The Biology of Four Haplochromine Species of Lake Kivu (Zaïre) with Evolutionary Implications

by

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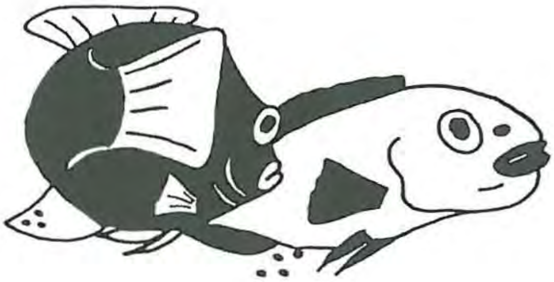

Thesis

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"La pensée est un oiseau de l'espace, qui dans une cage de mots peut ouvrir ses ailes mais ne peut voler." (Khalil Gibran, 1923)

Table of Contents

page

List of figures

List of tables

Acknowledgements

Abstract

I. Introduction 1

II. Lake Kivu 4

1. Introduction 4
2. Geological history 5
3. Limnology 10
4. Biotopes and their associated faunas 13

III. Study Area: Tshegera Island 18

1. Introduction 18
2. Physiographic features 19
3. Related faunas 21

IV. Taxonomy 22

1. Introduction 22
2. Characters used in species' identification 23
3. Diagnostic features of the species studied 25

Haplochromis astatodon

a. Taxonomy 26
b. Species' identification 26
c. Relation between form and function 29
d. Phyletic classification 30

Haplochromis olivaceus and *Haplochromis crebridens*

a. Taxonomy 31
b. Species' identification 31
c. Relation between form and function 37
d. Phyletic classification 38

Haplochromis paucidens

a. Taxonomy 39
b. Species' identification 39
c. Relation between form and function 43
d. Phyletic classification 43

V. Breeding Biology 44
1. Introduction 44
2. Material and methods 45
a. Monthly sampling 45
b. Reproductive seasonality 46
c. Fecundity 46
d. Condition factor 47
3. Results 48
a. Monthly sampling 48
b. Reproductive seasonality 51
c. Fecundity 53
d. Condition factor 55
4. Discussion 60

VI. Circadian Activity and Fish Distribution 64
1. Introduction 64
2. Material and methods 65
a. Circadian activity 65
b. Activity peak analysis 66
3. Results 67
a. Circadian activity 67
b. Activity peak analysis 71
4. Discussion 73

VII. General Discussion 75
1. Taxonomical and ecological aspects 75
2. Evolutionary implications 80
a. Mode of speciation in the African Great Lakes 80
b. Evolutionary status of Lake Kivu 82
c. Conclusion 83
3. Vulnerability of Lake Kivu 84

VIII. Bibliography 86

Appendix

A. Fish diversity in Lake Kivu.
B. Geological time scale and adaptive radiation of cichlids in African Great Lakes.
C. Bathometric map of Lake Kivu.
D. Agenda of sampling events.
E. Breeding territory distribution of the species studied.
  1. Description
  2. Illustration

List of Figures

Figure 1: Location of Lake Kivu and the study site, Tshegera Island (from Hecky and Degens, 1973) . . . 1

Figure 2: View on the latest eruption in June 1989 when a vent of the Nyamulagira exploded... . 4

Figure 3: A north-south profile of the Central African Rift (from Pouclet, 1978). . . . 5

Figure 4: Changes in geology and hydrology of the Western Rift Valley between Lake Edward and Lake Tanganyika from the late Pleistocene onwards . . . 6

Figure 5: Reconstruction of the lake level in Kivu for the last 15 000 years (from Hecky and Degens, 1973). . . . 8

Figure 6: The lava flow from the Nyamulagira volcano (1938-1940) almost cut the Basin of Kabuno from the Main Basin. . . . 9

Figure 7: Average values of temperature, conductivity and density obtained from 23 vertical profiles in the Main Basin (from Tietze, 1981). . . . 10

Figure 8: Variation in transparency and in the quantity of zooplankton over a one year period in Lake Kivu (from Verbeke, 1957a.) . . . 11

Figure 9: Dissolved oxygen profile of Lake Kivu (from Damas, 1937). . . . 12

Figure 10: A theoretical transect through the macrophytic environment along the sandy to muddy shoreline of Lake Kivu (from Van der Ben, 1959). . . . 15

Figure 11: Thsegera Island situated along the north-west coast of Lake Kivu. . . . 18

Figure 12: Bathometric and bottom type maps of the coastal zone at Thsegera Island. . . . 19

Figure 13: Characteristics of body and head shape used to differentiate the various species. . . . 23

Figure 14: The three basic types of tooth observed in the haplochromines and tooth nomenclature (from Barel et al.,1977) . . . 24

Figure 15: Shape of the tooth band illustrating the position of the outer and inner rows of teeth (from Barel et al., 1977). . . . 24

Figure 16: Sexually mature male and female *H. astatodon*. . . . 26

Figure 17: Head shape of female and male *H. astatodon*. . . . 27

Figure 18: Outer tooth description of *H. astatodon*. . . . 27

Figure 19: Colours displayed in the dorsal, caudal and anal fins of dominant *H. astatodon* males. 28

Figure 20: Classification of *H. astatodon* within the genus *'Haplochromis'* (Greenwood, 1979).. . 30

Figure 21: Sexually mature male and female *H. olivaceus*. . . . 31

Figure 22: Head shape of female and male *H. olivaceus* 32

Figure 23: Outer tooth description of *H. olivaceus*. 32

Figure 24: Colours displayed in the dorsal, caudal and anal fins of dominant *H. olivaceus* males.. 33

Figure 25: Sexually mature males and female *H. crebridens*. 34

Figure 26: Head shape of female and male *H. crebridens*. 35

Figure 27: Outer tooth description of *H. crebridens* comparatively to *H. olivaceus*. 35

Figure 28: Colours displayed in the dorsal, caudal and anal fins of dominant *H. crebridens* males.. 36

Figure 29: Classification of *H. olivaceus* and *H. crebridens* within the genus '*Xystochromis*' (Greenwood, 1979). 38

Figure 30: Mature male and females *H. paucidens*. 39

Figure 31: Head shape of male and female *H. paucidens*. 40

Figure 32: Outer tooth description of *H. paucidens*. 40

Figure 33: Colours displayed in the dorsal, caudal and anal fins of dominant *H. paucidens* males. . 41

Figure 34: Two dominant *H. paucidens* males chasing each other. 42

Figure 35: Classification of *H. paucidens* within the genus '*Paralabidochromis*' (Greenwood, 1980). 43

Figure 36: A male *H. paucidens* nudging its partner. 44

Figure 37: Two nets set parallel to the coastline in front of the vegetated zone at Tshegera Island.. 45

Figure 38: The reproductive stages during the female gonadal development. 46

Figure 39: Multiple box and whisker plot. 47

Figure 40: Total number of the four species caught in January and February 1988 during net selectivity trials. 48

Figure 41: Number of males and females caught per month. 49

Figure 42: Size distribution of both sexes combined for the total catches. 50

Figure 43: Percentage of males and females caught in 5 mm size classes. 51

Figure 44: Percentage of resting and developing, breeding and spent females per month, and mean GSI per month. 52

Figure 45: Relationship between standard length against fecundity. 54

Figure 46: Length - weight relationship of males and females separately. 55

Figure 47: Relationship between standard length and condition factor for females and males separately.. 57

Figure 48: Relationship between time and condition factor for females and males separately. . . . 58

Figure 49: Relationship between gonad maturation stages in the females and condition factor. . . 59

Figure 50: Fishing sites during the first, second and third 24-hour cycles at Tshegera. 64

Figure 51: Net sequence and position during the first, second and third 24-hour cycle at Tshegera Island. 65

Figure 52: Percentage of the species studied caught in each mesh size during the first and second 24-hour cycles. 67

Figure 53: Number of the 'species studied', 'other haplochromines' and 'non-haplochromines' caught per four-hour fishing period during the first, second and third 24-hour cycles.. . 68

Figure 54: Number of the species studied caught per four-hour fishing periods during the first and second 24-hour cycles in top and bottom set nets. 69

Figure 55: Percentage of the species studied relative to the total haplochromine catch and relative to one another for every 24-hour cycle. 70

Figure 56: Percentage composition of the species studied in the early morning and evening along the vegetated and rocky zones. 71

Figure 57: Analysis of the activity of the species studied in relation to change in light intensity in the early morning and evening along vegetated and rocky zones. 72

Figure 58: At Tshegera Island *H. astatodon* breeding males protected territories exclusively in the shallow vegetated zone. 77

Figure 59: Diagrammatic representation of altricial and precocial alternative phenotypic states and their associated characters (from Bruton, 1989) 78

Figure 60: Overview of morphological and ecological levels of specialization in the species studied. 79

Figure 61: Diversification in the African Great Lakes from generalized riverine species to highly diversified lacustrine species flocks. 81

List of Tables

Table 1: Change in transparency within the last 22 years measured by different authors in the Main Basin.. 12

Table 2: The invertebrate fauna in the two main littoral environments: the rocky and sandy shores (summarised from Verbeke, 1957a). 14

Table 3: A preliminary inventory of depth distribution of the Lake Kivu ichthyofauna [summarised from Vervoort (1981), Thys van den Audenaerde et al. (1982), Ulyel (1991) and own observations]. 16

Table 4: Total number of *H. paucidens* caught per month using gill nets and scuba. 49

Table 5: Total catches and sex ratios for each species studied. 50

Table 6: Percentage of resting females (with gonads in 2/4 stage) in the total samples. 51

Table 7: Relative fecundity, mean, maximum and minimum number of eggs produced in the ovaries. 53

Table 8: Mean, maximum and minimum egg height, and egg width. 53

Table 9: Length - fecundity relationship. 54

Table 10: Maximum size reached and size at first maturity. 56

Table 11: Length - weight relationship and mean condition factor with standard deviation for males and females for the species studied 56

Table 12: Trophic groups represented in Lake Kivu out of the 13 recognized in the African Great Lakes. 75

Table 13: Average body sizes, brood sizes and egg sizes in female mouthbrooders (Cichlidae), illustrating their range in diversity. 78

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Abstract.

Four species were selected within the littoral of Tshegera Island, and include *H. astatodon, H. olivaceus, H. crebridens* and *H. paucidens*. These species, identified on basis of the SMRS, express their individuality most strongly with respect to dentition, breeding colours, normal habitat and preferred breeding territory.

