditions.

In perspective, an assessment of the vulnerability and adaptation strategies of local communities to the decline of freshwater fish and climate change will be necessary. Concerning *P. obscura*, the current study should be extended to the whole of Africa to have a broad understanding of the evolutionary pattern and trajectory of fish populations and their ability to adapt to various environmental perturbations at the macro-geographic level. Likewise, the study of population dynamics, fish densities, competitors for food and resources, distribution, and characterisation of

quantitative trait loci carried by certain individuals that help them to resist to changes in environmental conditions such as temperature increase, pollution, etc. is necessary.

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APPENDICES

Appendix 1: Survey locations GPS coordinates

Country	Localities	Latitude	Longitude
Côte d'Ivoire	Krindjabo	5°23'59.44"N	3°12'41.61"W
Côte d'Ivoire	Alliekro	5°21'40.86"N	3°12'19.62"W
Côte d'Ivoire	Bianou	5°20'58.17"N	3°11'57.97"W
Côte d'Ivoire	Ayame	5°36'28.21"N	3° 9'40.85"W
Côte d'Ivoire	Dibobly	6°44'29.91"N	7° 1'13.06"W
Côte d'Ivoire	GUIGLO	6°32'27.85"N	7°29'26.75"W
Côte d'Ivoire	SAMOROSSO	9°34'24.39"N	6°30'16.34"W
Côte d'Ivoire	FAYE	4°59'34.98"N	6°38'28.44"W
Côte d'Ivoire	KOUBI	7° 7'43.39"N	5°10'52.58"W

Appendix 2: Survey questionnaire on “Fishers’ perceptions and experiences toward the impact of climate change and anthropogenic activities on freshwater fish biodiversity in Côte d’Ivoire” on “Fishers' knowledge of local names, habitats, uses, market prices, population dynamics and threats faced by the African snakehead fish, *Parachanna obscura*, in Côte d'Ivoire".

Questionnaire number:

Socio-demographic information

1. Locality
2. Watershed
3. Climate zone.....
4. Ethnic group
5. Gender 1) Male [...] 2) Female [...]
6. Age: 1) 20–29 [...]; 2) 30–39 [...]; 3) 40–49 [...]; 4) 50–59 [...]; 5) 60 and over [...]
7. Marital status: 1) Married [...]; 2) Single [...]; 3) Widowed [...]; 4) Divorced [...]; 5) No answer [...]
8. Household size 1) 1–5 [...]; 2) 6–10 [...]; 3) 11–15 [...]; 4) 16–20 [...]; 5) 21–25 [...]; 6) 26 and over[...]
9. Education level; 1) Illiterate [...] 2) Primary [...]; 3) Junior high school [...]; 4) Senior high school [...]; 5) University [...]
10. Main occupation
- 11 . Secondary occupation
12. Monthly income

SECTION ONE: Fishers’ perceptions and experiences toward the impact of climate change and anthropogenic activities on freshwater fish biodiversity in Côte d’Ivoire

Perception of climate change and its drivers

1. Are you aware of “climate change”? 1) yes [...]; 2) no [...]

2. What do you think is the major cause or driver of climate change? 1) greenhouse gas emissions [...]; 2) Land-use change [...]; 3) Deforestation; 4) Volcanoes; 5) Solar radiation [...]; 6) Other.....
3. Have you observed any change in the rainfall over the past years? 1) No change [...]; 2) Increase [...]; 3) Decrease [...]; 4) I don't know [...]
4. Have you observed any change in the timing of the rainy seasons over the past years? 1) No change [...]; 2) early arrival [...]; 3) late arrival [...]; 4) I don't know [...]
5. Have you observed any change in the length of the rainy seasons over the past years? 1) No change [...]; 2) lengthening [...]; 3) Shortening [...]; 4) I don't know [...]
6. Have you observed any change in the temperature over the past years? 1) No change [...]; 2) Increase [...]; 3) Decrease [...]; 4) I don't know [...]
7. Have you observed any change in flooding occurrence over the past years? 1) No change [...]; 2) Increase [...]; 3) Decrease [...]; 4) I don't know [...]

Perception of the impact of climate change and human activities on fish biodiversity.

1. Have you observed any decrease in fish abundance or quantity in your fishing watersheds over the past years? 1) No decrease [...]; 2) low decrease [...]; 3) moderate decrease [...]; 4) significant decrease [...]; I don't know [...]
2. How have temperature changes affected fish abundance or quantity? 1) No effect [...] 2) Increase [...]; 3) Decrease [...]; 4) I don't know [...]
3. How have rainfall changes affected fish abundance or quantity? 1) No effect [...] 2) Increase [...]; 3) Decrease [...]; 4) I don't know [...]
4. For you, what are the human actions or activities that affect/impact negatively fish biodiversity in your fishing watersheds?
.....
.....
.....
5. Have you noticed the scarcity or the depletion of populations or the disappearance of particular species of fish in your fishing watersheds? 1) Yes [...]; 2) No [...]
6. If yes, can you please provide the name(s) of this or these species?
.....

Any other comments?

.....
.....
.....
.....
.....

SECTION TWO: Fishers' knowledge of local names, habitats, uses, market prices, population dynamics and threats faced by the African snakehead fish, *Parachanna obscura*, in Côte d'Ivoire

1. How do you call *Parachanna obscura* in your ethnic?.....
2. In which habitat types do you catch this fish? 1) river [...]; 2) streams [...]; 3) ponds[...]; 4) wetlands [...]; 5) lakes; 6) floodplains, 7) other.....
3. Do you eat snakehead fish? 1) Yes [...]; 2) No [...].
4. Why do you eat this fish? 1) for its high nutritional quality [...]; 2) for cultural reasons [...]; 3) for its taste [...]; 4) other(list)
5. For which other purposes do you use this fish for? 1) traditional medicine [...] What disease(s) please.....; 3) traditional ritual [...] More information please.....4) Other (please specify)
6. How much the kilogram of snakehead fish is sold in your region? 1) less than 1000 FCFA (1.5€) [...]; 2)1000 to 2000 FCFA [1.5 to 3 €]; 3)2100 to 3000 FCFA [3.1 and 4.5 €]; 4) more than 3000 FCFA [more than 4.5 €].
6. Is this fish farmed in your region? 1) Yes [...]; 2) No [...].
7. Have you noticed a reduction in the populations of this fish in recent years? Yes [...]; 2) No [...]
8. If yes, what do you think could explain this decrease? 1) overexploitation (overfishing) [...]; 2) deforestation around watersheds [...]; 3) the increase in temperature in recent years [...]; 4) decrease in water level due to lack of rain [...]; Other(s) (please, specify)
9. Would you like this fish to be produced in aquaculture? Yes [...]; 2) No [...]
10. If yes,
why?.....

Any other comments?

.....

.....

.....

.....

.....

Appendix 3: GPS Coordinates of the locations of *Parachanna obscura* populations used the study

Country	Water body	Population abbreviation		Latitude	Longitude
		chapter IV	Chapter V		
Côte d'Ivoire	Bagoue river	BAG	BAG	9.578476	-6.51335
Côte d'Ivoire	Abengourou Lake		ABIN	6.706269	-3.50717
Côte d'Ivoire	Bia river		KRINB	5.360443	-3.20086
Côte d'Ivoire	Glo stream		GLO	6.759047	-7.13
Côte d'Ivoire	Baho stream		BAHO	6.747125	-7.12273
Côte d'Ivoire	Buyo Lake	SAS	SASA	6.769434	-6.99245
Côte d'Ivoire	Buyo Lake		SASB	6.554156	-7.08514
Côte d'Ivoire	Nzo river		NZOA	6.447769	-7.41535
Côte d'Ivoire	Nzo river	NZO	NZOB	6.543324	-7.47605
Côte d'Ivoire	Kan Lake	KAN	KAN	7.146202	-5.1801
Côte d'Ivoire	San-Pedro Lake	SANP	SANP	4.795008	-6.67068
Côte d'Ivoire	Sassandra river	SBR	SBR	5.742314	-6.59604
Côte d'Ivoire	Bia river	KRIN	KRINA	5.418801	-3.2127
Côte d'Ivoire	Wayadji stream		SIK	5.642733	-4.56151
Benin Republic	Nokoue lake		BIN	6.444704	2.406031

Appendix 4: Climate and habitat variables from the locations of the seven *P. obscura* populations sampled. Values are averages from measurements during the dry and wet seasons.

Population	T_Mean (°C)	RH (%)	Precipit (mm/day)	T_water (°C)	Depth (cm)	pH	Cond (µS/cm)	TDS (ppm)	ORP (mV)	Transp (cm)	Canopy (%)
BAG	26.2	65	3.4	28.4	171	6.9	41.7	27.2	281.4	42.5	50
KAN	26.7	75	3.5	30.8	222	7.2	118	68.5	271.2	65	48
KRIN	26.2	85	5	28.6	289	6.1	41.7	25	226.9	49.9	62
NZO	24.9	85	5.1	27.4	1273	7.1	67.5	45	276.3	36.8	37
SAS	25.2	82	4.8	28.9	1650	8.1	115	85	195	90	18
SBR	25.1	88	6	25.1	1607	7	96	67	197.2	98.5	23
SANP	25.6	87	6.5	26.2	142	7.6	1042	720.8	117.5	37.5	57
Origin	NASA	NASA	NASA	DM	DM	DM	DM	DM	DM	DM	DM

T_Mean= mean air temperature (°C), T_max= maximum air temperature (°C), T_min= minimum air temperature (°C), RH= relative humidity (%), precipit= mean precipitation (mm/day), T_water= water temperature (°C), Depth= Water depth (cm), Cond= electrical conductivity (µS/cm), TDS= total dissolved solids (ppm), ORP= redox potential (mV), Transp= transparency (cm), Canopy= canopy coverage of what vegetation (%). Data origin is either from NASA database or by direct measurements (DM).

Appendix 5: Proportion of missing genotypes among the 21 microsatellites (columns) in the 15 populations *Parachanna obscura* (rows). No individual with more than two missing genotypes were found, thus, all the 259 Individuals used for subsequent statistical analyses.

	Para137	Para136	Para025	Para042	Para039	Para038	Para128	Para107	Para134	Para023	Para018	Para110	Para059	Para027	Para036	Para049	Para026	Para041	Para104	Para037	Para040	Mean	
BAG	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ABIN	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.167	0.167	0.000	0.000	0.000	0.000	0.000	0.016
KRINB	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
GLO	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SASA	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
BAHO	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SASB	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
NZOA	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.083	0.000	0.000	0.000	0.004
NZOB	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.006
KAN	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SANP	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SBR	0.059	0.059	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.059	0.000	0.000	0.000	0.008
KRINA	0.026	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.026	0.000	0.000	0.000	0.003
SIK	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.200	0.000	0.000	0.000	0.010
BIN	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003
Total	0.008	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.004	0.000	0.004	0.004	0.019	0.000	0.000	0.000	0.003	

Appendix 6: Matrix of pairwise F_{ST} between the 15 *P. obscura* populations obtained using only the 19 microsatellite loci with low null allele frequencies.

	ABIN	BAG	BAHO	BIN	GLO	KAN	KRIN	KRINB	NZOA	NZOB	SANP	SASA	SASB	SBR
BAG	0.90													
BAHO	0.83	0.95												
BIN	0.70	0.83	0.74											
GLO	0.82	0.96	0.66	0.75										
KAN	0.80	0.92	0.85	0.63	0.85									
KRIN	0.57	0.71	0.53	0.39	0.53	0.41								
KRINB	0.58	0.79	0.56	0.43	0.55	0.50	0.01							
NZOA	0.84	0.94	0.04	0.76	0.61	0.85	0.55	0.59						
NZOB	0.89	0.93	0.07	0.84	0.59	0.88	0.64	0.72	-0.03					
SANP	0.60	0.76	0.52	0.54	0.57	0.54	0.32	0.33	0.54	0.65				
SASA	0.84	0.93	-0.02	0.78	0.55	0.85	0.56	0.62	0.01	0.05	0.55			
SASB	0.86	0.94	-0.07	0.79	0.61	0.87	0.58	0.64	0.07	0.11	0.58	0.00		
SBR	0.85	0.93	0.22	0.77	0.61	0.85	0.56	0.62	0.08	0.09	0.54	0.11	0.25	
SIK	0.58	0.89	0.69	0.61	0.66	0.68	0.47	0.46	0.71	0.80	0.46	0.72	0.77	0.70

Appendix 7: Output of BAYESCAN analysis for identifying candidate loci under selection. q-value: q-value for the model including selection. alpha: coefficient indicating the strength and direction of selection; A positive value of alpha suggests directional selection, whereas negative values suggest balancing or purifying selection. F_{ST} : the F_{ST} coefficient averaged over populations. Significant q-value (lesser than 0.05) are bolded.

Locus	q-value	alpha	F_{ST}
Para137	0.048	0.88	0.78
Para136	0.38	0.13	0.67
Para025	0.00	1.72	0.87
Para042	0.25	0.64	0.73
Para039	0.45	0.06	0.65
Para038	0.50	0.03	0.65
Para128	0.01	0.99	0.79
Para107	0.55	0.01	0.65
Para134	0.57	0.00	0.65
Para023	0.30	0.14	0.67
Para018	0.13	0.37	0.71
Para110	0.08	0.57	0.74
Para059	0.21	0.41	0.71
Para027	0.03	-0.88	0.48
Para036	0.53	0.01	0.65
Para049	0.47	0.05	0.65
Para026	0.00	1.38	0.84
Para041	0.18	0.44	0.71
Para104	0.41	-0.10	0.63
Para037	0.34	0.12	0.66
Para040	0.59	0.00	0.64

PUBLICATIONS

Research

Fishermen's perceptions and experiences toward the impact of climate change and anthropogenic activities on freshwater fish biodiversity in Côte d'Ivoire

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Abstract

Africa's freshwater ecosystems are impacted by many threats due to climate change and several anthropogenic activities. In Côte d'Ivoire, the economy relies mostly on agriculture, which covers around 64% of the land surface. The study aimed to investigate Côte d'Ivoire fishermen's perception of climate change, its drivers and other anthropogenic activities impacting freshwater fish biodiversity. The fish species locally threatened in the Ivorian freshwater ecosystems were also investigated. Face to face interviews and a structured questionnaire were used. The data obtained were analysed using descriptive statistics such as frequency, percentage, means, and standard deviation, minimum and maximum. The multinomial logit regression was also applied to test factors that influence fishermen's awareness and perception of climate change and their perception of change in fish abundance. The results show that around 72.7% of fishermen were aware of climate change. Decreases of precipitation (87.9%) and increases of temperature (76.1%) were observed by fishermen. Also, a significant decrease in fish quantity was observed by respondents. Climate change and anthropogenic activities such as gold mining, water withdrawal, use of small-mesh fishing nets, overfishing, industrial waste pollution, pesticides use for agricultural purposes along watersheds, obnoxious fishing practices and population growth, were highlighted as the main reasons for this decline. Species such as *Lates niloticus*, *Heterotis niloticus*, *Parachanna obscura*, *Malapterurus electricus*, *Sarotherodon galilaeus*, *Tilapia zillii*, *Polpyterus endlicheri* and *Labeo coubie* were listed by fishermen as locally threatened within Ivorian freshwater ecosystems. Actions and policies are needed to be taken by local authorities to ensure the sustainability of fisheries resources. The information obtained from this study constitutes a prerequisite for developing and implementing studies or policies aimed at mitigating and combating the negative effect of climate change and anthropogenic activities on the Ivorian freshwater ecosystem.