All four species are maternal mouthbrooders. This reproductive strategy is characterized by complete division of labour and polygamy. Breeding males compete for optimal territories and ready to spawn females. They are characterized by fast growth, large size and overall low condition factor. Females invest in few but large yolked ova and go through a fasting period while incubating the eggs. Females are generally characterized by slower growth, smaller size and higher condition factor when compared to males. In females the energy turnover during gonadal development and subsequent mouthbrooding is high, but the energy expenditure low. Mean fecundity varies between 25 and 36 eggs per brood and mean egg size between 2.6 and 2.7 mm. The right ovary, although small, is functional.

Breeding of variable intensity goes on throughout the year. The main dry season corresponds to synchronized breeding. During the other months of the year species breed asynchronously. Both types of breeding are related to food availability for adults and offspring. The major breeding peak which starts in July coincides to improved body condition in both sexes.

In similarity with the East African flocks, the Lake Kivu haplochromines display subdivision within the major trophic groups and invasion of the major lacustrine habitats. They are nevertheless morphologically and ecologically generalized. They tend to be plesiomorphic with low diversification within each trophic group, have a lake wide distribution (eurytopic) and incline to be altricial within their specialized reproductive guild.

The evolutionary status of the Lake Kivu haplochromines may be explained by survival of members of an ancestral fauna in an isolated bay during the Recent volcanic events which destroyed life in the Main Basin. The Lake Kivu flock, therefore, is a relict and is believed not to have evolved within the confines of the present-day lake.

I. Introduction.

Expectations from studies of the Great African Rift Lakes and their highly diversified species flocks are that the fauna of Lake Kivu would be another outstanding example of speciation. However, Lake Kivu is ecologically immature (Beadle, 1981) and is poor in fish diversity (Thys van den Audenaerde et al., 1982)(Appendix A). The number of endemic cichlid species in Lake Kivu is limited to 15 (Snoeks, in prep.) in contrast to 250+ in Lake Victoria (Van Oijen et al., 1981), 140+ in Lake Tanganyika (Brichard, 1978) and 400-500 in Lake Malawi (Ribbink et al., 1983). Interestingly, the haplochromine flock of Lake Kivu, regardless of its small size, is endemic and represents the most successful group of fish adapted to its environment through trophic diversification.

Factors affecting the degree of diversification are undoubtedly lake age (Greenwood, 1984) and habitat diversity (Van der Ben, 1959). Lake Kivu is young (ca. 15 000 years B.P.), but sediments in the Main Basin (figure 1) indicate the presence of a proto-lake there as far back as the Pliocene (Degens et al., 1973). In this basin, a haplochromine flock might have thrived and diversified until the abrupt event of volcanism in the late Pleistocene, resulting in extinction (Poll, 1939a & b). The relatively uniform and narrow shoreline of the present day basin might have been responsible for limiting diversification (Van der Ben, 1959).

Lake Kivu, therefore, might have been an evolutionary trap and may be an example of what could be the destiny of the highly diversified species flocks in the other Great African Rift Lakes. Today, not only natural catastrophic events, but also man in search of exploiting his environment could lead to fast destruction of our natural treasures as, for example, has happened in Lake Victoria since the introduction of *Lates* (Barel et al., 1985) and could happen in Lake Tanganyika where the ecosystem has to be defended against the invasion of oil companies (Coulter et al., 1986).

If a diversified cichlid species flock existed in the proto-lake Kivu, then its least specialized members had undoubtedly a much greater chance of survival during the volcanic phases, compared to more stenotopic species. Stenotopes tend to be more philopatric and poor disperses compared to eurytopes (Ribbink, 1991), giving them a smaller chance to escape in surrounding unaffected rivers. Because of the general instability of the lake during the last 15 000 years, the haplochromines of Lake Kivu might be expected to be more generalized (eurytopic) and less philopatric compared to the endemic lacustrine specialists of the African Great Lakes. The latter show a high regional endemicity (Ribbink, 1991).

My main interest in studying the fauna of Lake Kivu is (1) to test the hypothesis suggesting that the Lake Kivu haplochromines might be a remnant of a much older and more diversified species flock and tend to be generalists on a continuum from eurytopes to stenotopes and (2) understand how catastrophic volcanic events may have affected the ecology and evolution of the haplochromine flock. Is the ecology of the flock different from that of fish flocks in the other East and West African Rift Lakes? Is the small species flock as generalised as it is expected to be? Are there any highly specialized species present indicating that a more complex ancestral haplochromine flock might have existed before the late Pleistocene volcanic event?

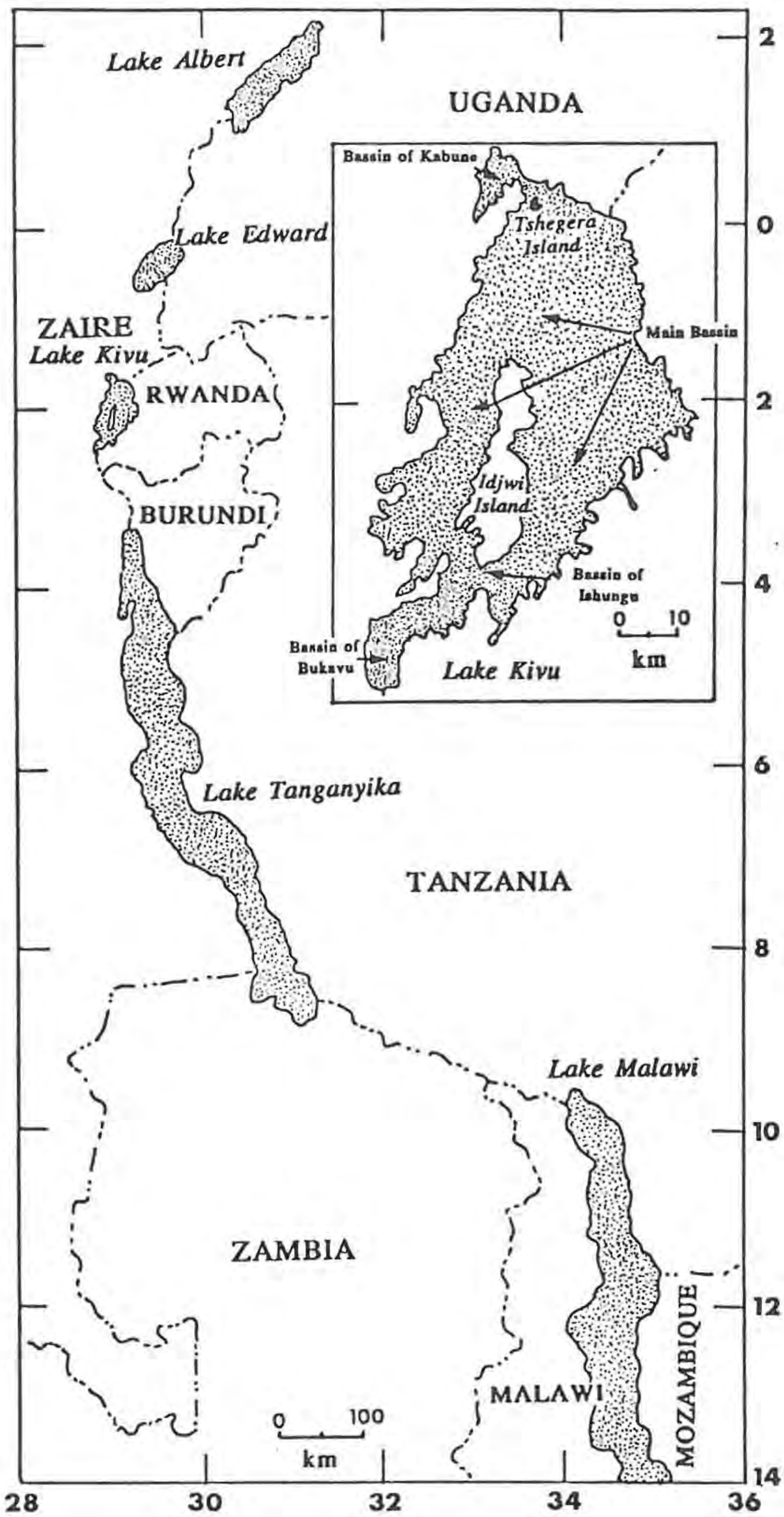


Figure 1: Location of Lake Kivu and the study site, Tshegera Island (from Hecky and Degens, 1973)

Answers to these questions are attempted after having clarified the geological history of the lake and its limnological features, and after having studied morphological aspects, habitat preferences, breeding periodicities, breeding behaviour and circadian activities of four of the haplochromine species.

Before starting the ecological work, the taxonomy of the haplochromine flock was first studied. A feature of haplochromine research in the African lakes has been the difficulty of distinguishing between closely related species. Inevitably, therefore, any research worker is drawn into the taxonomic complexities of the species flock being studied. Even in small flocks such as those of Lake Kivu it is difficult to identify member species without studying their morphology and elucidating their taxonomy. Of particular interest in the study of haplochromine morphology is that their diversification is mainly characterised by trophic specialisation through relative slight morphological modifications to a basic bauplan found in generalized riverine haplochromines (Greenwood, 1973). The older the lake, the more specialized and evolved a species flock will be and the greater the divergence of its members from the basic bauplan. For example, morphological diversity is highest and interspecific differences most trenchant among Lake Tanganyika species (about 5 my. B.P., but possibly as much as 20 my. B.P.; Greenwood, 1991), and least among the Lake Victoria species (about 750 000 years B.P.)(Appendix B). Therefore, the assessment of morphological features of the haplochromines of Lake Kivu is of direct value in estimating the degree of diversification from the ancestral riverine species and will refute or support the hypothesis.

Research was limited to Tshegera Island, situated on the north-west coast (figure 1), where four haplochromine species were selected. The species are part of a larger haplochromine community, but only those four species were chosen for the study because they were the most common members of the species flock along the coastline of the island. Because of the isolation of the fishing site it was essential that the selected species were abundant; ideally at least 30 specimens per month had to be caught without overfishing the site.

Field observations were carried out for 16 months. Such a short period is subject to sampling error as it precludes repetitive sampling and the exclusion of certain statistical procedures. Nevertheless, species specific patterns of resource utilisation and behaviour emerged, which showed that despite the generalized nature of these fishes they tend to inhabit species-specific parts of the habitat.