Keywords Anthropogenic activities · Climate change · Freshwater fish biodiversity · Fishermen · Côte d'Ivoire

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1 Introduction

The United Nations Framework Convention on Climate Change (UNFCCC) defined climate change as “a change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable periods” [1]. Most aquatic organisms are very sensitive to any variation in their environment. Combined effects of climatic factors, overfishing, increased human population growth, water pollution and alien invasive species, are amongst the stressors that contribute to the degradation of natural water resources, consequently threatening aquatic systems [2]. Recently, it was noted that aquatic biodiversity is threatened and subject to severe declines in many countries [2]. Among aquatic ecosystems, freshwater ecosystems are most sensitive to environmental disturbances [3]. Freshwater organisms have the highest proportion of known species globally categorized as extinct or threatened in the International Union for Conservation of Nature (IUCN) Red List [4, 5]. A report of the United Nations Educational, Scientific and Cultural Organization (UNESCO) indicated a faster decline of freshwater biodiversity than of terrestrial and marine biodiversity over the last three decades [6]. The decline is expected to accelerate even further with warmer temperatures, reduced precipitation and increased water withdrawal for agriculture and other human use [7, 8].

Africa harbours a diversified fish fauna resulting from a long history of complex climatic and geological events that resulted in geographic isolation followed by speciation for some populations, or extinction for others [9]. African ichthyofauna shows numerous exceptional features compared to other continents. However, Africa’s ichthyofauna shares affinities with those of both South America and Asia [9]. Thus, Africa’s freshwater fish biodiversity is reported to comprise more than 3000 species, more or close to that of Asia (more than 3600 species known) and South America (more than 4200 species known) [10]. Climate change and other anthropogenic perturbations such as dam construction, water extraction and overexploitation are some of the stressors impacting Africa’s freshwater biodiversity [9, 11]. Also, habitat modification, caused by various land uses and associated sedimentation is reported as one of the most widespread threats to freshwater fishes in Africa [12]. Sediments cover submerged surfaces, increase turbidity, and reduce suitable habitats for breeding and feeding of many fish populations [9]. Water pollution represents a problem for freshwater fish in several parts of Africa. Pesticides and fertilizers’ impact on African’s freshwater ecosystems have been well-documented [13, 14, 11].

In Côte d’Ivoire, the economy relies mostly on agriculture, which covers around 64% of the land surface [15]. From 1960 to 2018, the country’s rate of urbanization soared from 17.7% to over 50% [16]. The high rate of urbanisation, combined with agriculture expansion, are susceptible to impact aquatic ecosystems, especially those of the freshwaters, in this country. Pollution of aquatic ecosystems from the discharge of untreated domestic, industrial, and agricultural wastes have been reported in the country [17–19]. Regarding the climate of this country, from the 1980s to 2000s temperature increased on average by 0.5 °C, and from 2001 to 2010 a temperature rise of 0.8 °C was recorded [20]. The decades 1950s and 1960s were recorded to be comparatively wetter than those from 1970 to 1990s which were drier. Moreover, according to the prediction of The Intergovernmental Panel on Climate Change in 2014 under RCP4.5 scenario, temperature will rise of 3 °C by 2100, over most of the country from north to south, and the daily precipitation will drop by 8% relative to its current amount during the season from April to July over the next hundred years [20]. Thus, climate change and human activities may constitute a real threat to freshwater fish biodiversity in this country. Consequently, there is an urgency to provide a scientific assessment of the impact of climate change and human activities on Côte d’Ivoire freshwater biodiversity, which will guide management strategies.

Over time, Indigenous peoples throughout the world have preserved distinctive understandings, rooted in cultural experience, that guide relationships among human and non-human beings in specific ecosystems. These understandings and relationships constitute a system broadly identified as indigenous knowledge [21]. Indigenous knowledge is part of the heritage of humankind. It is the library of knowledge that people have of the environments where they live [22]. Fishermen are people depending directly on the services provided by the aquatic ecosystem for their livelihoods. Therefore, they are most affected by any environmental disturbance in this ecosystem, and also the key group well aware of the nature of the disturbance. Their perception of climate change (the existence, the impact, and causes) and knowledge of anthropogenic activities impacting freshwater fish biodiversity, being part of their indigenous knowledge, are essential for making and implementing decisions and policies related to the mitigation of these threats, and the management of freshwater fish biodiversity. Furthermore, fishermen’s knowledge and perception represent the baseline information for motivating and directing any research projects regarding this issue.

In this view, this study aimed to investigate Ivorian fishermen's knowledge and perception towards climate change, its drivers, and human activities impacts on freshwater fish biodiversity and the species locally vulnerable.

2 Materials and methods

2.1 Study area

The study was carried out in Cote d'Ivoire, West Africa. The country is divided by latitude into three principal climatic zones, with a fourth zone being the particular climate of the mountain zone. Our study was carried out in three climatic zones within Cote d'Ivoire: Guinean in the south, Sudano-Guinean in the middle and Sudanian in the northern (Fig. 1). Guinean zone, also known as Attiean zone, is characterized by a sub-equatorial climate with two rainy seasons and two dry seasons. Its annual precipitation is estimated to be more than 1500 mm [20]. Fishermen of Bia River, Ayame lake and Faye Lake within Krindjabo, Bianou, Alliekro and Ayame localities were randomly selected in this climate zone. The Sudano-guinean or Baoulean zone is characterized by an equatorial transition climate between the Guinean and the sudanian climates. This climate zone also has two rainy seasons and two dry seasons, with the annual precipitation comprising between 1200 and 1500 mm per year. Within this climate zone, fishermen of Kan lake, Buyo lake and Nzo river, from Koubi, Dibobly and Guiglo localities were selected for the study. Within the Sudanian zone, the fishermen of Bagoue river from Samorosso village were selected. The Sudanian zone is characterized by one rainy season and one dry season. The annual precipitation varies between 900 and 1200 mm.

2.2 Sampling of fishermen

The study was conducted as part of a project titled "Predicting the impact of climate change and anthropogenic activities on the distribution and genetic diversity of *Parachanna* species in Côte d'Ivoire" funded by the West African service centre of Climate Change and Adapted Land-use scholarship programme, for three years and half (started in September 2019). Thus, a preliminary investigation was done in the three selected climatic zones with 90 fishermen, to identify the proportion of them fishing or trading on *Parachanna* fish species among their global target species. The fishermen selected were those who were familiar with *Parachanna* species and who had already been involved in fishing or trading on *Parachanna* species. These fishermen were also involved in fishing or trading other common fish species found at the sampling sites. The survey was conducted among fishermen in different types of freshwater ecosystems, including

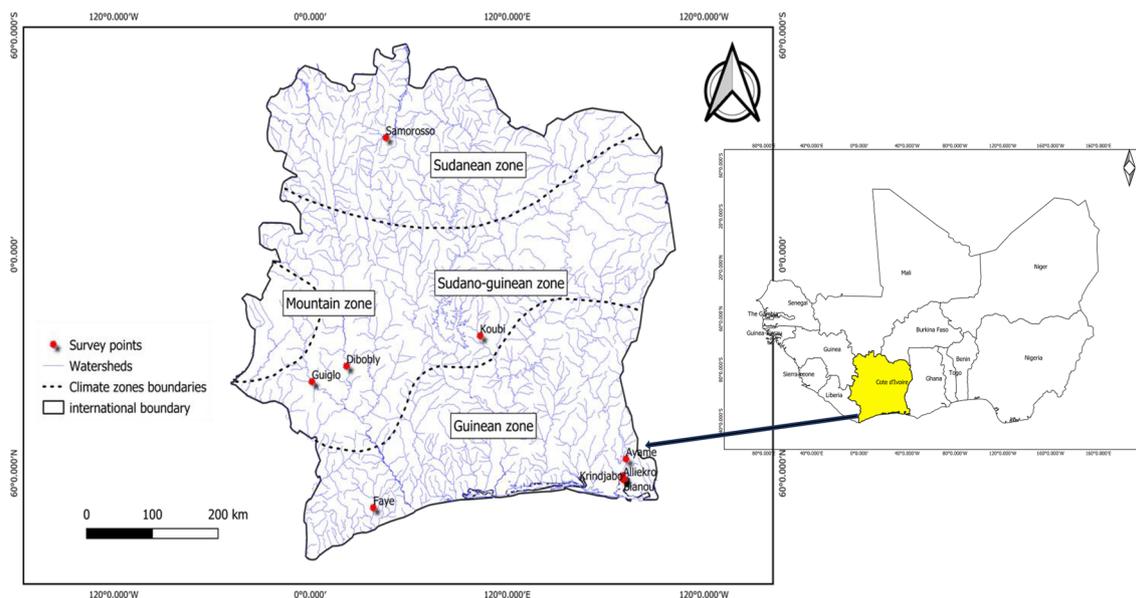


Fig. 1 The study area map, showing the borders of Côte d'Ivoire, its position in West Africa, the main climate zones and the locations where surveys were conducted

lakes, rivers and streams. The investigation resulted in the proportion of 60% of fishermen fishing on *Parachanna* among the global interviewed fishermen. This proportion was used in [23] formula with a 95% confidence level to calculate the necessary sample size:

$$N = \frac{U_{1-\alpha/2}^2 p(1-p)}{d^2}$$

N = the total number of fishermen to be surveyed; $U_{1-\alpha/2}^2$ represents the value of the normal random variable for a probability value of $1-\alpha/2=0.975$; $U_{1-\alpha/2}^2 = 1.96$; p represents the estimated proportion of fishermen fishing on *Parachanna* fish species among their target species, obtained from the preliminary investigation ($p=0.60$); d is the margin of error of a parameter estimated from the sample fixed at 0.05. From the formula, the sample size of 369 fishermen was the minimum needed, but to be more accurate, 381 fishermen were interviewed in this study.

2.3 Data collection

Face to face interviews were conducted using a structured questionnaire from October 2020 to February 2021. Fishermen were randomly selected on each sampling site. Fish landing sites within each sampling site were used as collection sites. The questionnaire was divided into three sections (Appendix 1). The first section was structured to assess the respondent's general demographic background (e.g., age, sex, household size, education level, occupation, monthly income, etc.) and the second section was on the fishermen's knowledge of climate change (e.g., awareness, causes and drivers, perceived change in variables, etc.). The last section was linked to respondents' perception of the impact of climate change and human activities on freshwater fish biodiversity (e.g., change in fish quantity, how climate change drew change in fish biodiversity, major human activities threatening freshwater fish biodiversity, locally threatened fish species).

2.4 Data analysis

Descriptive statistics (frequency, percentage, means and standard deviation, minimum and maximum) were calculated to analyse fishermen's demographic information, their perception related to climate change and its impact on freshwater fish biodiversity and their perception of human impact on fish biodiversity. The multinomial logit regression model (MLN) was applied to analyse factors that influence fishermen's awareness of climate change, their perception of climate change, and their perception of change in fish abundance. This model has been widely used in many studies to test factors that influence individual knowledge of climate change, climate adaptation and climate change risk perception [24, 25]. The multinomial logit regression is used to predict the probability of category membership of a dependent variable based on several independent (predictor) variables. The MLN model is a simple extension of the binary logit regression that allows for more than two categories of the dependent or independent variables. In this model, the independent variables can either be nominal or ordinal [26]. MLN uses maximum likelihood estimation to evaluate the probability of categorical membership in a dependent variable based on multiple predictor variables. In this study, we considered socio-demographic variables (e.g., age, gender, education level, household size, ethnic group) of fishermen as the predictors and perception variables (e.g., awareness of climate change, perceived change in climate or fish quantity) as dependent variables. The MLN results reflect the expected change in the probability that fishermen perceive climate change or fish quantity change or be aware of climate change with respect to a one-unit change in a predictor variable, keeping all the other predictors constant. Alpha (α) lesser than 0.05 was considered statistically significant. SPSS version 2.2 software was used for the descriptive statistics, while the multinomial logit regression was implemented in R 3.6.3 software.

3 Result

3.1 Socio-demographic background of respondents

A total of 381 questionnaires were successfully completed. 81.9% of respondents were males and 18.1% were females. Most (63%) of the respondents were between 30 to 49 years old, followed by those belonging to the ages ranging from 50 to 59 (17.8%), and 20 to 29 (13.6%). Only 5.5% of the respondents were 60 years and above. Among interviewed people, 84.5% were married, 15.2% single and 0.3% divorced. The household sizes of respondents were

principally between 1 to 10 persons (85.5%), followed by 11 to 15 persons (12.1%), 16 to 20 persons (1.0%), then 26 persons and above (1.3%). The largest proportion of the respondents (43.3%) were illiterates (no formal education). Then, 28.6%, 23.1% and 3.4% had primary, high school and university education, respectively (Table 1).

3.2 Livelihood strategies of the fishermen

Whereas 80% of the respondents were engaged in fishing as their main occupation, 14.2% were only engaged in fish trade. The remaining percentage was shared among farming, teaching and shopkeeping. Regarding the secondary occupation, respondents were mostly involved in farming (59.1%), followed by fishing (3.9%), fish trading (2.6%), live-stock farming (1.6%), and others (11.8%). Around 21% of respondents were not engaged in any secondary activities.

Concerning fishermen's monthly incomes, the arithmetic mean monthly income was about 130 EUR, with a minimum of 15 EUR and a maximum of 763 EUR. However, it varied among the climate zones. Thus, Guinean climate zone fishermen had the highest mean monthly incomes of about 145 EUR. Comparatively, Sudano-Guinean climate zone fishermen recorded the middle monthly mean income (126 EUR), more than those of Sudanian climate zone with the lowest one (93 EURO). The complete results of the interviewees' livelihood are presented in Tables 2 and 3.