II. Lake Kivu.

1. Introduction.

Lake Kivu is situated south of the Equator on the border of Rwanda-Zaire (1° 84' - 2° 30' S / 28° 50' - 29° 33 E) and forms part of the western branch of the East African Rift System (Beadle, 1981) (figure 1). The surface level is 1 462 m above sealevel. Maximum depth is 480 m and mean depth 240 m (Capart, 1956). The total surface area of the lake is 2 370 km^2 and the total volume 583 km^3(Verbeke, 1957a). The outline of the basin is highly complex with numerous bays, peninsulas and islands (Van der Ben, 1959). Idjwi, situated along the principal axis of the lake, with an escarpment reaching 2 000 m (above sealevel), is the largest island of the lake (figure 1). In the lake basin, four sub-basins can be recognized: the Basin of Bukavu, the Basin of Ishungu, the Basin of Kabuno, and the Basin of Kalehe also called the Great Lake or the Main Basin (Verbeke, 1957a)(figure 1).

The Kivu area has four seasons: two dry and two wet. The dry seasons extend from December to January and from July to September. The climatic cycle is not very distinct and water temperature does not change greatly between the seasons (Van der Ben, 1959). Mean water temperature near the surface varies between 23.1°C and 24.1°C (de Iong et al., 1984). Rainfall varies greatly between different localities. In general, along the western coast rainfall is higher compared to the eastern coastline. This is explained by the combined effect of wind, which blows predominantly in a south-easterly direction, and the influence of the escarpment of Idjwi Island on air movement (Van der Ben, 1959).

Lake Kivu is an oligotrophic lake and poor in fish species (Appendix A) and biomass (Beadle, 1981). 95% of the lakes' surface and 99% of its volume are uncolonized (Hulot, 1956). Life only thrives in the littoral and sublittoral zones leaving the pelagic environment devoid of fish (Verbeke, 1957a). The ecological immaturity of the lake and the reduced diversification of its fauna, two hallmarks of the Lake Kivu ecosystem, are believed to be an effect of the recent geological history of the lake which created an unstable environment affecting the limnology and disrupting the shape, boundaries and substrate of the proto-lake Kivu basin.

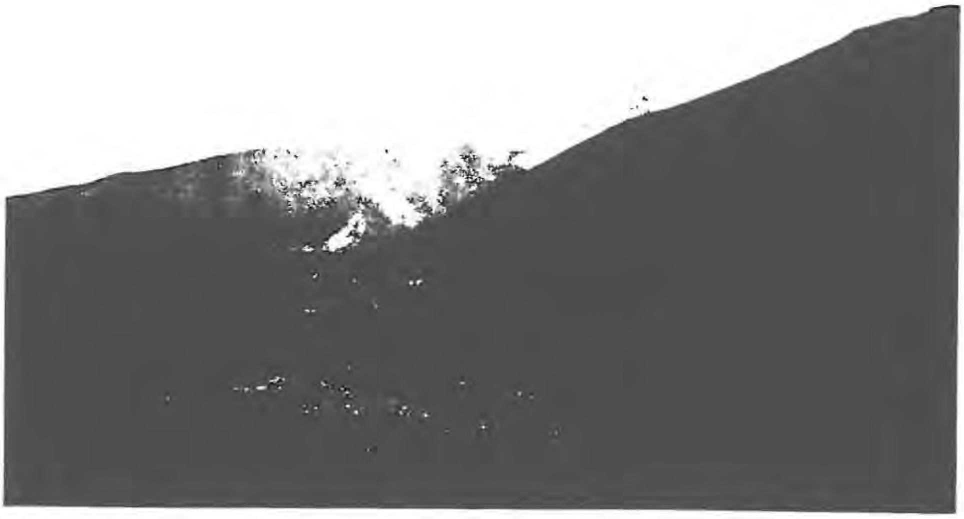


Figure 2: Since 15 000 years B.P. Lake Kivu has been strongly influenced by volcanic activity. The latest eruption, illustrated in this figure, took place in 1989 when a vent of the Nyamulagira exploded.

2. Geological history.

In this section, it is demonstrated that (1) an ancestral shallow lake existed at the same emplacement of the present-day Lake Kivu with lacustrine conditions which could well have allowed the presence of a speciose haplochromine flock and (2) that the geological instability since the late Pleistocene affecting the Lake Kivu basin resulted in major extinction phases and most likely inhibited diversification of any survivor.

The Central African Rift consists of a series of lake basins and sills (figure 3). On these sills volcanic areas are situated. By analogy with the Eastern Rift Valley, it was believed by the first explorers that during the formation of the rift valley all lakes were connected and formed a single lake. They would have been separated later during periods of regression, by rifting processes and tectonic activity (Delhaye and Salée, 1923; Sluys, 1958). However, apart from Lake Edward and Albert which once formed a single lake during the lower and middle Pleistocene, Lake Kivu and Lake Tanganyika have since their formation been separate basins (Pouclet, 1978).

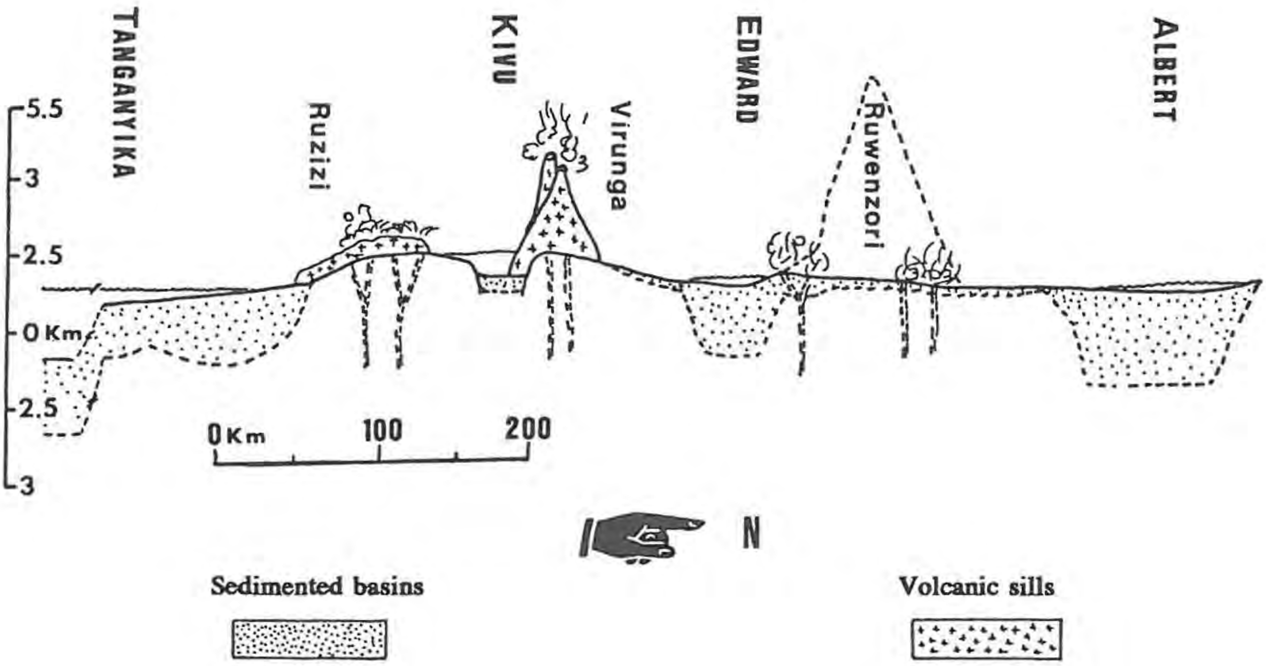


Figure 3: A north-south profile of the Central African Rift (from Pouclet, 1978).

On the basis of sediment distribution patterns two stages in the formation of Lake Kivu can be recognized: i) a shallow and ii) a deep water stage. The former lasted for most of the lake's history, between one to five million years (Degens et al., 1973). During the shallow water stage the lake included only the Main Basin (figure 4a), as indicated by a 400 to 500 m thick sediment layer, and was drained by water running from the Kihezi and Rwanda Highlands and the Mitumba Mountains (figure 4a). The lake was shallow then, there was no stratification and the water column was completely mixed. Phytoplankton production was high and eutrophic conditions prevailed (Hecky and Degens, 1973).

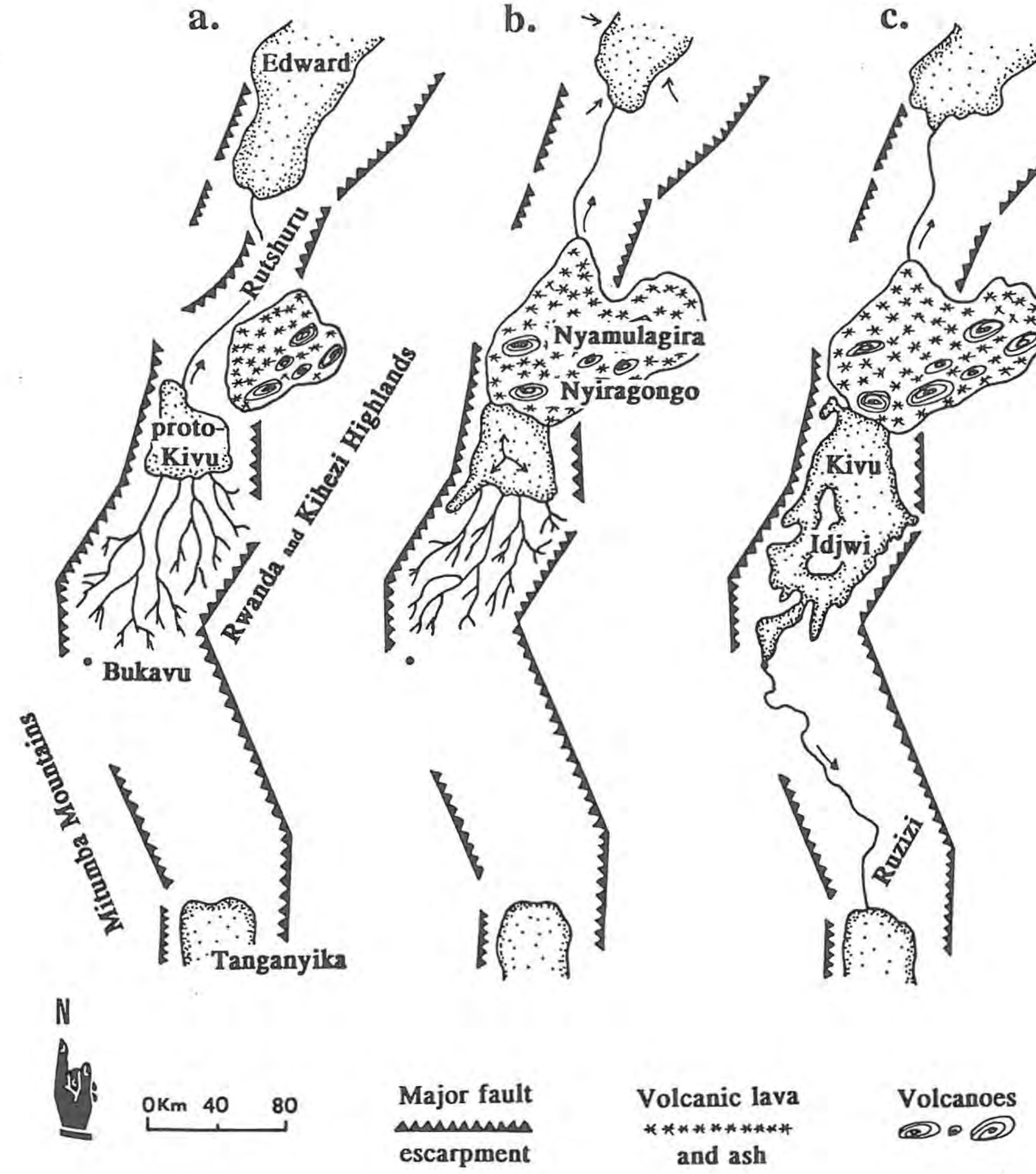


Figure 4: Changes in geology and hydrology of the Western Rift Valley between Lake Edward and Lake Tanganyika from the late Pleistocene onwards:

a) 13 000 years B.P.:Lake Kivu included only the Northern Basin, with drainage from the SE, S and SW Kivu; occasionally water overflowed towards the N via the Rutshuru River into Lake Edward.

b) 12 000 years B.P.: eruption of the Nyiragongo and Nyamulagira volcanoes blocked the northern outlet and Lake Kivu level started to rise whereas Lake Edward level dropped.

c) 10 000-9 000 years B.P.: the lake level rose to an altitude of 1 650 m and overflowed southwards via the Ruzizi River into Lake Tanganyika (from Beadle, 1981 with modifications)

Apart from the sediment deposits recorded in the Main Basin, and which are the undeniable proof of a Pliocene-Pleistocene lake existence, no indications are present of what the fauna in this basin was like (Beadle, 1981). But, as at that time the Kivu basin was shallow, splitting and reunion of small isolated lakes as well as periods of complete desiccation might have given rise to periods of speciation and extinction, in a similar way as described for Lake Victoria (Greenwood, 1964). Until the late Pleistocene, a large species flock such as those observed today in Lake Victoria or even Malawi or Tanganyika might well have diversified in Lake Kivu (Beadle, 1981).

During this shallow water stage, Lake Edward from its formation in the early Pleistocene is assumed to have been in contact with Lake Kivu until the late Pleistocene volcanic event via the Rutshuru River (Beadle, 1981)(figure 4a). The connection between these lakes most likely flowed sufficiently slowly to allow exchange of lacustrine fauna and biota (Beadle, 1981). The present-day lake Victoria, the youngest of all three lakes, originated near the end of the middle Pleistocene, and in turn, is believed to have been in contact with the Edward basin until the end of the late Pleistocene (25 000 to 30 000 years B.P.) (Fryer and Iles, 1972; Beadle, 1981)(Appendix B).

From this geological evidence it can be concluded that the fauna of Lake Kivu was not derived from ancestors which already had undergone adaptive radiation in Lake Victoria as suggested by Fryer and Iles (1972) for Lake Kivu is much older. It must also be stressed that despite the contact that might have existed between Lake Kivu, Edward and Victoria, exchange of the most derived species (i.e specialized) is believed to be almost excluded, because of increased habitat restriction with increased specialisation (Ribbink, 1991). Thus, faunal exchange could only have involved the least specialized forms of the various trophic lineages as observed today in Lake Victoria (Greenwood, 1974), but such exchange may not have occurred.

The phases of the history of Lake Kivu which resulted in its present form started at about 13 700 years B.P. (Hecky and Degens, 1973). At that time the water level started to rise and at about 12 500 years B.P. the lake was about 100 m deep. More stable stratification developed, leading to deoxygenation of the deeper water and diminishing the amount of nutrients contributed from deep water for phytoplankton production. The water was saline and alkaline and could be compared to the sodium bicarbonate lakes of the modern East African Rift Valley (Hecky and Degens, 1973), such as Lake Turkana.

At about 12 000 years B.P., the volcanoes Nyiragongo and Nyamulagira arose on the sills and their lava flows blocked the northern outlet, the upper Rutshuru River, towards Lake Edward (figure 4b) (Degens et al., 1973). This volcanic activity on the sills coincided with a moister climate, sublacustrine volcanic activity and deep water saline spring activity (Degens et al., 1973). During this first volcanic period Lake Kivu became isolated and several species disappeared both from the Lake Kivu and Lake Edward basins (Beadle, 1981).

Despite a period of lake level lowering between 11 000 and 10 000 years B.P. (figure 5) (Hecky and Degens, 1973), at the end of the Pleistocene or early Holocene (about 10 000 years B.P.) the lake level had risen to 1 650 m altitude, inundating the valleys on both sides of Idjwi (figure 4c)(Pouclet, 1978).

At about 9 400 years B.P. Lake Kivu excavated an outlet towards the south via the Ruzizi River into Lake Tanganyika (Haberyan and Hecky, 1987)(figure 4c), but faunal exchange was

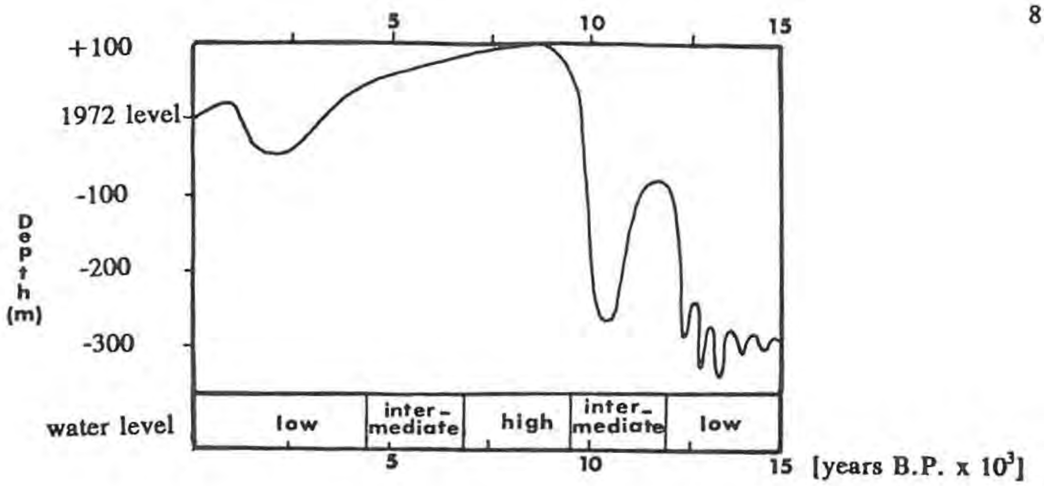


Figure 5: Reconstruction of the lake level in Kivu for the last 15 000 years (from Hecky and Degens, 1973).

prohibited by the Panzi falls (Beadle, 1981). This outlet was at a higher elevation than at present (Pouclet, 1978).

Between 9 000 and 5 500 years B.P. there was a warming trend and the thermocline became more stable as the temperature differential between the surface and deep water increased. This led to reduced mixing and lower productivity (Hecky and Degens, 1973).

Catastrophic events occurred between 5 500 and 5 000 years B.P. in the lake basin, due to increasing volcanic activity. Salinity reached 3 ppt and the lake became strongly stratified (Haberyan and Hecky, 1987). Hydrothermal spring activity in the deep anoxic water became stronger, and planktonic production fell. This drop in productivity was either due to an increase in toxic substances from hydrothermal activity or to changes in quantity and nature of food (Hecky and Degens, 1973). Sudden overturn events which introduced high concentrations of CH_4, H_2S and H^+ into the surface waters probably resulted in sudden faunal extinctions as indicated by the sharpness of the sedimentary changes (Haberyan and Hecky, 1987). This short geological period most likely represented a second major extinction period for the fauna within the Lake Kivu Basin.

At about 4 000 years B.P. a dryer and cooler period began and the outlet towards the north became interrupted, resulting in a closed basin at about 3 500 years B.P. The surface waters became cooler and more saline; hydrothermal gases and heavy metals of the lower anoxic water body, rich in nitrogen and phosphorus, gradually mixed with the surface waters and gave rise to intense primary production (Hecky and Degens, 1973).

A wetter and warmer climate followed this cooler mixing period and at about 1 200 years B.P. the lake was reopened towards the south (Hecky and Degens, 1973). Another pulse of hydrothermal and volcanic activity reestablished the thermohaline structure, which has persisted up to the present (Hecky and Degens, 1973).

In conclusion, since the late Pleistocene volcanic events and related two major extinction phases, Lake Kivu has become an isolated basin. Repopulation of the present day lake from Lakes Edward or Victoria could not possibly have taken place as since then, the Virunga volcanoes prevented any faunal exchange. The absence of truly limnitic zooplankton (Dumont, 1986) in the pelagic zone also supports the hypothesis of the destruction of the biotic system of the ancestral lake basin and its complete isolation since then. The Lake Kivu ichthyofauna fauna we are perceiving today must therefore be considered as the remnant of a previously older lake fauna, with no possible recent members from any other major water body. The only chance that some fraction of the endemic lake fauna could have survived extinction periods would be by rapid dispersion in surrounding stable riverine environments (Thys van den Audenaerde et al., 1982). However, as clearly pointed out by Kornfield and Echelle (1984), extant endemic fish faunas are never found in the riverine environments as reduced volume and spatial complexities would have inhibited colonisation by spatially specialized lacustrine species. Therefore, only trophic generalized lacustrine species could have survived a transition in surrounding rivers and have been the seed for new recolonizations during the stable phases of the lake.

Today, of the Virunga Volcano Chain, the two volcanoes situated at the western end are still active (figure 4). The latest eruption of the Nyiragongo (3 470 m) occurred in 1976. The Nyamulagira (3 056 m), with its several associated vents, has been erupting at intervals since first discovered by a European in 1894. The most violent eruption occurred between 1938 and 1940, when a lava flow of more than 100 km in area (Beadle, 1981) flowed southwards towards Sake where it eventually poured into Lake Kivu (figure 6). The bay of Kabuno was almost cut off from the Main Basin, but a connecting channel 150 m wide and 15 m deep remained. This event destroyed the entire fauna within the bay, which has subsequently been repopulated through the connecting channel (Verbeke, 1957a).

The latest eruption of a vent of the Nyamulagira volcano started in May 1989 and was active for about two months (figure 2). Volcanic activity seems over time to be moving towards the west and it is believed that in the future new volcanoes may arise in the Massissi Mountains (pers. comm. Shohei Hirose), and thus move away from the Lake Kivu basin.