Table 1 Overview of the socio-demographic background of 381 respondents to a questionnaire on the perception of climate change and changes in fish biodiversity and their potential drivers in Côte d'Ivoire

Respondents	Frequency	Percentage	Respondents	Frequency	Percentage
Gender			Ethnic group		
Female	69	18.1	Abron	1	0.3
Male	312	81.9	Agni	75	19.7
Total	381	100.0	Apollo	4	1.0
Age			Bambara (Mali)	17	4.5
[20–29]	52	13.6	Baoulé	65	17.1
[30–39]	119	31.2	Bozo (Mali)	63	16.5
[40–49]	121	31.8	Dioula	8	2.1
[50–59]	68	17.8	Guéré	57	15.0
≥ 60	21	5.5	Keke (mali)	3	0.8
Total	381	100.0	Koroboro (Mali)	7	1.8
Marital status			Samogo	57	15.0
Married	322	84.5	Senoufo	14	3.7
Single	58	15.2	Songhaï (Mali)	9	2.4
Divorce	1	0.3	Tagbana	1	0.3
Total	381	100.0	Total	381	100.0
Household size			Watershed		
[1–5]	154	40.4	Bia river	58	15.2
[6–10]	172	45.1	Lake Ayame	58	15.2
[11–15]	46	12.1	Lake Buyo	48	12.6
[16–20]	4	1.0	Lake faye	55	14.4
≥ 26	5	1.3	Lake Kan	64	16.8
Total	381	100.0	River Bagoue	54	14.2
Education level			River Nzo	44	11.5
No formal education	165	43.3	Total	381	100.0
Primary	109	28.6	Climate zone		
Junior high school	63	16.5	Guinean climate	171	44.9
Senior high school	25	6.6	Sudano-guinean climate	156	40.9
University	13	3.4	Sudanian climate	54	14.2
Koranic school	6	1.6	Total	381	100.0
Total	381	100.0			

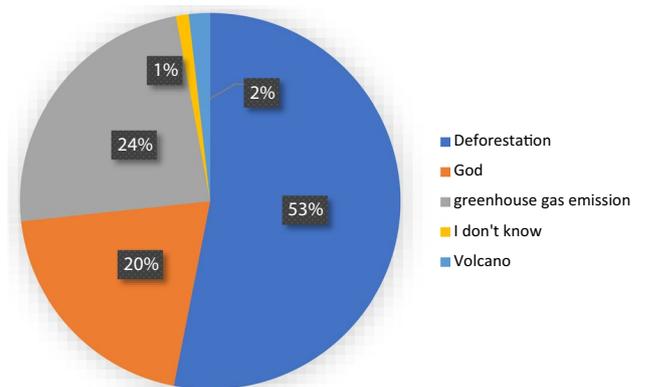
Table 2 Livelihood strategies of 381 respondents to a questionnaire on the perception of climate change and change in fish biodiversity and their potential drivers in Côte d'Ivoire

Respondents	Percentage	Respondents	Percentage
Main occupation		Secondary occupation	
Fishing	80	Fishing	3.9
Fish Trading	14.2	Farming	59.1
Farming	3.4	Fish Trading	2.6
Teaching	0.3	Livestock farming	1.6
Shopkeeping	2.1	None	21
Total	100.0	Other	11.8
		Total	100

Table 3 Monthly income of 381 respondents to a questionnaire on the perception of climate changes and changes in fish biodiversity and their potential drivers, from three Ivorian climatic zones

Climate zone	Mean	Standard Deviation	Minimum	Maximum	% of Total N
Monthly income (EUR)					
Guinean climate	145	7.34	15	610	44.9%
Sudano-guinean climate	126	8.24	17	763	40.9%
Soudanean climate	93	7.63	15	183	14.2%
Total	130	4.91	15	763	100.0%

Fig. 2 Circular diagram summarizing in percentage the perception of 381 Ivorian's fishermen of causes and drivers of climate change



3.3 Fishermen's perception of climate change, its drivers, its impact on Ivorian freshwater fish abundance

About 72.7% of fishermen were aware of climate change, whereas 27.3% were not. Of the total percentage of the respondents who were aware of climate change, 53% and 24% believed that the drivers of climate change are deforestation and greenhouse gas emissions, respectively, whereas 20% of the respondents attribute the cause of climate change to the will of God, and 2% believe that natural processes such as volcanic eruptions are the main cause of climate change (Fig. 2). A decrease in precipitation (87.9%) and an increase in temperature (76.1%) were observed by respondents. Additionally, interviewees testified to have observed delay in the onset of the rainy season and its length shortening (Fig. 3). Concerning the occurrence of floods, 55.6, 3.7, and 40.7% of the respondents observed an increase, decrease and no change respectively (Table 4).

Most of the fishermen reported significant decreases in fish abundance (81.6%), while 10.0, 3.4, and 5% observed little, moderate and no decrease, respectively. Concerning the impact of climate change on fish abundance, the respondents stated that change in temperature has mainly led to a decrease in fish abundance (65.9%), while 3.4% of the respondents argued that change in temperature has led to an increase in fish abundance, 22.8% observed no effect and 7.9% did not know. As far as the effect of change in precipitation on the fish abundance is concerned, 71.1% of the respondents specified that it has led to a decrease, 8.1% to an increase, and 5% did not know. For the remaining 15.7%, change in precipitation has not affected fish abundance.

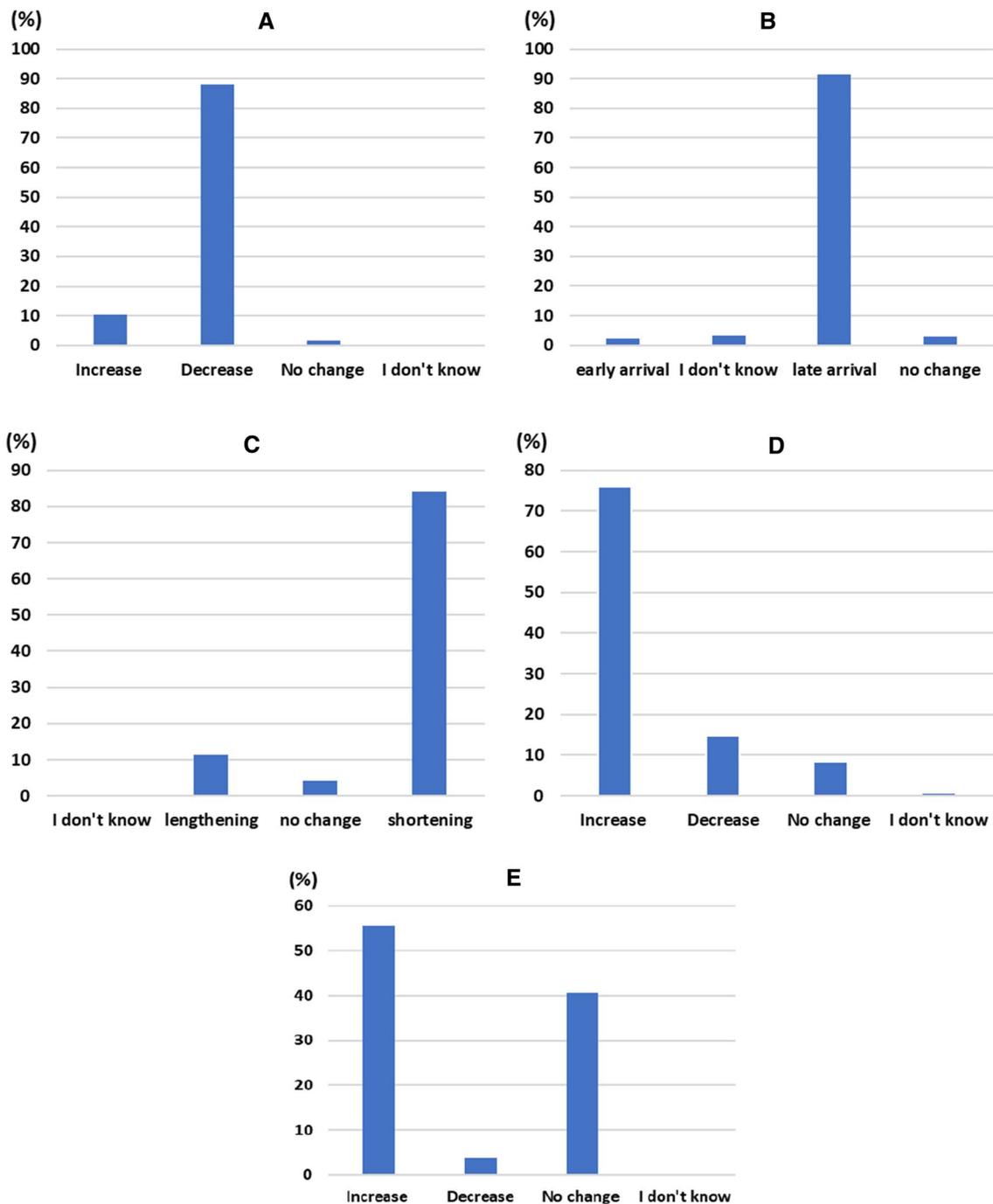


Fig. 3 381 Fishermen's responses concerning their perception of **A** change in rainfall, **B** change in rainy season timing and **C** length, **D** change of temperature, and **E** change in flooding occurrence in Côte d'Ivoire. **y** axis is the respondent percentage, **x** axis represents the categories of responses in the considered change climate attribute

3.4 Fishermen's perception of the Anthropogenic stressors on freshwater fish

Table 4 shows the perception of interviewees on the impact of human activities on the Ivorian freshwater fish. Gold mining, water withdrawal for human needs, use of small-mesh fishing nets, overfishing, industrial waste discharge, pesticides use for agricultural purposes along watersheds, obnoxious fishing practices and increase in human

Table 4 Anthropogenic activities threatening Ivorian freshwater fish biodiversity according to fishermen of the watersheds sampled

Watershed	Stressor	Percentage (%)
Bia river (N= 58)	Obnoxious fishing practices	44.8
	Gold mining	22.4
	Overfishing	31.0
	Use of small-mesh fishing nets	1.7
	Total	100
Lake Ayame (N= 58)	Gold mining	44.8
	Overfishing	41.4
	water withdrawal for human needs	6.9
	Obnoxious fishing practices	6.9
	Total	100
Lake Faye (N= 55)	Use of small-mesh fishing nets	16.4
	Water withdrawal for human needs	14.6
	Industrial waste discharge	12.7
	Overfishing	10.9
	Hydrological dams	1.8
	None	43.6
Lake Buyo (N= 48)	Total	100
	Pesticides use for agricultural purposes along watersheds	66.7
	Overfishing	10.4
	Water withdrawal for human needs	4.2
	Obnoxious fishing practices	4.2
Nzo river (N= 44)	I don't know	14.6
	Total	100
	Pesticides use for agricultural purposes along watersheds	97.7
	I don't know	2.3
Lake Kan (N= 64)	Total	100
	Overfishing	40.6
	Pesticides use for agricultural purposes along watersheds	18.8
	None	40.6
River Bagoue (N= 54)	Total	100
	Overfishing	42.6
	Obnoxious fishing practices	20.4
	Increase in population growth	3.7
	None	20.4
	I don't know	12.9
Total	100	

population, were identified by Ivorian fishermen as the major anthropogenic perturbations affecting Côte d'Ivoire freshwater fish biodiversity. Specifically, fishermen of Bia River argued that the river is mainly impacted by obnoxious fishing practices (44.8%), overfishing (31.0%) and gold mining (22.4%). The use of small-mesh fishing nets (1.7%) was also identified as a stressor for the fish biodiversity of this river. Fishermen in the artificial lake Ayame, resulting from the construction of the hydroelectric dam on Bia River, identified in decreased order, gold mining (44.8%), overfishing (41.4%), water withdrawal and obnoxious fishing practices as stressors of the fish biodiversity in this lake. Use of small-mesh fishing nets, water withdrawal and industrial waste discharge were recognised as factors threatening fish diversity of lake Faye. Pesticides used for agricultural purposes along watersheds were implicated as the main human activity that threatens Buyo lake and Nzo River fish communities. Regarding Kan Lake located within the Sudano-Guinean climate zone and Bagoue river located in the Sudanian climate zone, overfishing was perceived to be the principal factor of fish biodiversity decline.

3.5 Fish species locally under threats according to the fishermen

This section summarizes the fish species within Ivorian freshwaters for which fishermen perceived drastic population declines, such that they are considered to be very scarce over the past years. *Tilapia zillii* and *Malapterurus electricus* were the principal fish species listed by Bia River fishermen, while those of Ayame lake mainly identified *Heterotis niloticus* and *Parachanna obscura*. *Labeo cubii*, *Parachanna obscura* and *Tilapia zillii* species were mostly reported threatened within buyo Lake. Meanwhile, *Heterotis niloticus* was the only species reported threatened by Faye Lake fishermen. About 89.1% of the interviewees from the area surrounding Kan Lake identified *Tilapia zillii* as under threat in this lake. About River Bagoue and lake Nzo, no species was identified by the fishermen as being threatened in these water bodies (Table 5).

3.6 Factors influencing fishermen's awareness of climate change and perception of change climate

Tables 6 and 7 present the results of the multinomial logit regression models concerning the variables that influence respondents' awareness and perception of climate change.

Variables such as climatic zone, household size and education level were significantly associated with respondents' awareness of climate change. Positive relationships between respondents' education level and awareness of climate change were found, meaning that respondents' awareness increased with high education level. The same positive relationship was found with respondents' household size, which increased fishermen's awareness of climate change. However, a negative relationship was obtained between fishermen's awareness of climate change and the climate zone. Thus, respondent awareness of climate change decreased when going from the Guinean forest zone to the Sudanean savanna zone.

Concerning fishermen's perception of climate change, age, household size, gender, and education level were strongly influencing fishermen's perception of change in rainfall. A decrease in rainfall was mainly observed by young adults, males, and low education level fishermen. Perceived change in temperature was significantly influenced by fishermen's fishing watersheds and ethnic groups. Perception of temperature decreases decreased when going from Bia River, Lake Ayame, Lake Buyo, Lake Faye, Lake Kan, Bagoue River to Nzo River fishermen. Perceived change in flooding was significantly determined by watersheds, ethnic group, main occupation and household size.

3.7 Factors determining fishermen's perception of change in fish quantity

Change in fish abundance was significantly associated with respondents' age, education level, ethnic group and climate zone. Perceived decrease in fish abundance (low, moderate, and significant) increases with an increase in respondents' ages. Positive relationships between fishermen's education level and their perception of significant decrease in fish abundance were observed (Table 8). Fishermen's perception of significant decrease in fish abundance increased when going from the Guinean climate zone to the Sudanean zone.