The five other volcanoes (figure 4), of which the Mikeno is the oldest having first erupted about 100 000 years ago, are extinct. They are magnificent remnants of a chaotic geological period and display a unique alpine vegetation which has become the last refuge of the mountain gorilla, *Gorilla gorilla graueri.*

Figure 6: The lava flow from the Nyamulagira volcano (1938-1940) almost cut the Basin of Kabuno from the Main Basin.

3. Limnology

After the destructions of the biotic system of the ancestral lake basin and its complete isolation since then, the Kivu basin became transformed into an oligothrophic lake. Several limnological features of the present day lake are responsible for the poverty of its fauna.

Lake Kivu is a striking example of a meromictic lake, showing a distinct permanent stratification (Beadle, 1981). It is the most firmly stratified lake known of Africa (Beadle, 1981). A number of separate layers can be distinguished, each possessing an exceptional constancy of measured parameters (mixed layers) and layers with a very marked variation within a small depth interval (gradient layers) (figure 7). There are seven well mixed layers (ML) and six gradient layers (GL) (Tietze, 1981). This condition is explained by deep seepage of warm saline water of volcanic origin (Degens et al., 1973). The warm water has a higher density than the surface water, and because of the heat transported into the lake a so-called "double diffusive convection " develops, giving rise to the various GL and ML (Tietze, 1981).

Water density increases down to a depth of 50 m due to a decrease in temperature. Below that it increases due to increasing salt content, though this effect is somewhat reduced because temperature increases too (figure 7).

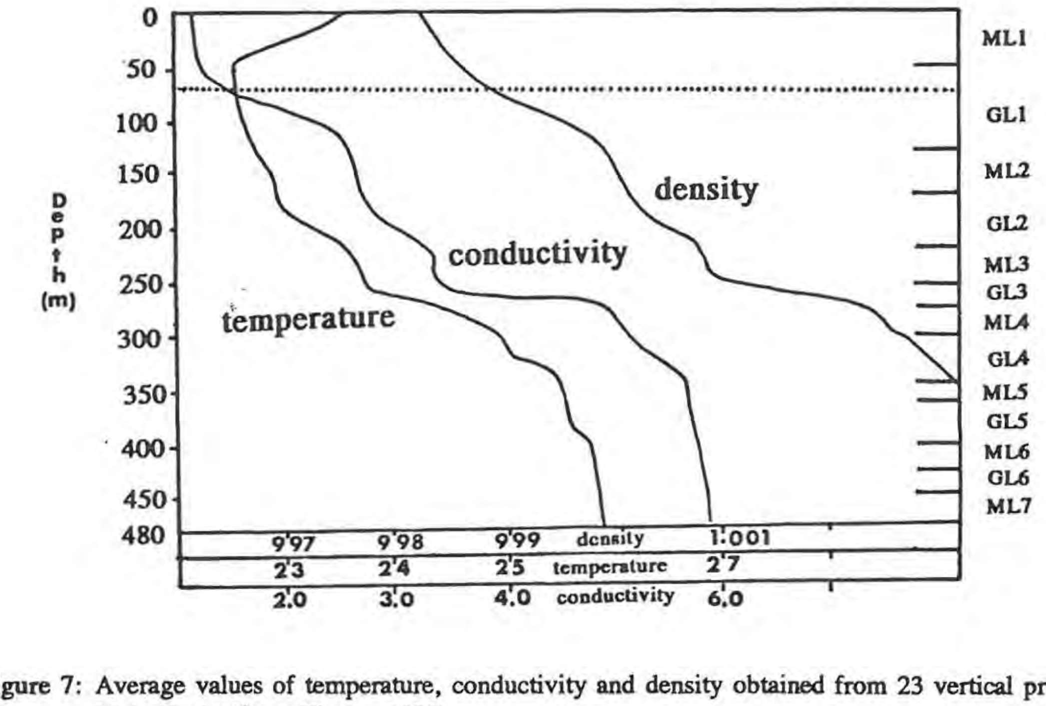


Figure 7: Average values of temperature, conductivity and density obtained from 23 vertical profiles in the Main Basin (from Tietze, 1981).

An expected thermal gradient exists in the lake down to a depth of 50 m, with temperature decreasing with depth (figure 7). At about 35 m a temperature gradient layer, called metalimnion, exists which can shift in depth down to 50 to 70 m and may also vary in structure. The lake has a distinct epilimnion, metalimnion and hypolimnion. The water freely mixes to a depth of 50 to 70 m, as can be seen from the conductivity curve which shows a homogeneous condition down to this depth (figure 7). Below 50 to 70 m the stratification remains stable. Lake Kivu can therefore be regarded as a lake of about 70 m deep floating upon a dense and more saline water (Beadle, 1981). Most of the nutrients become locked into the stagnant water body leaving the pelagic environment, which covers 90% of the lake surface, depleted of nutrients (Verbeke, 1957a).

Towards the end of the dry, cooler and windy seasons, however, a small amount of mixing between ML1 and GL1 in the Great Lake results in an annual outburst of production as judged by the decrease in transparency of the water and increased quantity of zooplankton (Damas, 1937; Verbeke, 1957a) (figure 8).

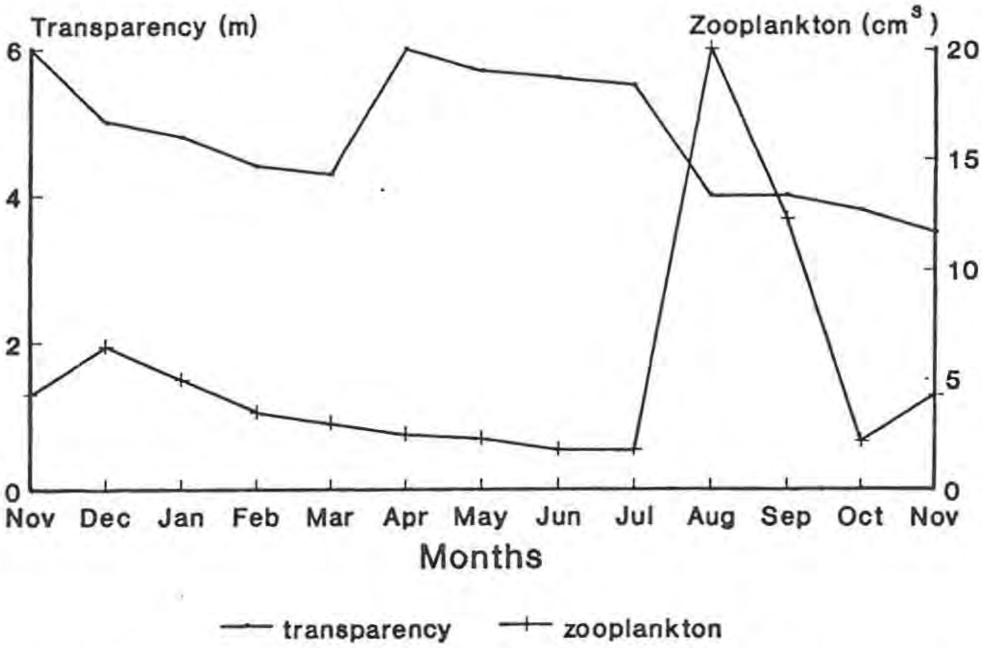


Figure 8: Variation in transparency and in the quantity of zooplankton over a one year period in Lake Kivu (from Verbeke, 1957a.)

Close to the exposed shoreline, transparency values do not differ much from those observed in the open water, but in some protected bays they are lower and are indicative of different ecological conditions, such as accumulation of organic material, reduced water agitation, shallow depth, higher water temperatures and higher salinities, rapid oxygen decrease with depth and abundant phyto- and zooplankton. The transparency and colour values in these cases vary from bay to bay (Verbeke, 1957a). The Bay of Kabuno is a striking example, as when entered from the Main Lake via the narrow pass, the water colour changes from predominantly blue to mainly green.

The dissolved oxygen profile is given in figure 9. In the upper 20 m oxygen remains constant during the whole year and varies between 6 and 7.5 mg/l, i.e. 85 to 110 % saturation. The lower limit of oxygen changes during the various seasons (Tietze, 1981) and from basin to basin (Verbeke, 1957a). In general, the oxygen concentration decreases rapidly below 50 m to become zero at 70 m (Tietze, 1981).

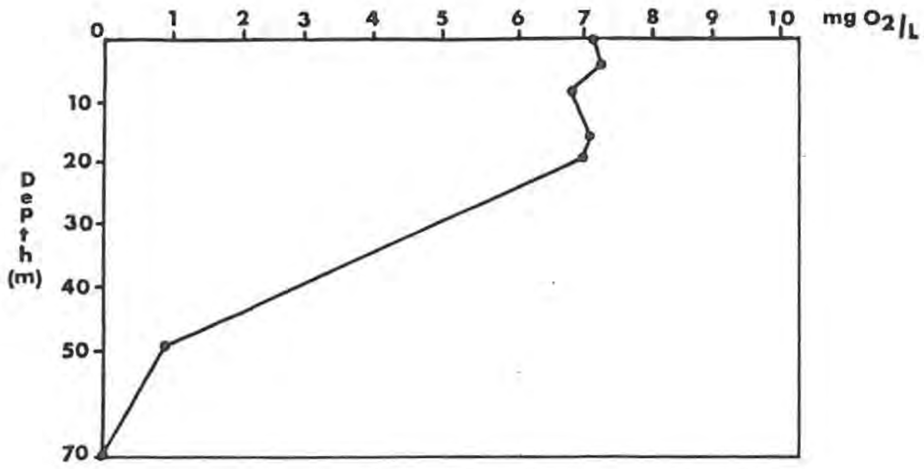


Figure 9: Dissolved oxygen profile of Lake Kivu (from Damas, 1937).

Total salinity is 1.0 g/l at the surface and 1.35 g/l at 90 m deep (Verbeke, 1957a). The high alkalinity of the water, associated with the high salinity most likely diminishes photosynthesis in phytoplankton and thus primary production (Beadle, 1981). This lowered phytoplankton production, together with the loss of organic productivity from the uppermost layer to the stagnant water below contribute to the lake's oligothrophic condition. Life can only thrive in the upper 50 to 70 m because of the strong stratification features preventing oxygen penetration into the deeper waters of the lake.