4 Discussion

Climate change has become the focus of scientists, politicians, policymakers and the general public since the last decade. The representatives of indigenous peoples have been pushing to engage with climate change agreements since the adoption of the Kyoto Protocol in 1997 [27]. This study, which aims to capture Ivorian local fishermen's perceptions and personal experience of climate change, represents an important contribution to the global effort of combating and reducing climate change. Fishermen are directly dependent on the aquatic ecosystems for their livelihoods. Thus, understanding their perception and knowledge of climate change is an essential step towards developing and implementing adaptation and mitigation strategies to deal with the effects of climate change on aquatic ecosystems.

The high proportion of awareness of climate change obtained is consistent with a study by [28] who argued that the majority of Africa's citizens are aware of change in climate patterns. Many other studies conducted in several parts of Africa found similar results with households [29], farmers [24] and fishers [30, 31]. Since the twentieth century, increases in temperature and decreases in precipitation have been experienced in Cote d'Ivoire [20, 32]. In our study, fishermen mainly observed an increase in temperature, a decrease in precipitation and an increase in flood occurrence. Ivorian

Table 5 Fish species locally threatened according to fishermen of the sampled watersheds

Watershed	<i>Heterotis niloticus</i>	<i>Tilapia zillii</i>	<i>Malapterurus electricus</i>	<i>Lates niloticus</i>	<i>Parachanna obscura</i>	<i>Sarotherodon galilaeus</i>	<i>Labeo cubii</i>	<i>Polypyterus endlicheri</i>	None species	Total (%)
Bia river (N = 58)	-	36.2	27.6	10.3	8.6	3.5	-	-	13.8	100
Lake Ayame (N = 58)	50	8.6	3.5	-	31	1.7	-	-	5.2	100
Lake Buyo (N = 48)	22.9	-	-	-	27.1	-	39.6	2.1	8.3	100
Lake Faye (N = 55)	12.73	-	-	-	-	-	-	-	87.27	100
Lake Kan (N = 64)	-	89.1	-	-	1.6	-	-	-	9.4	100
River Bagoue (N = 54)	-	-	-	-	-	-	-	-	100	100
River Nzo (N = 44)	-	-	-	-	-	-	-	-	100	100

Values are given in percentage (%) per total number of respondents(N) in the specific sampling site

Table 6 Results of multinomial logistic regression of socio-demographic factors determining Ivorian fishermen's awareness of climate change

Explanatory variable	Awareness of climate change Coef ^{sig} (St. Err)
Climatic zone	– 0.730* (0.287)
Fishing watershed	– 0.012 (0.101)
Age	0.119 (0.146)
Ethnic group	– 0.068 (0.051)
Gender	0.016 (0.445)
Household size	0.411* (0.189)
Education level	0.580** (0.104)
Main occupation	0.036 (0.276)
Residual Deviance	361.11
AIC	379.11

Significant correlations in bold, with level of significance indicated by stars, and standard errors in brackets
* $\alpha < 0.05$; ** $\alpha < 0.01$

Table 7 Results of multinomial logistic regression of socio-demographic factors determining Ivorian fishermen's perception of change in climate

Explanatory variable	Perceived Change in rainfall		Perceived Change in temperature		Perceived Change in flooding	
	Increase	Decreased	Increase	Decreased	Increase	Decreased
	Coef ^{sig} (St. Err)	Coef ^{sig} (St. Err)	Coef ^{sig} (St. Err)	Coef ^{sig} (St. Err)	Coef ^{sig} (St. Err)	Coef ^{sig} (St. Err)
Climatic zone	– 3.117 (2.384)	– 0.907(2.307)	0.478 (0.401)	0.671 (0.628)	– 1.445** (0.302)	0.519 (0.819)
Fishing watershed	– 0.539 (0.514)	– 0.733 (0.486)	0.214 (0.175)	– 0.641** (0.248)	0.670** (0.106)	– 0.370 (0.328)
Age	– 1.235 (0.690)	– 1.527* (0.663)	0.458 (0.238)	– 0.069 (0.309)	– 0.230 (0.141)	– 0.245 (0.337)
Ethnic group	0.543 (0.398)	0.616 (0.392)	– 0.280** (0.069)	– 0.197* (0.089)	– 0.302** (0.049)	– 0.039 (0.120)
Gender	12.139** (0.412)	14.398** (0.412)	1.884 (1.342)	3.366** (1.388)	0.271 (0.416)	1.115 (1.182)
Household size	– 2.195** (0.821)	– 1.773** (0.762)	0.140 (0.330)	0.496 (0.397)	0.261 (0.188)	0.695* (0.344)
Education level	– 1.814* (0.728)	– 1.530* (0.717)	– 0.016 (0.127)	– 0.053 (0.161)	– 0.058 (0.089)	0.141 (0.198)
Main occupation	– 0.066 (0.794)	– 0.870 (0.764)	– 0.319 (0.460)	– 0.007(0.463)	0.305 (0.204)	– 12.793** (0.00002)
Residual Deviance	236.66		421.86		483.83	
AIC	272.66		475.86		519.83	

Significant correlations in bold, with level of significance indicated by stars, and standard errors in brackets

* $\alpha < 0.05$; ** $\alpha < 0.01$

fishermen are therefore well informed of the climate trend. Being aware of local perception and knowledge of climate change is essential for formulating climate change education, communication interventions, and for effectively implementing risk reduction strategies [25]. Our result, which suggests that most of the Ivorian fishermen are well informed of climate change, is a positive feature for global actions against climate change in Cote d'Ivoire. Local fishermen should be associated with the process of decision-making concerning climate change adaptation and mitigation strategies.

According to previous studies, the demographic background of individuals represents an important factor that influences their awareness and perception of climate change [24, 29, 33, 25]. For instance, [25] have shown that socio-demographic factors such as gender, age and education have a great influence on farmers' knowledge and perception of climate change. The result of the multinomial logit regression model, which highlighted the significant importance of demographic variables such as age, gender, household size ethnic group and education level in fishermen awareness and perception of climate change, corroborates these findings. Interviewees' awareness of "climate change" was positively influenced by educational level. Our finding is consistent with those of [29] and [34] which showed an increase of respondents' knowledge of climate with education level. Thus, people with higher educational levels are more likely to get access to information related to climate change than those with low educational levels. The same observations were

Table 8 Results of multinomial logistic regression of socio-demographic factors influencing Ivorian fishermen's perception of change in fish abundance

Explanatory variable	Perceived Change in fish abundance		
	Low decrease Coef ^{sig} (St. Err)	Moderate decrease Coef ^{sig} (St. Err)	Significant decrease Coef ^{sig} (St. Err)
Climatic zone	0.156 (1.041)	0.378 (1.160)	2.364* (0.965)
Fishing watershed	− 0.294 (0.301)	− 0.851 (0.483)	− 1.009** (0.274)
Age	1.604** (0.556)	1.909** (0.646)	1.607** (0.532)
Ethnic group	0.219 (0.164)	0.858** (0.227)	0.123 (0.156)
Gender	1.633 (2.231)	0.249 (3.157)	− 1.205 (2.175)
Household size	− 0.430 (0.539)	− 1.123 (0.855)	0.100 (0.479)
Education level	0.365 (0.240)	0.083 (0.347)	0.491* (0.220)
Main occupation	− 3.218 (2.427)	0.222 (2.906)	1.708 (2.165)
Residual Deviance	334.245		
AIC	388.245		

Significant correlations in bold, with level of significance indicated by stars, and standard errors in brackets
* $\alpha < 0.05$; ** $\alpha < 0.01$

done by [35], where higher levels of knowledge of individuals allowed them to better assess the threats posed by climate change and reduced the perceived level of uncertainty related to climate change and the impact of pro-environmental behaviours.

Freshwater fishes represent an important and vital component of the food of many people in sub-Saharan Africa [11]. Our study suggests that most of the respondents observed significant declines in fish quantity. Climate change, especially change in temperature and rainfall were acknowledged to contribute to this decline in Ivorian freshwater fish abundance. Additionally, many anthropogenic activities including gold mining, water withdrawal for human needs, use of small-mesh fishing nets, overfishing, industrial waste discharge, pesticides use for agricultural purposes along watersheds, obnoxious fishing practices and increase in human population, were listed by fishermen as other stressors contributing in depletion of Ivorian freshwater fish abundance. Since the independence of Côte d'Ivoire, a set of laws and regulations has been adopted for the sustainable management of the fisheries sector [36]. The most recent is the law n° 2016–554 of 26 July 2016 on fisheries and aquaculture, which provides dispositions relating to the regulation and sustainability of aquatic resources, in particular in its articles 8, 9, 10, 11 and 12 [37]. The dispositions in these articles define the set of measures such as the types of fishing engines allowed, the size of fishing nets allowed, the prohibition of fishing on protected species, the prohibition of the use of any explosive materials, toxic substances or baits likely to weaken, stun, excite or kill aquatic resources or to infect their habitats, etc. However, based on information provided by fishermen, there is clear evidence of a lack of application of these measures by fishermen communities. Thus, awareness-raising campaigns on the important values of freshwater ecosystem biodiversity, especially those of fish species, for human livelihoods, and the necessity to preserve these ecosystems for the benefit of future generations are necessary. Similarly, populations living in areas surrounding freshwater habitats should be informed on practices that negatively impact the biodiversity of freshwater ecosystems. In addition, further measures such as a prohibition on fishing during reproduction seasons of fish species, introduction of laws imposing prison sentences to those engaged in obnoxious fishing practices, establishment of buffer zones between watersheds and agriculture farms in order to prevent pesticides used in agriculture to get water bodies, enforcement of mining and agricultural industries to treat their waste before discharging it into waterways, should be taken by the Ivorian government in agreement with local fishery management authorities. These additional measures will contribute to strengthening the existing aquatic resources management policy, then allow the sustainable use of these resources. To reduce the effect of climate change on fish abundance, greenhouse gas emissions and deforestation must be reduced, and reforestation campaigns should be increased all over the country. Another solution for the mitigation of climate change is the protection of watershed forests.

The listed factors threatening Ivorian freshwater fish biodiversity in our study are among the wide spectra of factors threatening Africans' freshwater ecosystems in general. Indeed, according to [11], climate change, water pollution, habitat loss due to deforestation, overfishing, mining, and agriculture represent the greatest threats to freshwater fishes in Africa and specifically in West Africa [11]. For instance, impact of climate change was observed in Lake Chad located in West Africa between 1960s and 2001, where the surface area of water was reduced to 5.4% of its initial level (50% caused

by climate change), leading to the loss of many aquatic organisms taxa [9, 38]. Also, according to [39], natural disasters (e.g., droughts) represent the second most serious cause of decline for around 70% of the freshwater fishes in northern Africa. In Kinshasa and Lagos, pollution from oil exploration, cars in the cities, factories or other urban industries, and from boat traffic are impacting freshwater ecosystems. Pollution from oil exploration, combined with habitat loss, specifically threatens many restricted-range species in the Niger Delta and may pose a threat to species in coastal freshwater of the Republic of Congo, Cabinda, Gabon and Angola [9]. Congo freshwater ecosystem was additionally reported to suffer from mercury discharge linked to gold mining activities. In Lower Guinea, freshwater species are particularly threatened by intensive land use and pollution from rubber, banana, and palm oil plantations [9]. Another example is the case of eastern slopes of Mount Cameroon, where freshwater fish biodiversity is impacted by habitat loss due to agriculture. In Benin and the Volta region of Africa, overfishing was reported to cause changes in fish community structures and distributions [40, 11].

Research studies examining the survival of extremely rare, cryptic or possibly extinct species often rely on local knowledge rather than on direct study of these species. While there is considerable potential for error and bias in the collection and interpretation of traditional ecological knowledge from local informants [41], this research approach provides a unique source of data with substantial applicability for conservation [42, 43]. Fish species populations declines have been supported by fisher's perceptions in several studies that have assessed freshwater fish species [42] and the marine one as well [44–46]. The study by [44] in the Eastern Brazilian Marine Park corroborated the decline of seven of the reef fish species by fishers. These declines were mostly due to heavy fishing pressure and overfishing along the Brazilian coast [44]. Another example is the study by [42], which demonstrated the strong awareness of fishers of the major declines in many fish species in the Yangtze River in recent decades. In our study, the species reported by respondents as locally scarce or under threat or with their populations in depletion are all classified in the category of least concern in the IUCN red list. *Heterotis niloticus* is a pelagic species that frequent shallow waters of rivers and lakes for the adults, and marshy places among aquatic vegetation for the young [47]. *Tilapia zillii*, *Parachanna obscura* and *Lates niloticus* are demersal and potamodromous species. *Tilapia zillii* is caught in shallow marginal waters, drowned forest areas and also on sandy shores [48]. *Lates niloticus* inhabits channels, lakes and irrigation canals, prefers sandy bottoms, but is also found in rocky to muddy bottoms. Vegetated areas in calm waters provide shelter for its larvae and young [49]. *Parachanna obscura* is a deep-water inhabitant and migratory freshwater species found mainly in floodplains, swamps, rivers, lakes, ponds and streams [50]. This species breeds throughout the year, but preferably during and just after floods. *Sarotherodon galilaeus* is also demersal and occurs in the shallow coastal waters of lakes and prefers open water, but juveniles and breeding adults can be found offshore [51]. In lakes, it is often associated with beds of submerged vegetation. *Malapterurus electricus* inhabits shallow waters with muddy or sandy bottoms, close to rocky areas, and prefers stagnant or slow-moving water [52]. *Labeo coubie* is a benthopelagic and potamodromous species living in rivers and lakes, and mainly sheltered bays [53]. All of these species breed on seasonal floodplains, overflowed areas or in marginal vegetated areas of the catchment. Thus, any change in the rainy season pattern (late or early arrival, shortening, etc.) or any reduction in rainfall can disrupt their reproduction and spawning. Also, given that fish are often adapted to a certain level of hydrological variability, changes in this variability could have negative effects on fish populations [54]. Unusually large floods or seasonal pulses can displace adults and displace or injure juveniles and larvae, and droughts or prolonged dry spells can lead to population declines as well as reductions in abundance and changes in species composition [55, 54]. According to the fishermen, there has been a decrease in rainfall and a change in the onset and length of the rainy season as well as an increase in floods occurrence. Thus, this can probably explain why these species were reported as locally threatened by respondents. Freshwater fish are all exotherms, unable to regulate their body temperature by physiological means and having a body temperature virtually identical to that of their environment [54]. Consequently, increasing global temperatures can affect them by altering physiological functions such as thermal tolerance, growth, metabolism, food consumption, reproductive success and the capacity to maintain internal homeostasis in the face of a variable external environment [56]. Fish populations that experience changing thermal regimes may increase or decrease in abundance, experience range expansions or contractions, or be threatened with extinction [54]. The increase in temperature observed by fishermen can illustrate the decline of the population of these species. In addition, due to the preference of these species for vegetation or forest areas, agriculture expansion and pesticide use along watersheds may pose a threat to their habitat and populations. Agriculture and pesticide use along watersheds were listed by the fishermen in this study among anthropogenic activities threatening the Ivorian freshwater ecosystem. Most of the species listed are among the main species of the Ivorian fishery [57]. Overfishing has been reported by fishermen as one of the threats to the biodiversity of Ivorian freshwater fish. Thus, it may represent one of the probable causes of the rarity of these species. According to the result of a recent study on the assessment of the conservation status and the vulnerability of the ichthyofauna

of the Bandama River in Côte d'Ivoire, species such as *Lates niloticus*, *Labeo coubie*, *Heterotis niloticus* and *Sarotherodon galilaeus*, despite their status as species of least concern, were assessed as vulnerable to fishing pressure [17]. Many other studies carried out on the African continent have reported that these species are locally threatened by many humans' actions and climate change. *Lates niloticus* is reported to suffer from over-exploitation in much of its native range, and to a lesser extent, pollution [58]. *Heterotis niloticus* and *Parachanna obscura* are also affected by overfishing in central and western Africa respectively, where they represent commercially important fish species [47, 59]. *Malapterurus electricus*, *Sarotherodon galilaeus*, *Tilapia zillii* and *Labeo coubie* are threatened by dam constructions, water pollution, groundwater extraction and drought in northern Africa, whereas *Malapterurus electricus* and *Sarotherodon galilaeus* are additionally affected by overfishing in eastern Africa [51, 53, 52, 48].

5 Conclusion and perspectives

Côte d'Ivoire is a climatically diverse country with a great diversity of freshwater ecosystems.

The results of this study show good awareness among local fishermen of climate change and its drivers. That climatic awareness represents a positive prerequisite for the implementation of measures toward climate mitigation and population adaptation. Fish abundance reduction was reported as a consequence of climate change and several anthropogenic activities. In response to this reduction in fish quantity, the government must ensure the strict application of policies and regulations in force in the fisheries sector, through the establishment of local management and monitoring committees. These should be done by involving fishermen associations (or cooperatives) in the process of decision making, their implementation, and monitoring. This will improve the effectiveness of actions and contribute to the sustainable management of fishing resources. In addition, to enable fishing communities to adapt to the decline of fish, they need to be trained to diversify their sources of income. For example, training them in agriculture (livestock, aquaculture, etc.) or other activities such as mechanics, commerce, electricity, etc. This will not only strengthen their adaptive capacities but also reduce excessive pressures on aquatic ecosystems. All these measures should be implemented through fishermen associations or cooperatives. In Côte d'Ivoire, fishermen are mainly organized in cooperatives or associations [60]. The roles of these are most often to contribute to food security, poverty eradication, promotion of collective action, empowerment of fishermen to respond to environmental and socio-economic changes, and sharing of responsibility in the practice of responsible fishing, but also to have a good voice in the social-economic process. However, the movement of cooperatives or associations in the fisheries sector is characterised by a lack of dynamism in Côte d'Ivoire. Those function with difficulty, thus giving the impression that there are no existing fisheries actors in Côte d'Ivoire [60]. Thus, the government should first revitalise the associations or cooperatives by providing financial supports, but also train them on their roles and duties.

The information provided by fishermen constitutes basic information on the evolutions and the main factors impacting fish abundance in Ivory Coast. These are useful for directing and approving adaptation and management strategies of fish resources. These results should be supported by further studies that will focus on quantifying the level of decrease in fish quantity, the contribution of each threat in this decline, the level of correlation between these threats, the identification of the most impactful threats, and the assessment of the vulnerability and the already existing local adaptation strategies in Ivorian local fishermen communities. These will give a clear view on which management strategies will be more appropriate for the sustainability of fish resources and how to improve the existing adaptation strategies.

Fish species listed by fishermen as being threatened are economically among the most important fish species for the livelihood of many African countries, especially in Côte d'Ivoire. The reassessment of the local status of these species using IUCN criteria is needed to guide management and conservation policies. Furthermore, more research studies are needed to assess and quantify the vulnerability of these species to climate change and human activities. The assessment of the distribution, genetic diversity and population dynamics of these species will also be necessary to develop appropriate management and conservation policies.

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Authors' contributions AAI participated in the collection and analysis of the data, as well as the writing of the manuscript. ONB and AK participated in the writing of the manuscript and in the data analysis. TM and KEP guided and supervised the project, reviewed and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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Appendix 1: Survey questionnaire on “Fishermen’s perceptions and experiences toward the impact of climate change and anthropogenic activities on freshwater fish biodiversity in Côte d’Ivoire”.

Questionnaire number:

Socio-demographic information

1. Locality
2. Watershed
3. Climate zone.....
4. Ethnic group
5. Gender 1) Male [...] 2) Female [...]
6. Age: 1) 20–29 [...]; 2) 30–39 [...]; 3) 40–49 [...]; 4) 50–59 [...]; 5) 60 and over [...]
7. Marital status: 1) Married [...]; 2) Single [...]; 3) Widowed [...]; 4) Divorced [...]; 5) No answer [...]
8. Household size 1) 1–5 [...]; 2) 6–10 [...]; 3) 11–15 [...]; 4) 16–20 [...]; 5) 21–25 [...]; 6) 26 and over[...]
9. Education level; 1) Illiterate [...] 2) Primary [...]; 3) Junior high school [...]; 4) Senior high school [...]; 5) University [...]
10. Main occupation
11. Secondary occupation
12. Monthly income

Perception of climate change and its drivers

1. Are you aware of “climate change”? 1) yes [...]; 2) no [...]
2. What do you think is the major cause or driver of climate change? 1) greenhouse gas emissions [...]; 2) Land-use change [...]; 3) Deforestation; 4) Volcanoes; 5) Solar radiation [...]; 6) Other.....
3. Have you observed any change in the rainfall over the past years? 1) No change [...]; 2) Increase [...]; 3) Decrease [...]; 4) I don't know [...]
4. Have you observed any change in the timing of the rainy seasons over the past years? 1) No change [...]; 2) early arrival [...]; 3) late arrival [...]; 4) I don't know [...]

5. Have you observed any change in the length of the rainy seasons over the past years? 1) No change [...]; 2) lengthening [...]; 3) Shortening [...]; 4) I don't know [...]
6. Have you observed any change in the temperature over the past years? 1) No change [...]; 2) Increase [...]; 3) Decrease [...]; 4) I don't know [...]
7. Have you observed any change in flooding occurrence over the past years? 1) No change [...]; 2) Increase [...]; 3) Decrease [...]; 4) I don't know [...]

Perception of the impact of climate change and human activities on fish biodiversity.

1. Have you observed any decrease in fish abundance or quantity in your fishing watersheds over the past years? 1) No decrease [...]; 2) low decrease [...]; 3) moderate decrease [...]; 4) significant decrease [...]; I don't know [...]
2. How have temperature changes affected fish abundance or quantity? 1) No effect [...] 2) Increase [...]; 3) Decrease [...]; 4) I don't know [...]
3. How have rainfall changes affected fish abundance or quantity? 1) No effect [...] 2) Increase [...]; 3) Decrease [...]; 4) I don't know [...]
4. For you, what are the human actions or activities that affect/impact negatively fish biodiversity in your fishing watersheds?
.....
.....
.....
5. Have you noticed the scarcity or the depletion of populations or the disappearance of particular species of fish in your fishing watersheds? 1) Yes [...]; 2) No [...]
6. If yes, can you please provide the name(s) of this or these species?

Any other comments?

.....
.....
.....

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RESEARCH ARTICLE

Population genetics of the African snakehead fish *Parachanna obscura* along West Africa's water networks: Implications for sustainable management and conservation

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Abstract

An essential factor for aquatic conservation is genetic diversity or population divergence, which in natural populations reflects the interplay between geographical isolation with restricted gene flow and local evolution of populations. The long geological history of Africa may induce stronger among-population divergence and lower within-population divergence in fish populations of African watersheds. As an example, we studied population structure of the African snakehead fish *Parachanna obscura*. Our study aimed: (1) to develop a set of highly polymorphic microsatellite markers suitable for the analysis of genetic diversity among *P. obscura* and (2) to study the genetic diversity and structure of *P. obscura* populations from the West Africa region and mostly from Côte d'Ivoire, with respect to the effects of climate region and geographical distance on the genetic differentiation. A total of 259 specimens from 15 locations of *P. obscura* were collected over the West Africa region reflecting a high variability of pairwise geographical distances and variability of hydrological connectivity of the area. We developed a set of 21 polymorphic microsatellite markers for studying population genetics of the fish. The results showed relatively low intragenetic diversity for all the 15 locations, certainly attributable to confinement of fish in segregated catchments, resulting in limited gene flow. We also found evidence for local adaptation processes, suggested by five out of 21 microsatellite loci being under putative selection, according to BAYESCAN analysis. In turn, there was strong genetic differentiation ($F_{ST} > 0.5$) among fish from most locations, reflecting the allopatric development in watersheds without hydraulic connectivity. Neighbor-joining dendrogram, Principal Coordinate Analysis, and analysis of ancestral groups by STRUCTURE suggested that the 15 locations can be divided into three clusters, mainly matching the dominant climate zones and the segregation of the watersheds in the region. The distinct genetic structure of the fish from the 15 locations obtained in this study suggests that conservation and sustainable management actions of this fish resource should avoid genetic mixing of potentially locally adapted populations.

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KEYWORDS

genetic differentiation, genetic diversity, hydrological networks, paleogeographic history, snakehead fish

TAXONOMY CLASSIFICATION

Population genetics

1 | INTRODUCTION

Tropical regions host the world's richest freshwater fish faunas. According to estimates, there are over 3000 species of freshwater fish in Africa, which is comparable to the number of species in Asia (over 3600) and South America (over 4200; Lévêque et al., 2008). Complex climatic and geological events have caused a long history of geographical isolation followed by diversification for some and extinction for other populations, ultimately resulting in the diversified fauna of the African freshwater ecosystems (Amoutchi et al., 2021; Darwall et al., 2011). Since the division of Gondwanaland in the early Cretaceous, many African rivers went through complex geological histories involving changes in the structure of their catchments and river beds (Goudie, 2005). The evolution of Africa's fauna and landscapes has been influenced by the cycles between the Pleistocene and Pliocene dry and rainy eras (deMenocal, 2014; Maslin et al., 2014; Van Steenberge et al., 2020). Along with fluctuations of water levels in the African Great Lakes, these climate cycles have caused alternating expansions and contractions of savannah and forest-like habitats (Malinsky & Salzburger, 2016). According to Tedesco et al. (2005), these climatic shifts led to migration, extinction, and allopatric divergence, which resulted in the current diverse fish faunas. In addition, the long geological history of Africa also affects the interplay between the contemporary distribution of populations and their genetic diversity, with longer periods of spatial segregation and allopatric development than those typically found for the much younger post-glacial landscapes of the Palearctic or Nearctic.

An essential factor for aquatic conservation is genetic diversity or population divergence, which in natural populations reflects population history and the evolutionary potential of a species (Jaisuk & Senanan, 2018). Within a fish species, population subdivision results from the interaction of distinct genetic changes within isolated populations and restricted gene flow among them (Hedrick, 2011). Conspecific populations typically diverge from one another in the absence of gene flow due to mutation, natural selection, and genetic drift (Freeland, 2005). In addition, the degree to which landscape shapes patterns of genetic variation among populations is determined by life-history features linked to migration and fish dispersal capabilities (Pilger et al., 2017). Geographical factors favoring population division include geographical distance between locations (Beneteau et al., 2009; Crookes & Shaw, 2016), the presence of barriers (Neville et al., 2006; Yamamoto et al., 2004), the complexity of a river network (Pilger et al., 2017), and habitat fragmentation (Sterling et al., 2012).

The freshwater ecosystem in Côte d'Ivoire in Africa is characterized by a large and complex system consisting of four major

river basins: Sassandra, Cavally, Bandana, and Comeo ranging in length from 650 to 1160 km and rising in geographically wide-ranging areas beyond the Côte d'Ivoire. In addition to these systems, there are many coastal rivers such as the Tabou, San Pedro, Niouniourou, Boubo, Agneby, Bia, and Me Rivers as well as two tributaries of the Niger River and many lakes (Girard et al., 1971). These habitats are endowed with numerous economically important fish species.

Among the economically important fish, *Parachanna obscura* (Gunther, 1861), is the most popular and widespread African fish species from the Channidae family. It is commonly known as African snakehead fish and has great economical and commercial values for local African communities. This species is benthopelagic and a strict freshwater habitant. It is generally distributed in the intertropical convergence zone where the water temperature ranges from 26°C to 28°C principally in West Africa. Nevertheless, it is also found in the upper course of the White Nile, the Lake Chad basin, and the Congo River basin (UA, 2013). Given the complexity and geological history of the region, the resulting patterns of genetic variation merit investigation in *P. obscura*. For example, Bezault et al. (2011) suggested that paleo-geographic history, climatic events of Africa, and geographic barriers have induced strong genetic differentiation among *Oreochromis niloticus* populations from different parts of Africa. Strong genetic differentiation was also detected among African freshwater river and lake populations of *Lates niloticus*, reflecting the complexity of freshwater systems originating from the geological history of the continent (Basiita et al., 2018). Furthermore, the long-time isolation of populations can favor adaptations to local environmental conditions with the occurrence of particular alleles. The adaptive capacity of populations depends on microevolution, e.g., the selection of local genotypes better adapted to changing environmental conditions (Canale & Henry, 2010; Hoffmann & Sgrò, 2011). These adaptation processes will likewise influence the amount and distribution of genetic diversity among populations (Pauls et al., 2013). Thus, assessment of the genetic diversity of *P. obscura* is necessary for understanding the evolutionary patterns of this species, and its capacity to cope with future environmental conditions, as well as for planning conservation policy for sustainable management of this species as fisheries resource.

Previous studies on *P. obscura* have mostly focused on biology (Bolaji et al., 2011; Odo et al., 2012), reproduction (Vodounnou et al., 2017), aquaculture potential (Azrita & Hafrijal, 2015), and phylogenetic range of the fish (Adamson et al., 2012; Conte-grand et al., 2017; Li et al., 2003). However, there is no information about the genetic diversity among populations of this species. Since no previous studies have been conducted on the genetic diversity of

P. obscura, genetic markers, for example, microsatellites, were not available. Accordingly, the objectives of our study were (1) to develop a set of highly polymorphic microsatellite markers suitable for the analysis of genetic diversity among *P. obscura* fish and (2) to study the genetic diversity and structure of *P. obscura* fish from 15 locations from the West Africa region and mostly from Côte d'Ivoire. According to the geological history of the region with potentially long periods of geographical isolation, we expected low genetic diversity and high genetic differentiation for this species. Furthermore, we expected that the genetic differentiation was affected by geographical isolation caused by the interplay between connectivity barriers, landscape structure, and geographical distances among locations.