In the stagnant anoxic water below 70 m, gases of organic and volcanic origin accumulate, such as dissolved methane, carbon dioxide, nitrogen and hydrogen sulphide. These toxic gases could lead to mass destruction of the fauna during violent stormy weather, bringing water to the surface from the stagnant anoxic and toxic gas charged layers, such as reported from many tropical lakes (Beadle, 1981). However, owing to the very steep density gradient, the stability of the lake appears sufficient to resist disturbance by violent weather (Beadle, 1981).

Although Lake Kivu is most likely still close to its pristine condition, during the past 22 years there has been a trend towards increased transparency (table 1). The water is alkaline but over recent time has also shown a tendency to become more acid. In 1957 the pH in the Main Basin fluctuated between 9.1 and 9.3 (Verbeke, 1957a), whereas in 1980 the pH measurements taken in front of Gisenyi were between 8.2 and 8.8 (de Iongh-Spliethoff and de Iongh, 1980). Some pH measurements made by myself along the coastline of Goma (1988-1989) also showed a pH between 8 and 9. These small changes in both parameters are the first symptoms of water pollution due to human activity around the lake basin (Reyntjens, 1982).

Table 1: Change in transparency within the last 22 years measured by different authors in the Main Basin.

Author	Stratification period Rainy season	Mixing period Dry season
Verbeke (1957a)	4.25 - 6 m	3.5 - 4 m
de Iongh-Spliethoff and de Iongh (1980)	5.5 - 8 m	-
Own observations (1988-1989)	9 - 12 m	6.5 - 8 m

4. Biotopes and their associated faunas.

"*A rich milieu in which all resources occur in large amounts will tend to favour the development of specialists, whereas an impoverished milieu favour generalists*" (Allen, 1976). The biotopes of Lake Kivu are restricted in range and diversity because of the nature of the substratum and the shape of the basin (Van der Ben, 1959). The uniformity of the physical environment might have contributed to the poverty of the Lake Kivu fauna and have hampered diversification to take place.

SUBSTRATUM: A unique feature of Lake Kivu is that independent of the substrate type, the bottom of the lake down to 35 m is covered by calcareous magnesium rich deposits which precipitate because of the water's richness in alkaline elements (Verbeke, 1957a). The deposits limit the development of the aquatic vegetation and have important consequences on the biology of the lake by for example inhibiting the diversification of organisms which biology is dependant on unconsolidated sand or mud (Van der Ben, 1959).

SHAPE OF THE BASIN: Lake Kivu is situated in a trough with very steep sides (Appendix C). The 70 m contour is so close to the shore that only 12% of the total area of the bottom is in contact with the oxygenated waters. The endemic ichthyofauna, especially the haplochromines which are mainly substratum dwellers (Thys van den Audenaerde et al., 1982), thrive within this restricted narrow zone (Verbeke, 1957a). The pelagic environment is devoid of fish apart from *Limnothrissa miodon* (so-called Lumpu) introduced in the early sixties (Collart, 1960).

The ecological factors which determine the distribution of the flora and fauna within the narrow coastal zone are depth, water agitation and bottom type (Van der Ben, 1959).

90% of the shoreline consists of a rocky surface covered, as mentioned above, by calcareous magnesium rich deposits and an algal mat of *Cladophera*, leaving 10% for sandy to muddy environments covered by macrophytes (Verbeke, 1957a). Photosynthesis is limited to 8 m and restricts the extent of *Cladophera* growth down to this depth (Van der Ben, 1959). Depending on the exposure and dip of the rocky shore, the degree of water agitation varies resulting in two biotopes with similar vegetation but different fauna as follows (Verbeke, 1957a):

- firstly, wave washed areas characterised by steeply dipping slopes exposed to strong water agitation (0 to 5 m deep). Organic material is completely absent and variation in water temperature is limited because of the permanent contact with the open lake. The oxygen content is always high. The fauna present are comparable to those of running water and are characterized by non-swimming, but climbing invertebrates which are adapted to adhere to the substratum (table 2).

- secondly, more sheltered areas characterized by slowly dipping slopes and reduced water agitation. Organic material may be present, temperature variations may be high, and the oxygen concentration is lower compared to the exposed zone. This environment is often mixed with patches of macrophytic vegetation and could be called an intermediate zone between the exposed rocky environment and the more sheltered vegetation zones. Almost the same fauna is found as in the exposed environment but the abundance of the invertebrate fauna changes. However, Turbellaria are completely absent (table 2).

Table 2: The invertebrate fauna in the two main littoral environments: the rocky and sandy shores (summarised from Verbeke, 1957a).

Bottom type:	Rocky		Sandy to muddy	
Vegetation:	Cladophera carpet		Macrophytes	
Water agitation:	Strong	Low	Strong	Low
Fauna				
Turbellaria	+++	-	-	-
Hirudinea	+++	++	-	-
Oligochaeta	+	+++	-	-
Nematoda	+	+++	-	-
Cladocera	+	+++	-	-
Ostracoda	+	+++	-	-
Copepoda	+	+++	-	-
Decapoda	-	+++	++	+++
Acarina	++	+++	-	-
Collembola	++	?	+++	+++
Ephemeroptera	+++	+++++	+++++	+++++
Odonata	+	+++	(++)	(+++)
Hemiptera	-	+++	++	+++
Trichoptera (larvae)	+++++	+++	+	+
Coleoptera	+	+++	+	+
Diptera total	+++	+	-	-
Chironomidae	+++++	+++	+++++	+++++
Gastropoda	++	+	++	++

Legend: +++++: typical +++: abundant ++: common +: rare -: absent

The uniformity of the *Cladophera* carpet, as suggested by Verbeke (1957a), is presumably an underestimate of the number of algal species present. But, because of the lake's recent instability, the algae are likely to be less species rich, as for example in Lake Malawi, where the algal mat is comprised of 41 different components (Reinthal, 1990).

At the mouths of the rivers and in protected bays a sandy to muddy substratum covered by macrophytes predominates. This zone can again be subdivided into two major biotopes (Verbeke, 1957a):

- firstly, an environment with little accumulation of organic material and moderate agitation,
- secondly, one with high accumulation of organic material, close to the river mouths.

These two conditions are associated with different bottom types, temperature, oxygen concentration, salinity, nitrate content, water transparency, turbidity and therefore phytoplankton production and food availability. A theoretical transect across the macrophytes along the shore of Lake Kivu is illustrated in figure 10. The invertebrate fauna composition for the two types of biotopes is given in table 2. Again, the species composition in both biotopes is very similar and only the abundance of the fauna changes. Interestingly, the fauna associated with the macrophytes is less diverse when compared to that with the *Cladophera* and is likely to affect fish distribution.

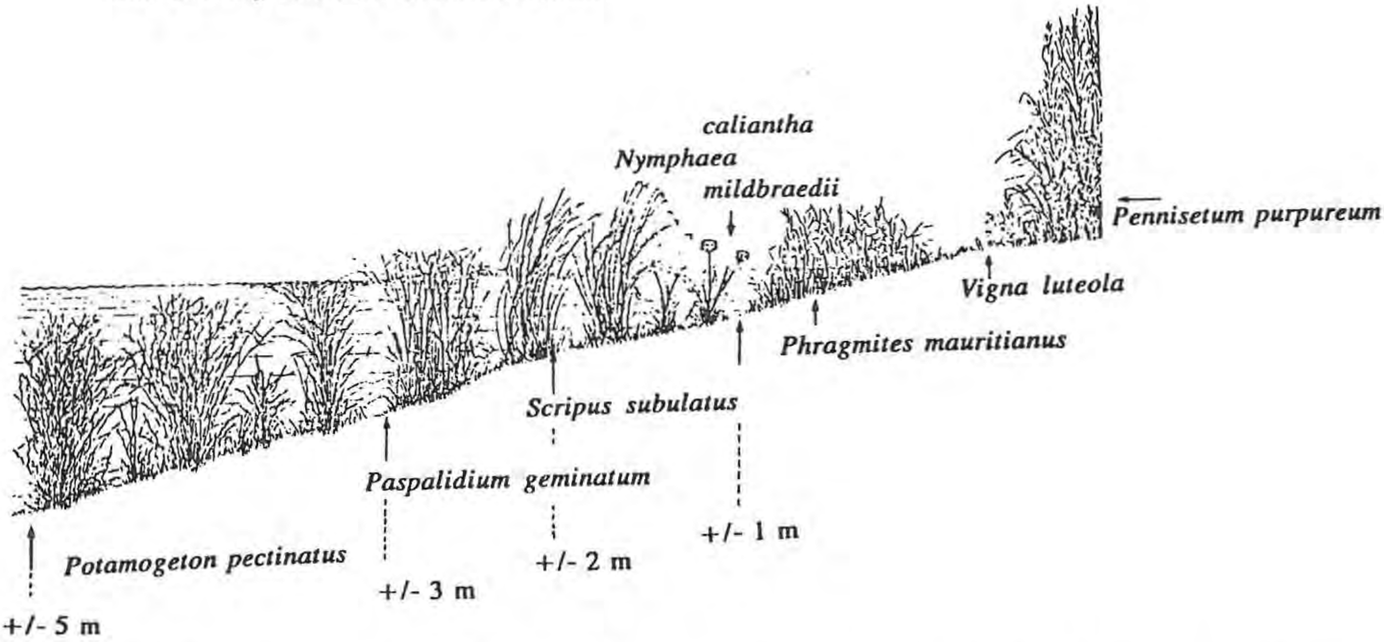


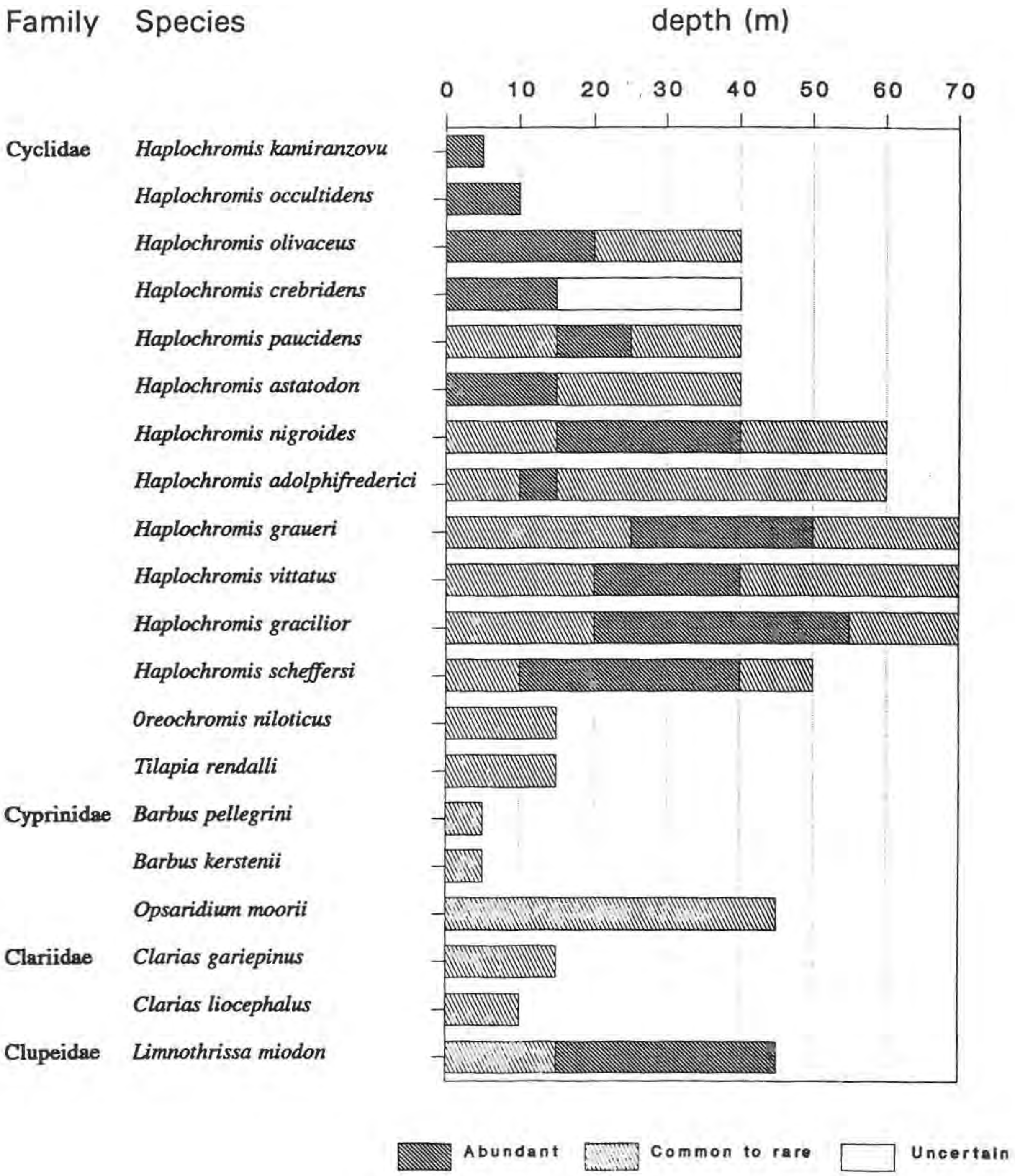
Figure 10: A theoretical transect through the macrophytic environment along the sandy to muddy shoreline of Lake Kivu (from Van der Ben, 1959).

In the algal zone, Chironomidae, Ephemeroptera and Trichoptera larvae are quantitatively equivalent and their total represent the most important fraction of the invertebrate fauna. Their total life weight is 100 kg/hectare/generation (Verbeke, 1957a). In the macrophytic environment, the Chironomidae and Ephemeroptera larvae represent the greatest biomass of 60 kg/hectare/generation (Verbeke, 1957a).

It is interesting to note that the invertebrate fauna of Lake Kivu is much more speciose than the ichthyofauna. This phenomenon is most likely explained by the ease of dispersion and transport of these organisms which allowed them to invade more readily new and vacant biotopes during periods of lake stability (Verbeke, 1957b).

The surface water of the lake are inhabited by Copepoda and Cladocera (Verbeke, 1957a). This zooplankton community is variably distributed within the lake (Kiss, 1966), but in general, the volume of the zooplankton reaches a maximum twice a year in response to strong water agitation (figure 8) (Verbeke, 1957a). In contrast with the plankton blooms during the windy seasons, the macrophytes and *Cladophera* carpet become highly reduced (Van der Ben, 1959). The latter represent an essential food source for the haplochromine community (Verbeke, 1957a). This alternative cycle of plankton blooms during the windy seasons and *Cladophera* vegetation during the rainy seasons are likely to have an important influence on the biology of the haplochromines.

Table 3 : A preliminary inventory of depth distribution of the Lake Kivu ichthyofauna [summarised from Vervoort (1981), Thys van den Audenaerde et al. (1982), Ulyel (1991) and own observations].



The ichthyofauna occupies the narrow stretch of coastline between 0 and 70 m deep (table 3). Within this narrow habitat range, the haplochromines display the broadest distribution with each species showing its own depth preference. This depth preference is wide when compared to that of some of the highly stenotopic rock dwelling species of Lake Malawi, which live within a five meter depth range (Ribbink, 1991). But it nevertheless demonstrates that within the Lake Kivu basin, the haplochromines have invaded most successfully the lake in a similar way as in the other East African Rift Lakes and show the widest diversification with respect to habitat preference.

Although some haplochromine species, such as *Haplochromis graueri* and *vittatus*, extend their depth range to the oxygen limit (Vervoort, 1981), all members of the haplochromine flock are believed to be dependant on the littoral zone for optimal breeding (personal observations). This is in contrast with the other East African Rift Lakes where many species occur in deep water for their entire life cycle, such as for example the deep dwelling cichlids of Lake Tanganyika (Coulter, 1966). The dependence of all Lake Kivu haplochromines on the nutrient rich oxygenated waters of the littoral, especially for breeding, supports the hypothesis suggesting a fairly recent descendants of the present day haplochromines from riverine ancestral species.

III. Study Area: Tshegera Island.

1. Introduction.

The inside of Tshegera Island (figure 11), situated at the north-west of Lake Kivu (figure 1) was chosen as the study site. This island represents the crater of an ancient volcano (caldera) and forms the northern limit of the Virunga National Game Park. The selection of this site for research had the following advantages: the island was isolated from the mainland by 100 m deep water (Appendix C) and was not inhabited by humans. Fishing activities were limited to artisanal fishermen using traditional fishing methods as for example hand-made gillnets and ropes with hooks. They did not use the more destructive fishing methods such as dynamite or poison which are commonly used along the coastline. Other advantages of the study site were its close proximity to the laboratory, the protection it afforded from storms so that the gill nets could be set out year round independent of the weather and its small size made it manageable.

Fishing activities and most diving observations were limited to 10 m deep. The algal zone in the coastal water, which does not extend beyond 10 m, represents the breeding grounds of the haplochromines. It is also believed that the algae and associated invertebrate fauna are an essential food source for the ichthyofauna (Verbeke, 1957a). In addition, diving duration in this depth zone is unlimited with respect to decompression times.

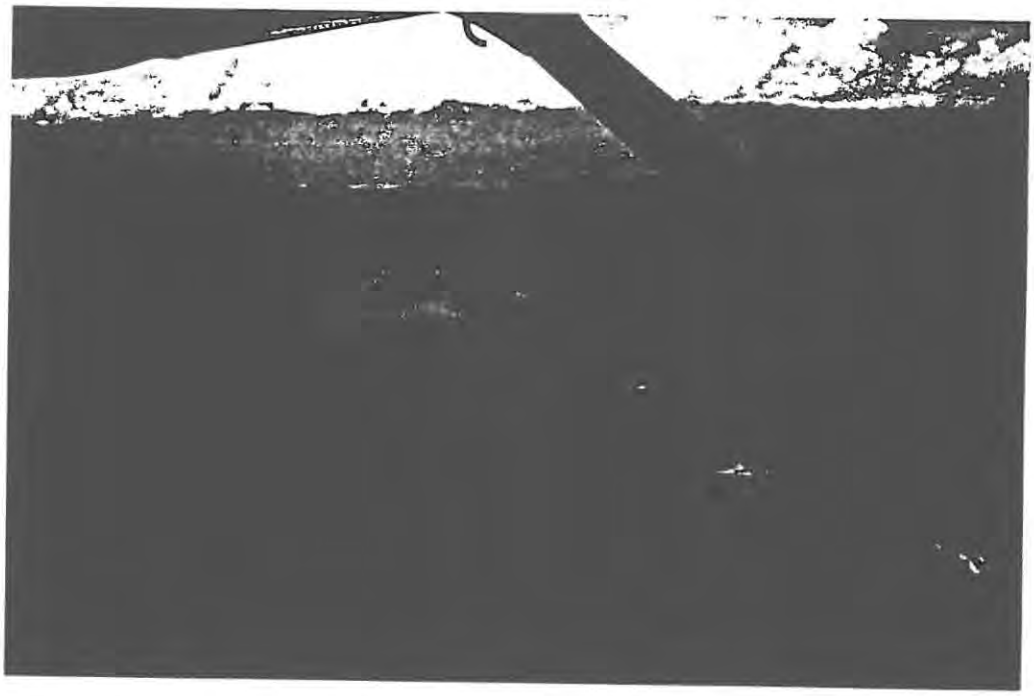
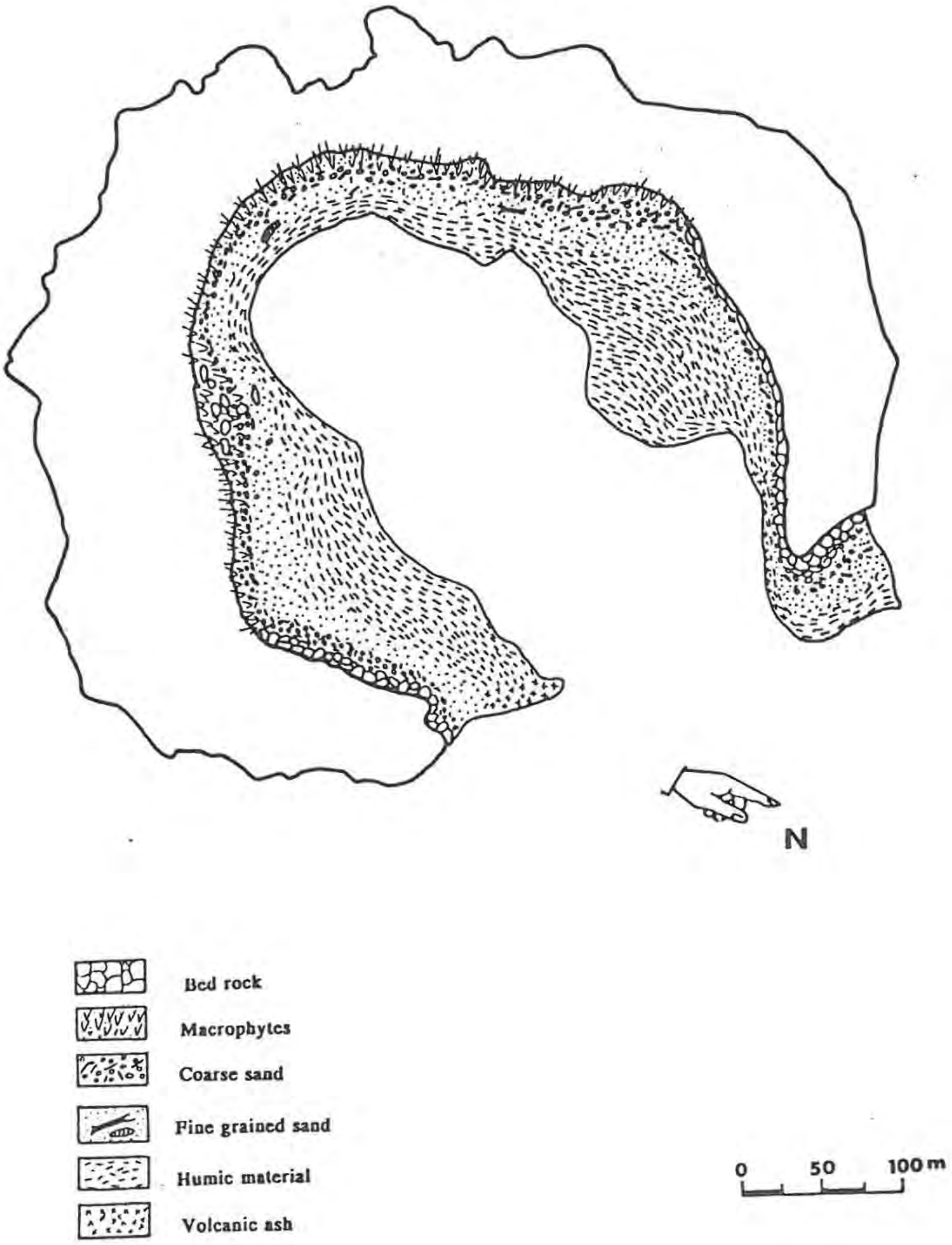