2 | MATERIALS AND METHODS

2.1 | Study area and collection of samples

A total of 259 specimens of *P. obscura* from 15 locations were collected over the West Africa region from Côte d'Ivoire (14 locations) and Benin republic (one location; see Figure 1 and Table 1). The sampling sites were selected to represent a high variability of pairwise geographical distances. In Côte d'Ivoire, individuals were sampled from Bia river (KRINA, and KRINB, locations about 7 km distant from each other), Wayadji stream (SIK), Sassandra river (SBR), San-Pedro Lake (SANP), and Abengourou lake (ABIN). This region is

characterized by a sub-equatorial climate (Guinean climate zone) including two rainy and dry seasons, with an estimated annual precipitation of more than 1500 mm (Bernard, 2014). Specimens were also collected from Kan Lake (KAN), Baho (BAHO) and Glo (GLO) streams, Buyo Lake (SASA and SASB, sampling distance of about 26 km), and Nzo River (NZOA and NZOB, sampling distance of about 13 km), in the center and centre-western Cote d'Ivoire, characterized by an equatorial transition climate (Sudano-guinean climate zone), with two rainy and dry seasons, and an annual precipitation of 1200 to 1500 mm per year. Finally, individuals were collected in Bagoue river (BAG), situated in the north Cote d'Ivoire, characterized by a tropical climate (Sudanean climate zone) with a very hot and dry season from November to March and a rainy season from April to October. Specimens sampled from Benin republic were collected in Nokoue lake (BIN), located in the southern part characterized by a sub-equatorial climate with two rainy and dry seasons.

Parachanna obscura fishermen from each sampling site were employed for fish samples collection using traps and fish nets. The intended sample size per location was 25–30 individuals; however, for several sites this number could not be obtained. For molecular analyses, approximately 1 cm of pectoral fin was clipped from each individual and stored in individual Eppendorf tubes containing 95% ethanol. The rest of the entire specimens were fixed in 10% formaldehyde solution and transported to laboratory for further analysis. The molecular analysis was performed in the genetic laboratory of the Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin.

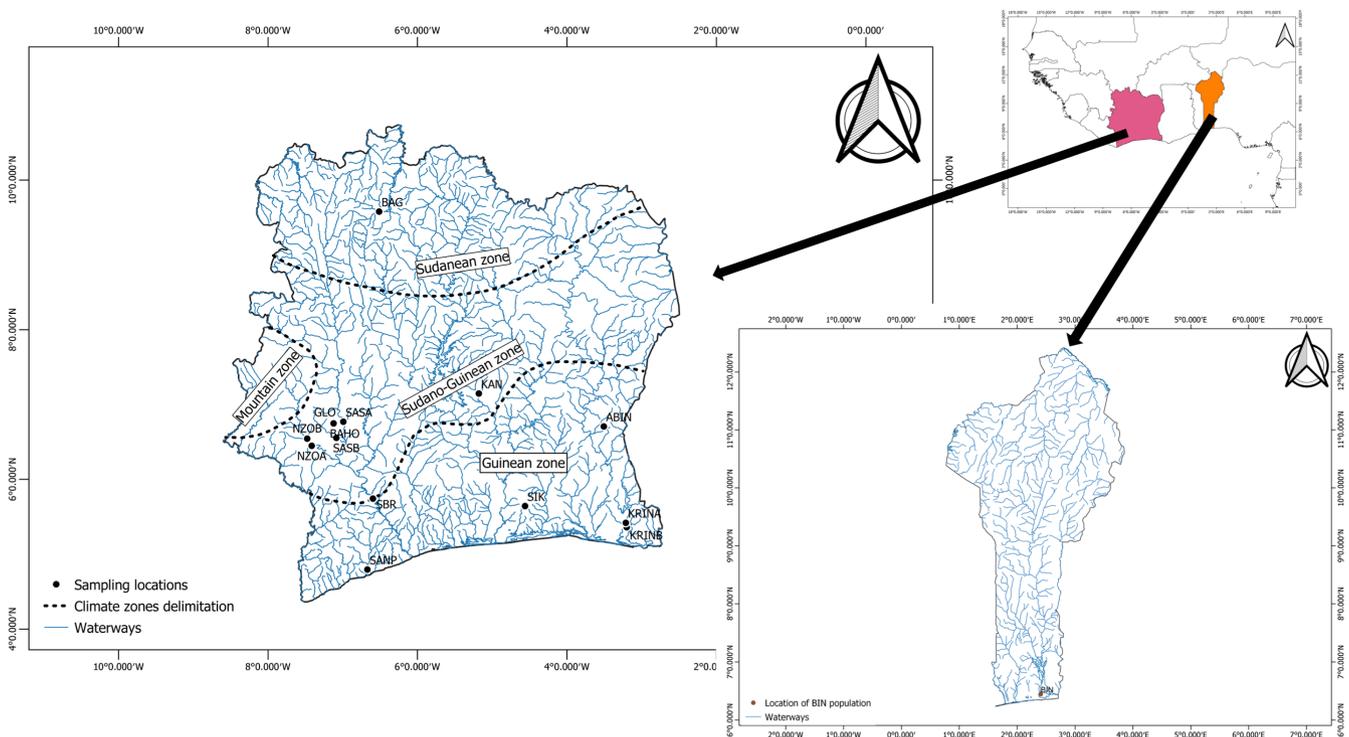


FIGURE 1 Map of the study area, showing sampling locations and abbreviations of locations (Table 1) from which *Parachanna obscura* specimens were collected, in Côte d'Ivoire (left) and in Benin republic (right down), and position of these countries in West Africa. The climate zones of Côte d'Ivoire are also shown.

TABLE 1 Information on samples sizes, basins, country, and climate of locations of 15 samples *Parachanna obscura* (with total sample size of 259 individuals).

River basin	Water body	Location	Sample size (N)	Country	Climate
Comoe	Abengourou Lake	ABIN	6	Côte d'Ivoire	Subequatorial
Coastal river Bia	Bia river	KRINA	38	Côte d'Ivoire	Subequatorial
Coastal river Bia	Bia river	KRINB	13	Côte d'Ivoire	Subequatorial
Coastal river San-Pedro	San-Pedro Lake	SANP	26	Côte d'Ivoire	Subequatorial
Sassandra	Sassandra river	SBR	17	Côte d'Ivoire	Subequatorial
Coastal river Agneby	Wayadji stream	SIK	5	Côte d'Ivoire	Subequatorial
Sassandra	Baho stream	BAHO	7	Côte d'Ivoire	Equatorial transition climate
Sassandra	Glo stream	GLO	6	Côte d'Ivoire	Equatorial transition climate
Bandama	Kan Lake	KAN	18	Côte d'Ivoire	Equatorial transition climate
Sassandra	Nzo river	NZOA	12	Côte d'Ivoire	Equatorial transition climate
Sassandra	Nzo river	NZOB	40	Côte d'Ivoire	Equatorial transition climate
Sassandra	Buyo Lake	SASA	16	Côte d'Ivoire	Equatorial transition climate
Sassandra	Buyo Lake	SASB	17	Côte d'Ivoire	Equatorial transition climate
Niger river	Bagoue river	BAG	22	Côte d'Ivoire	Tropical climate
Fed by Ouémé and Sô Rivers	Nokoue lake	BIN	16	Benin	Sub-equatorial

2.2 | Molecular genetics analyses

Genomic DNA from fin clippings was isolated using the DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer protocol. The development of microsatellite markers suitable for the analysis of population genetics of *P. obscura* was conducted by the commercial company GenoScreen. Their procedure consisted of two steps: (1) GenoSat library preparation using 5 µg DNA from an equimolar pool of 10 DNA samples followed by high throughput DNA sequencing run on Nano 2x250 v2—MiSeq Illumina and bioinformatic analysis and primer design. (2) Biological validation of 142 primer pairs on eight *P. obscura* DNA samples from different populations including PCR amplification and analysis of the obtained profiles on QIAxcel (Qiagen). GenoScreen usually considers as validated those primer pairs with a specific PCR product at the expected size for at least 5 samples. This was the case for 120 (or 84.5%) of the tested 142 primer pairs. Based on the delivered list of validated primers with comments for each pair and migration profiles generated by QIAxcel ScreenGel 1.6.0, the number of potentially suitable primer pairs was further reduced by excluding those with weak, very weak, or no visible PCR product for one or more samples and focusing on those indicating polymorphism on the migration profiles. This screening resulted in 29 primer pairs selected for testing on a larger number of individuals using the PCR protocol described below. However, only 21 primer pairs (Appendix A) turned out to be suitable for routine genotyping based on the observed polymorphism.

Each forward primer of the 21 loci was synthesized with either DY751 or Cyanine 5 or BMN-6 fluorescent dyes attached to its 5' end. A set of eight multiplex reactions were conducted (Appendix B). PCR amplification was conducted using Qiagen Multiplex PCR kits, following the recommendations of the manufacturer. PCR

amplification was carried out in 11.3 µl reaction volumes, containing 10 µl PCR mix and 1.3 µl DNA (~20 ng/µl). The composition of the PCR mix of each of the multiplex reactions is described in Appendix B. The primer concentration was 10 pmol/µl. The thermocycling profile started with an initial denaturation step at 95°C for 15 min, followed by 35 cycles of 30 s at 94°C, 55°C, and 72°C and ended with a final extension step of 30 min at 60°C. Denatured fragments were resolved on an automated DNA sequencer (Beckman Coulter CEQ 8000) using 0.83 µl of PCR product and a mixture of 30 µl formamide (SLS; Sciex) and 0.5 µl size standard-400 (Sciex). Genotypes were identified using the GenomeLab™ GeXP Genetic Analysis System version 10.2 (Beckman Coulter) fragment analysis module.

2.3 | Statistical data analyses

The majority of the analyses and graphical output were created using R 4.1.2 (R Core Team, 2021). Allele polymorphism at each of the 21 microsatellite loci and the intra-population genetic diversity metrics, such as number of alleles per location and allelic richness A_R , were quantified by PopGenReport 3.0 package (Adamack & Gruber, 2014). Potential existence of individuals with missing genotypes among the loci was evaluated using poppr 2.9.3 (Kamvar et al., 2014) package in R. Null allele frequencies per locus were calculated in the genepop 1.1.7 package (Rousset, 2008). The inbreeding coefficient (probability that the two alleles at one locus of an inbred individual are identical alleles per descent (Gazal et al., 2014); F_{IS}) was estimated in genepop_in_R. The significance of this coefficient was evaluated based on 95% confidence intervals calculated using bootstrapping ($N = 100$) in hierfstat 0.5–11

package in R (Jerome & Thibaut, 2022). Deviations from Hardy-Weinberg equilibrium (HWE) at the location level were tested by the exact (probability) test using genepop v1.1.7 in R. Probabilities of HWE deviations (Guo & Thompson, 1992) per locus per location were corrected by the false discovery rate for multiple tests (Benjamini & Hochberg, 1995), supplemented by U-tests on excess homozygotes. We conducted an Analysis of Molecular Variance (AMOVA, Excoffier et al., 1992) using the R-package pegas 1.1 (Paradis, 2010) to compare within- and between-location variance for the 15 locations.

Through the genepop v1.1.7 package in R, genetic differentiation was estimated by F -statistics between locations (F_{ST} ; Weir & Cockerham, 1984), with the significance of differentiation assessed by exact conditional contingency table tests for genotypic differentiation. Using the poppr v2.9.3 package in R, a neighborhood tree (Saitou & Nei, 1987) based on Prevosti's pairwise genetic distance (Prevosti, 1974) was constructed to identify genetic relationships between *P. obscura* locations. The 259 individual genotypes were also subjected to a principal coordinate analysis (PCoA), which is a multidimensional metric scaling, in order to visualize the distribution of individuals and location centroids in reduced space. This analysis was carried out in ade4 v1.7-19 (Thioulouse et al., 2018), while adegraphics v 1.0-16 (Siberchicot et al., 2017) was used to visualize the resulting graphs.

Bayesian approaches as implemented in the standalone program STRUCTURE v2.3.4 (Pritchard et al., 2000) were used to estimate and visualize the genetic structure among samples from the 15 locations. After a burn-in period of 100,000 iterations, the number of Markov-chain Monte Carlo iterations was set to 100,000 using admixture model's default parameters and locations' correlated allele frequencies. Ten runs were performed for

each K (ancestral groups or clusters) between 1 and 15. The greatest mean estimate of the posterior probability based on the ad hoc ΔK statistics was used to determine the optimum K (Evanno et al., 2005).

Mantel correlation tests were performed between the pairwise genetic distance matrices calculated as $F_{ST}/(1-F_{ST})$ values and the natural logarithm (ln) of the pairwise straight-line geographic distances (km) to assess the effect of geographic isolation or distance on the genetic structure among *P. obscura* sample locations. The genetic distance matrix was calculated in the genepop package of R, while the geographical distance matrix was calculated with QGIS 3.22.6 using the global positioning system (GPS) coordinates of the sampling locations. Mantel correlation tests with 1000 permutations were performed by the vegan v 2.6-2 package (Oksanen et al., 2022) in R.

To examine non-neutral evolutionary forces acting on the microsatellite loci, a scanning analysis was realized using the BAYESCAN v2.1 software (Foll & Gaggiotti, 2008) to detect candidate loci under selection. BAYESCAN was run with a sample size of 5000, a number of pilots runs of 20, length of pilot runs of 5000, a burn-in of 50,000, and the false discovery rate (FDR) threshold of 0.05.

3 | RESULT

3.1 | Genetic structure within populations

In total, 0.3% missing genotypes were obtained among all microsatellites for the 259 individuals from the 15 locations (Appendix C). Loci Para041 (1.9%) and Para023 (1.5%) had the highest proportions

TABLE 2 Genetic diversity of *Parachanna obscura* fish from 15 sampling locations at 21 microsatellite loci

Location	N_A	H_O	H_S	\bar{A}_R	F_{IS}	95% CI for F_{IS}
ABIN	33	0.16	0.18	1.4	0.09	[-0.17; 0.33]
BAG	27	0.02	0.023	1.1	-0.04	[-0.06; 0.00]
BAHO	23	0.02	0.03	1.1	0.28	[0.00; 0.37]
BIN	57	0.30	0.30	1.9	-0.01	[-0.15; 0.14]
GLO	22	0.02	0.02	1.0	-0.25	[-0.25; -0.25]
KAN	28	0.09	0.10	1.2	0.09	[-0.05; 0.22]
KRINA	57	0.35	0.33	1.9	-0.06	[-0.14; -0.01]
KRINB	55	0.33	0.34	2.0	0.01	[-0.08; 0.13]
NZOA	23	0.04	0.04	1.1	0.07	[-0.22; 0.29]
NZOB	25	0.04	0.04	1.1	0.09	[0; 0.11]
SANP	35	0.27	0.26	1.6	-0.05	[-0.22; 0.12]
SASA	25	0.04	0.05	1.1	0.19	[-0.09; 1]
SASB	25	0.02	0.03	1.1	0.40	[-0.03; 0.54]
SBR	24	0.06	0.05	1.1	-0.16	[-0.19; -0.13]
SIK	34	0.30	0.26	1.6	-0.14	[-0.41; 0.13]

Abbreviations: 95% CI, 95% confidence interval; F_{IS} , inbreeding coefficient; H_O , observed heterozygosity; H_S , expected heterozygosity; N_A , Observed number of alleles; \bar{A}_R , Mean allelic richness.

of missing genotypes. Among locations, ABIN (1.6%) and SIK (1.0%) recorded the highest proportions of missing loci. No individual with more than two missing loci was found. Therefore, all individuals and loci were used for further analyses.

A total of 87 alleles were observed across the 21 microsatellite loci. All microsatellite markers developed in this study were variable. The allele number (N_A) per locus ranged from two found at Para038, Para128, Para136, and Para137 loci to 12 found at Para027 locus (Appendix D). Among the loci genotyped, Para027 was the most variable one ($H_E = 0.67$, $H_O = 0.42$), while the lowest variability was detected at locus Para042 ($H_E = 0.21$, $H_O = 0.03$). Following maximum likelihood estimates (Dempster et al., 1977), relatively high null allele frequencies were estimated for loci Para038 (16%) and Para059 (59%). However, since no difference was observed in the estimates of genetic differentiation among locations after removing these loci (pairwise F_{ST} values; Appendix E), we included all 21 loci in the analyses.

The genetic diversity was low in most of the locations (Table 2). However, KRINA ($N_A = 57$, $H_O = 0.35$, $H_S = 0.33$, $\bar{A}_R = 1.9$), KRINB ($N_A = 55$, $H_O = 0.33$, $H_S = 0.34$, $\bar{A}_R = 2.0$) and BIN ($N_A = 57$, $H_O = 0.302$, $H_S = 0.30$, $\bar{A}_R = 1.9$) had a higher genetic diversity than the other locations. The estimated inbreeding coefficient (F_{IS}) value was low for all locations, and the confidence intervals showed that the F_{IS} coefficients were non-significant for all locations. Except for SASA (Para 107), SASB (Para027) and KRINA (Para104) locations where deviations from HWE at single loci were found (Appendix F), most of the samples did not deviate from HWE for all 21 analyzed microsatellite loci after correction by the false discovery rate for multiple tests.

3.2 | Genetic structure between populations

The pairwise F_{ST} was high and significantly differentiated all location pairs of *P. obscura*, except the few locations from the same watershed only few kilometers apart (Table 3). BAG was most genetically differentiated, with the highest pairwise F_{ST} values (all above 0.7) recorded relative to the other location pairs. Estimation of the pairwise F_{ST} was extremely low (close to zero) between SASA, SASB, NZOA, NZOB, and BAHO from Sassandra river basin and between KRINA and KRINB from Bia river.

The result of AMOVA showed significantly ($p < .05$) high genetic variation among locations (66.7%) and within individuals (33.5%), while no significant variance was detected among individuals within locations (-0.2%; Table 4).

The neighbor-joining dendrogram obtained based on Prevosti's genetic distance separated the locations into three major clusters (Figure 2). The locations SIK, KRINA, KRINB, SANP, KAN, and BIN fish representing cluster I are located in southern regions characterized by sub-equatorial climate, except KAN from the central Côte d'Ivoire. The second cluster (II) was composed of BAG (Bagoue river) and ABIN (Abengougou lake) from northern (with a tropical climate) and south-eastern Côte d'Ivoire (with sub-equatorial climate), respectively. The third cluster (III) included SASA, SASB, NZOA, NZOB,

TABLE 3 Matrix of pairwise F_{ST} between the 15 *P. obscura* locations (lower diagonal), and their p -values as obtained by G-tests (upper diagonal)

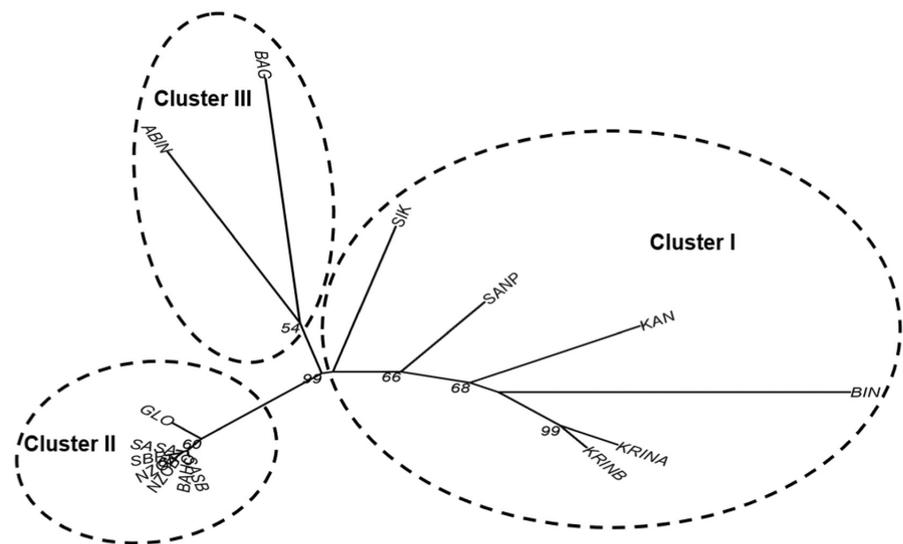
	ABIN	BAG	BAHO	BIN	GLO	KAN	KRINA	KRINB	NZOA	NZOB	SANP	SASA	SASB	SBR
ABIN														
BAG	0.90													
BAHO	0.81	0.95											1	0.006
BIN	0.67	0.82	0.72											
GLO	0.80	0.96	0.66	0.73										
KAN	0.79	0.93	0.85	0.63	0.85									
KRINA	0.56	0.72	0.52	0.38	0.53	0.42								
KRINB	0.56	0.80	0.55	0.41	0.54	0.50	0.01							
NZOA	0.83	0.95	0.04	0.74	0.61	0.85	0.54	0.59						
NZOB	0.88	0.94	0.07	0.83	0.59	0.88	0.64	0.72	-0.03					
SANP	0.58	0.78	0.51	0.54	0.56	0.53	0.34	0.34	0.53	0.63				
SASA	0.83	0.94	-0.02	0.76	0.55	0.85	0.56	0.61	0.01	0.05	0.54			
SASB	0.85	0.95	-0.07	0.78	0.61	0.87	0.57	0.63	0.07	0.11	0.57	0.00		
SBR	0.84	0.94	0.22	0.76	0.61	0.85	0.56	0.61	0.08	0.09	0.53	0.11	0.25	
SIK	0.56	0.89	0.68	0.59	0.65	0.68	0.47	0.45	0.71	0.80	0.46	0.72	0.76	0.70

Note: Significant pairwise differentiation indicated in bold.

TABLE 4 Analysis of molecular variance for 259 *Parachanna obscura* individuals originating from 15 locations sampled for this study

	df	Sum Sq	Mean Sq	Sigma	% of variation	p
Variance between locations	14	2958.9	211.3	6.2	66.7	.01
Variance between samples within locations	244	747.6	3.1	-0.02	-0.2	.59
Variance within individuals	259	805.0	3.1	3.1	33.5	.01
Total variance	517	4511.5	8.7	9.3	100	

FIGURE 2 Neighbor-joining dendrogram of *Parachanna obscura* fish from 15 sampling locations, based on Prevosti's genetic distance. Only bootstrap values >50% are shown.



GLO, SBR, and BAHO locations fish from central-western region of Côte d'Ivoire with an equatorial transition climate. Principal coordinate analysis (PCoA) of individuals confirmed the classification of locations obtained from the dendrogram (Figure 3). The first five axes explained around 77.4% of the total predicted variation with 36.9%, 21.7%, 7.5%, 5.8%, and 5.3% of predicted variation, respectively. The projection of the 259 specimens over the first two axes is shown in Figure 3. PCoA-Axis 1 principally separated samples of cluster II (negative PCoA-values) and samples of cluster I (positive PCoA-values). PCoA-Axis 2 isolated cluster III locations BAG and ABIN with negative PCoA-values from the other locations.

A complex spatial genetic structure of *P. obscura* samples was revealed by the correlation between pairwise genetic distances ($F_{ST}/(1-F_{ST})$) and the natural logarithm of the pairwise Euclidean geographical distance between the 15 locations. Although there was a significant positive trend between genetic and geographical distances, there were strong deviations from the linear pattern at 5.5 and 6.5 ln geographical distances, caused by the strong genetic distances between BAG and SASA, SASB, NZOA, NZOB, BAHO, and BAHO locations (Slope = 0.96, Adj $R^2 = 0.052$; Mantel test $p = .04$, Figure 4).

The fish from the 15 locations could be divided into three ancestral genetic groups (Figure 5), following the peak value $\Delta K \sim 100$ (Figure 5a Evanno et al., 2005). However, a second small peak of ΔK (~ 18) was recorded at $K = 9$, suggesting that nine ancestral groups would be an alternative splits worth exploring. With $K = 3$, the

STRUCTURE clustering diagram corresponded to differentiation among locations into three clusters as proposed previously in the distance-based and Principal coordinate analysis. However, individuals of SANP and SIK locations displayed a more complex genetic structure with shared membership of ancestral origins from clusters I and II. Also, ABIN defined as belonging to cluster III shared memberships with clusters I and II. Considering $K = 9$, the STRUCTURE clustering diagram showed that the locations of the previously defined cluster II were clearly differentiated from the other locations, with two admixed ancestral genetic groups (yellow and orange). The other locations were unique with dominance of one ancestral group in each location, except KRINA and KRINB which belong to the same ancestral group.

3.3 | Detection of loci potentially under selection

The BAYESCAN analysis indicated five among the 21 loci with a q -value of less than 5%, suggesting that they are under selection (Figure 6). Of these five loci, Para027 with lowest F_{ST} and negative alpha (coefficient indicating the strength and direction of selection) was putatively under balancing selection, while the other four loci (with highest F_{ST} and positive alpha) were under putatively directional selection (see Appendix G). However, the F_{ST} estimates showed high values for all loci (>0.4), also for those with $q > 0.05$ (Figure 6).

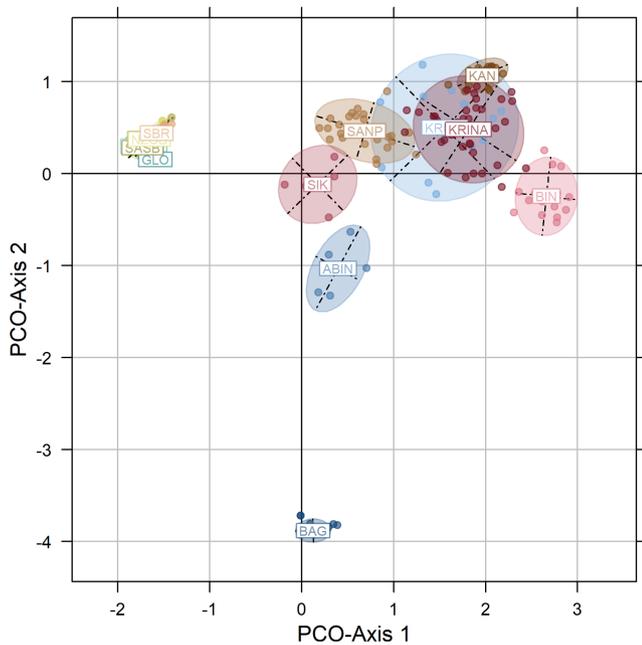


FIGURE 3 Axes 1 and 2 of the principal component analysis (PCoA) of 259 *Parachanna obscura* individuals (dots) and inertia ellipses representing 15 sampling locations.

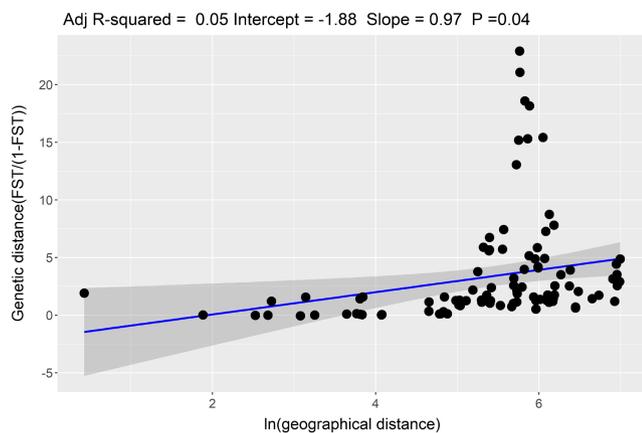


FIGURE 4 Multilocus estimates of pairwise genetic distances ($F_{ST}/(1-F_{ST})$) between fish from 15 sampling locations plotted against natural logarithm (\ln) of pairwise Euclidean geographical distance (km). p was obtained based on Mantel test.

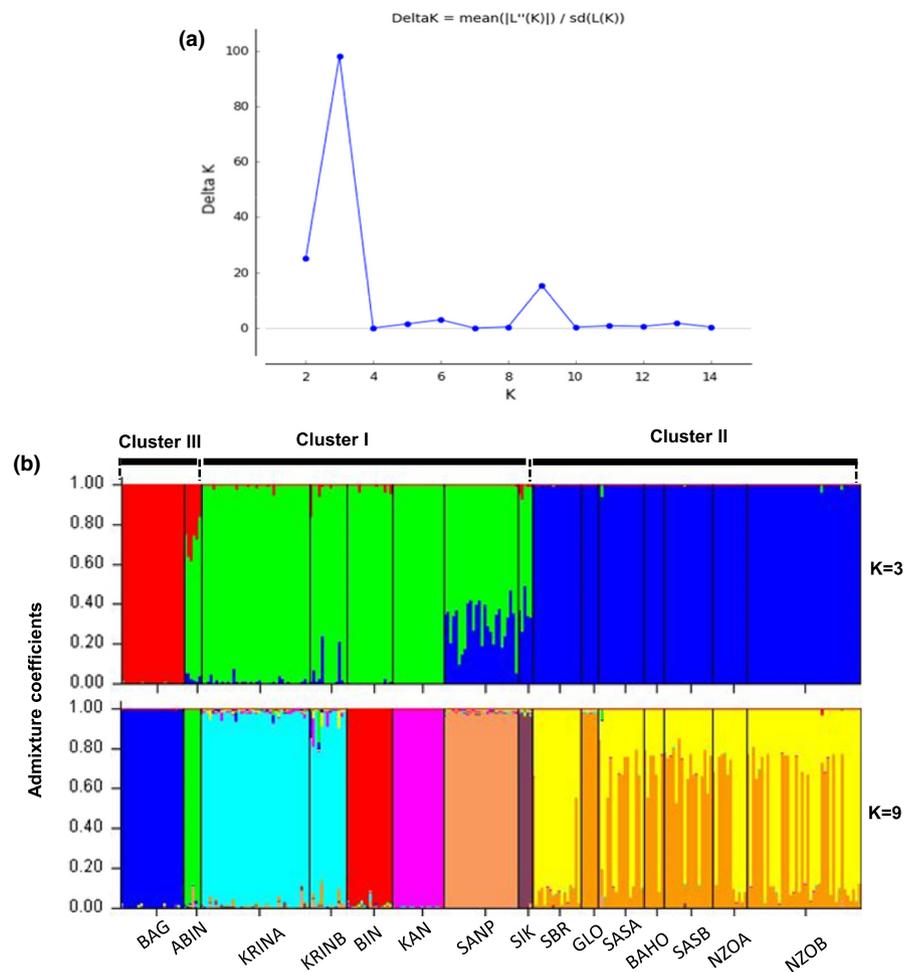
4 | DISCUSSION

We characterized the genetic structure and diversity of *P. obscura* fish from 15 locations in the West Africa region (mostly Côte d'Ivoire), using the set of polymorphic microsatellite markers developed in the current study. Among the 120 produced and validated markers, a group of 21 polymorphic microsatellites were deemed suitable for the analysis of genetic differentiation among the sampling locations. However, some of these markers had a slightly increased frequency of null alleles. Microsatellite null alleles have been documented in studies of population genetics and PCR primer characterization (Dakin & Avise, 2004) and have been discovered in a wide variety

of taxa. Examples include insects (Lepidoptera, reviewed in Meglecz et al., 2004; Diptera, Lehmann et al., 1997; and Orthoptera, Chapuis et al., 2005) and mollusks (Astaneï et al., 2005; Li et al., 2003). It is generally not advised to include null allele loci in population genetics because they may affect estimates of population differentiation (Chapuis & Estoup, 2007). However, we did not exclude any locus from our study because it has been demonstrated that the influence of null alleles in studies of population genetics may be minimal compared to other parameters such the number of loci (Carlsson, 2008). Moreover, for our data, the estimation of the populations differentiation (F_{ST}) using only 19 microsatellites showed no difference in the value compared to the original data including null alleles. Jaisuk and Senanan (2018) also found no change in population differentiation of *Garra cambodgiensis* after removing alleles with high null alleles frequencies.

The estimated within-population genetic diversity was low for all the 15 locations. In contrast to our result, high genetic diversity was obtained in other fish species occurring in Africa and other parts of the world using microsatellite loci. Angienda et al. (2011) reported a relatively high genetic diversity for *Oreochromis esculentus* ($H_O = 0.795-0.81$, $H_S = 0.745-0.77$, $\bar{A}_R = 7.13-8.13$) and *Oreochromis niloticus* ($H_O = 0.70-0.78$, $H_S = 0.71-0.79$, $\bar{A}_R = 7-8.38$) populations in eastern Africa. Mehner et al. (2021) found high genetic diversity in the European *Coregonus cisco* populations ($A_R = 3.4-6.3$). Many studies on the genetic diversity of other species from the Channidae family such as *Channa striata* (Adamson et al., 2012; Robert et al., 2019; Tan et al., 2016) and *Channa marulius* (Pathak et al., 2018) showed relatively high genetic diversity. The low within-population genetic diversity observed in our study is likely a result of limited gene flow among populations. Also, the very low genetic diversity observed in SASA, SASB, NZOA, NZOB, and GLO, all originating from the same basin (Sassandra river basin), may be due to the Wahlund effect, which occurs when genotypic proportions are computed from heterogeneous samples where individuals belonging to genetically differentiated entities (subpopulations) are pooled (De Meeûs, 2018), resulting in an excess of homozygotes. This assumption is supported by the STRUCTURE results ($K = 9$, Figure 5) with the mix from two ancestral groups in these samples, as well as the positive F_{IS} obtained for these samples. Furthermore, confinement of populations in segregated catchments have probably facilitated local adaptation, thus further reducing genetic diversity. Microsatellite markers are normally neutral to selection. However, adaptive micro-evolutionary mechanisms may reduce genetic diversity both at selected loci under adaptation and in those parts of the genome that are hitchhiking with them (Via, 2009; Via & West, 2008). Genetic hitchhiking is a process that allele frequencies change without being under natural selection, because these genes are located on the same DNA chain near to another gene that is undergoing a selective sweep. The hitchhiking process may affect larger regions of the genome in particular in small populations (Charlesworth et al., 1997). As a result, genetic diversity of populations may decrease fast in response to environmental changes, lowering the population's ability

FIGURE 5 Admixture analysis by STRUCTURE of *Parachanna obscura* fish obtained from 15 sampling locations. (a) Line plot of successive ΔK from $K = 2$ –14. (b) Bar plots of genetic clusters for $K = 3$ and $K = 9$ ancestral groups, where each color corresponds to a unique ancestral group. Markov-chain Monte Carlo iterations were set at 100,000 after a burn-in period of 100,000.



to respond to future selection pressures. We found high F_{ST} for all loci and five loci suggested to be under selection in the BAYESCAN analysis, indicating that micro-evolutionary mechanisms may have contributed to the reduction of the genetic diversity.

The estimation of the pairwise genetic differentiation (F_{ST}) showed highly significant differences among most of the locations of *P. obscura* except among locations from connected river networks. This result suggests that the fish from most of the different locations belong to distinct populations, except those collected from interconnected water networks, which may form one unique population together. In our study, SASA, SASB, NZOA, NZOB, and BAHO are samples from interconnected rivers (Nzo River, Baho and Glo streams) and therefore had low values of pairwise genetic differentiation (F_{ST} close to zero). Nzo River, Baho and Glo streams are tributaries of Buyo lake, which is an artificial lake created by dam construction on Sassandra river. Thus, fish from these five locations can be considered as belonging to one population. KRINA and KRINB are both from Bia River, with samplings only a few km apart, and therefore likewise can be considered belonging to the same population.

Aquatic species, and freshwater fishes in particular, frequently display strong population structure probably as a result of their confinement to the network structure of aquatic systems in the landscape (Loxterman, 2011; Pérez-Espona et al., 2008). The

pattern of genetic differentiation obtained in our study suggests an allopatric evolution of populations of *P. obscura*. The freshwater systems of the area where populations were collected are heterogeneous and complex, characterized by geographical barriers and lack of connectivity, which has favored the isolation of populations and prevented gene flow. Isolation of fish populations based on height of watershed boundaries and relatively frequent occurrence of movement barriers within watersheds, have generally been demonstrated to generate significant genetic differentiation (Faulks et al., 2010; Gomez-Uchida et al., 2009; Loxterman & Keeley, 2012; Pfrender et al., 2004; Taylor et al., 2003). The results are in line with the hypothesis developed by Meffe and Vrijenhoek (1988) for explaining population genetic patterns for aquatic organisms inhabiting stream networks. Indeed, these authors predict that genetic isolation will occur among stream networks that do not have hydrological connections, resulting in an imbalance between drift and gene flow (where gene flow is effectively zero). A study on *Channa argus*, another Channidae species, revealed significant genetic differentiation among populations related to the structure of the river system (Yan et al., 2018). Loxterman and Keeley (2012) also demonstrated that watershed boundaries have probably driven the genetic isolation obtained among Cutthroat trout (*Oncorhynchus clarkii*) populations from western North America.

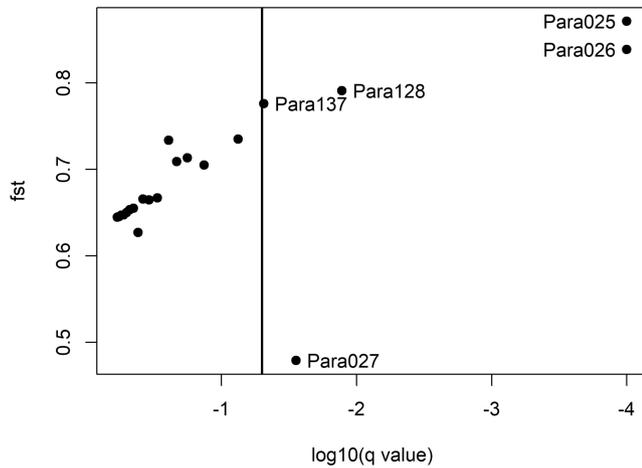


FIGURE 6 Plot representing the BAYESCAN results searching candidate loci under selection. The vertical line represents a false discovery rate (FDR) threshold of 0.05. Points to the right of the vertical line represent loci under selection. Q-value: Minimum false discovery rate at which a locus may become significant; F_{ST} , Coefficient to measure the difference in allele frequency between the common gene pool and each population, calculated as a posterior mean using model averaging.

The high values of the genetic differentiation obtained between locations from unconnected water networks (F_{ST} higher than 0.5 in most cases) and the high genetic variation obtained among locations (66.7%) from AMOVA in our study, suggest that the populations have been isolated for long period of time, probably matching with the paleogeographic history of the formation of the hydrological systems on the African continent. Indeed, various paleogeographic (such as the disruption of fluvial drainages) and paleoclimatic (such as wet-dry cycles) events have had a significant impact on the African ichthyofauna from the Miocene to the Pleistocene by altering the connectivity between the various hydrographic systems (Bezault et al., 2011; Drake et al., 2011; Lévêque, 1997). A study by Bezault et al. (2011) demonstrated that paleo-geographic events have resulted in high genetic differentiation among *Oreochromis niloticus* populations across Africa. Using mitochondrial DNA based markers, Mwanja et al. (2013) found different lineages of *Lates* sp, which may have developed during geographical isolation during the Pleistocene and have remained largely allopatric without gene flow since that time, on the African continent. The effect of paleo-historical lake level variations on genetic diversity of African cichlids has also been demonstrated (Egger et al., 2007).

Although there was a significant and positive trend between genetic and geographical distances, some location pairs strongly deviated from the expected linear pattern. This pattern suggests that genetic diversity may additionally be shaped by insurmountable barriers resulting from landscape characteristic between the different sampling locations that prevent any exchange of genetic material among populations from non-connected water bodies. The population most strongly differentiated from all others was from Bagoue River (BAG), situated in the north Cote d'Ivoire, characterized by a tropical climate. As seen on the map, the watersheds of Bagoue

River are completely disconnected from the watersheds of the other populations analyzed, making geographical separation very likely. This separation is likely induced by the geography of the area, which is characterized by a mountain ridge south of Bagoue River that prevents the river flowing to the south, as most of the other rivers in the southern part. Similar observations were taken on salmonid fishes for which it has been suggested that landscape characteristics such as the complexity of the drainage network and differences in channel gradients between habitats are likely to limit dispersal between their populations (Angers et al., 1999; Castric et al., 2001; Guy et al., 2008; Hebert et al., 2000).

The classification of *P. obscura* populations into three clusters from both the neighbor-joining dendrogram and the principal coordinate analysis suggested that the genetic diversity of the populations may have probably been shaped by isolation due to geographical barriers and micro-evolutionary adaptive mechanisms, with climate-related environmental conditions as a potential driver. Indeed, the location of the populations in these clusters partly matched the climatic zones of Ivory coast and Benin republic. In the first cluster, five populations are combined, which originate from regions with a sub-equatorial climate. Only fish from the KAN location were collected in an area characterized by an equatorial transition climate. The second cluster was composed of samples from an equatorial transition climate, except the SBR. SBR is linked to other populations of this cluster by habitat connectivity which facilitate gene flow. The third cluster included two populations, with BAG located in the tropical climate regions and ABIN located in sub-equatorial climate regions. The population structure characterized by the ancestral groups inferred by admixture coefficients in STRUCTURE has given the same classification ($K = 3$) but showed that ABIN shared a higher admixture with those populations from the sub-equatorial climate areas, which form cluster I. Therefore, it is more likely that ABIN location also belongs to cluster I. The partly match between clusters and climate zones suggests that regional climate conditions may have contributed to the patterns of genetic diversity of *P. obscura* in West Africa. However, more appropriate types of markers (e.g., SNP data obtained through RAD-seq) should be applied in future for confirming this hypothesis of regional climate as driver of the pattern of genetic diversity in *P. obscura*. In contrast, the population structure at higher resolution with classification into nine ancestral groups ($K = 9$) reflects the geographical configuration of the network of watersheds with populations from the same watersheds belonging to the same cluster. Hence, hydraulic connectivity or isolation have shaped gene flow among the habitats, facilitating differing evolution of the populations.

5 | CONCLUSIONS

Using the collection of polymorphic microsatellite markers developed in the present work, we characterized for the first time, the

genetic diversity, and structure of *P. obscura* populations from West Africa, representing an important baseline for further exploration of the population dynamics in this species. Understanding the genetic diversity of wild populations can help establishing aquaculture breeding programs as well as conservation initiatives to preserve fish stocks and their unique genetic identities (Yan et al., 2018). The low genetic diversity of *P. obscura* demonstrated that particular attention has to be paid for conservation and sustainable management of this fish resource. Regarding the high genetic differentiation between populations attributable to habitat heterogeneity and local adaptation, in situ conservation will be required in order to maintain genetic integrity. These population may serve as reservoirs or stocks for future selection programmes in aquaculture as well as improving population fitness and ability to respond to future environmental disturbance.

AUTHOR CONTRIBUTIONS

Petra Kersten: Data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); validation (equal); writing – review and editing (equal). **Asja Vogt:** Data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); validation (equal); writing – review and editing (equal). **Klaus Kohlmann:** Formal analysis (equal); investigation (equal); methodology (equal); validation (equal); writing – review and editing (equal). **Essetchi Paul Kouamelan:** Conceptualization (equal); supervision (equal); writing – review and editing (equal). **Thomas Mehner:** Conceptualization (equal); formal analysis (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); software (equal); supervision (equal); validation (equal); writing – review and editing (equal). **Amien Isaac Amoutchi:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); project administration (equal); software (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The sequences of microsatellite markers developed and used in this study have been submitted to Genbank (<https://www.ncbi.nlm.nih.gov/genbank/>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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