Figure 11: Thsegera Island situated along the north-west coast of Lake Kivu.

(b)


N
Bed rock
Macrophytes
Coarse sand
Fine grained sand
Humic material
Volcanic ash
0
50
100 m

2. Physiographic features of Tshegera Island.

A depth and a bottom type profile of the caldera was established. From an aerial photograph 20 sites with recognition points on the island were chosen. At each site a depth profile to 10 m was taken with an echosounder, checked beforehand with a depth meter using scuba. A 100 m rope with knots every 10 m was attached to a branch on the coastline. The depth was measured every 10 m perpendicular from the coastline until a depth of 10 m was reached. The bathometric map is illustrated in figure 12a.

To obtain a bottom type profile, I swam with a depth meter, a slate and a compass perpendicular from the coastline at each of the 20 sites to 10 m depth. Change in substrate in relation to depth was noted on the slate. Each transect was immediately copied onto a note book in the boat. The bottom type map is presented in figure 12b.

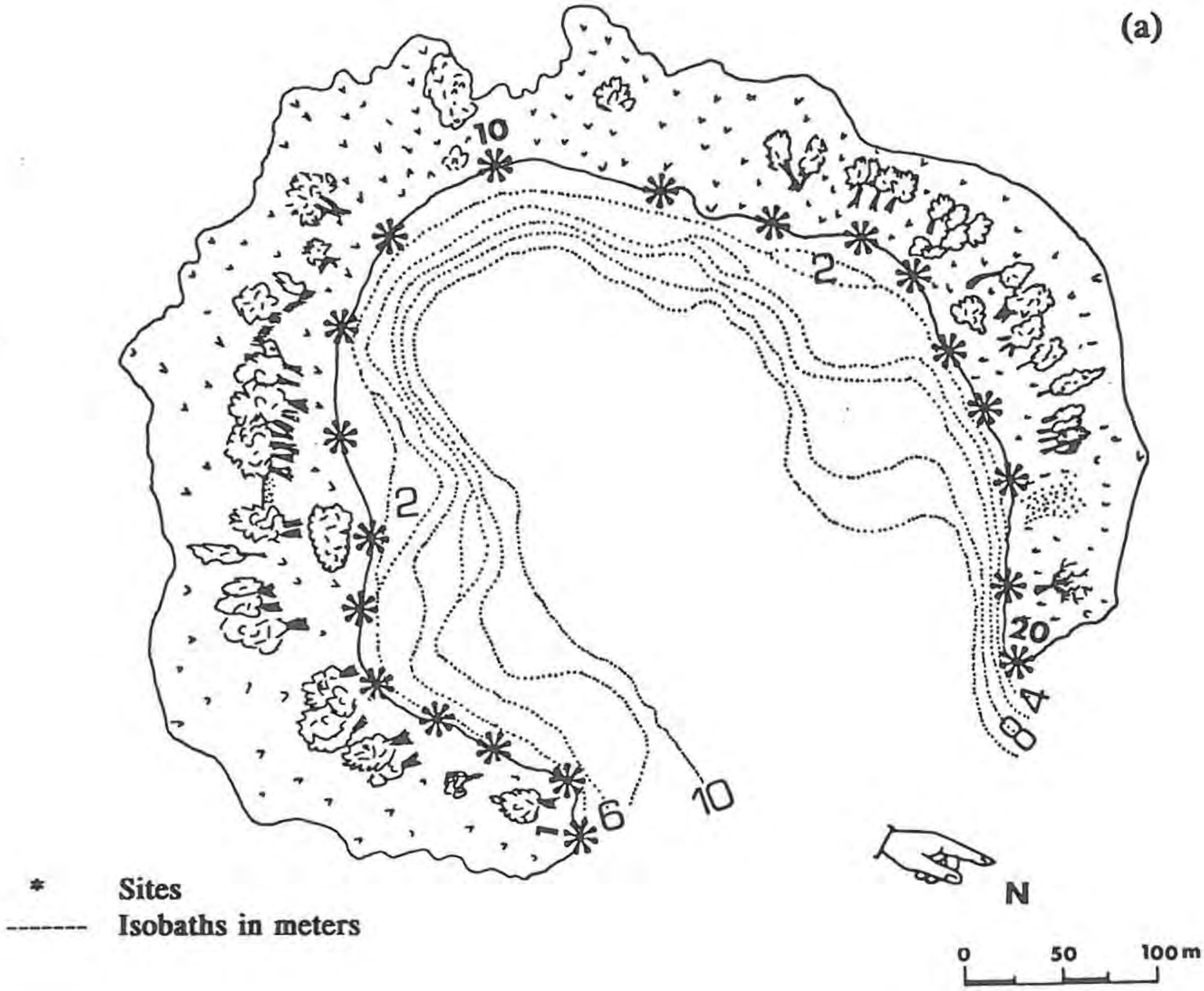


Figure 12: (a) Bathometric map and (b) bottom type map of the coastal zone at Thsegera Island.

Within the study area a moderately exposed rocky and sandy shore was present:

i. The rocky shore.

This environment is situated at the north-eastern and north-western arms of the crater, towards the subsided sides of the caldera (figures 12b). Rocks of all shapes and sizes, exclusively volcanic basalt, occurred in profusion on the bottom successively composed of bed rock, bolders, pebbles, coarse gravel and occasionally volcanic ash as moving from the shore to deeper water. The slopes of the rocky zone at the extremities of the north-eastern and north-western arms were abrupt down to six meters, after which they became more gradual (figure 12a). Towards the vegetation zone, the slope from the coastline onwards was gentle, and resembled the intermediate zone described on page 13.

At some time on almost any day of the year the water among the rocks was in a state of turbulence due to wave action. In calm conditions, the configuration of the bottom could be seen from the surface to 10 m deep when viewed with a mask. During windy periods, the visibility decreased from the tips of the north-eastern and north-western arms towards the inside of the crater.

Macrophytic vegetation was entirely lacking due to the nature of the substratum. The upper surfaces of the rocks were covered by an algal mat of *Cladophera*. The entire felt represented "Aufwuchs" and, as described by Fryer (1959) for Lake Malawi, is believed to be of fundamental importance in the biological economy of the rocky shore (Verbeke, 1957a & b).

ii. The sandy shore.

The sandy shore pitched very gently to 10 m depth (figure 12a & b). Close to the shoreline the yellowish brown sand was fairly fine grained and compact, becoming darker and more humic away from the coast. It was a monotonous substratum, apart from an area between three and five meters where occasionally mineralised tree stumps and isolated boulders were observed.

The water while clear during periods of calm weather could become at times very turbid during long windy periods, although breakers never reached the inshore coastline.

Along the shoreline macrophytes were represented by *Pennisetum purpureum, Phragmites mauritianus* and *Scirpus subulatus*. *Pennisetum* only occurred on the dry land along the water edge and *Phragmites* in shallow water of 0.50 m deep, whereas *Scirpus* extended further into the deeper water up to sometimes 10 m from the coastline. Macrophytes were most extensive in the southern bay of the crater and became reduced to a very thin fringe towards the rocky zones. The straplike leaves of the *Scirpus* vegetation were probably coated with a periphyton community (Aufwuchs), as haplochromine fish were observed to scrape and pick the leaves in a similar way as was observed on the *Cladophera* carpet in the rocky zone.

The substratum of both the rocky and sandy shore beyond eight meters deep was very similar: the slope pitched slowly down to 30 m towards the centre of the crater where the bottom surface became covered by an increasingly thick layer of decomposed humic material (at least one meter thick).

3. Related faunas.

Despite the isolation of the island, the ichthyofauna within the coastal water of Tshegera was found to be comparable to that observed along the main northern coast of the lake. This wide range in distribution is an essential feature of the Lake Kivu haplochromines. It accentuates their generalized nature compared to the haplochromines of the other East African Rift Lakes where regional endemicity, as illustrated by the Mbuna of Lake Malawi (Ribbink, 1991), is a hallmark of the haplochromine flocks.

Because of this lake wide dispersal of the Lake Kivu ichthyofauna in general, it is assumed that any observations made on the island on fish distribution, inter and intraspecific competition for food and breeding sites, shelter from predators and timing of breeding and breeding behaviour within the specified habitats can be safely extrapolated to similar sites along the northern coast. This makes Tshegera Island an ideal site for a biological study on the ichthyofauna of Lake Kivu.

Along both rocky and sandy coastal biotopes of Tshegera Island, the haplochromines were the most numerous fishes. All other species appeared to be "visitors" and included breeding *Tilapia* species; the sardine, *Limnothrissa miodon*, feeding in schools in early evening and morning; the solitary catfish, *Clarias gariepinus*, and at night the Tanganyican *Opsaridium moorii* and various *Barbus* species. *Clarias liocephalus* was rarely observed hiding within crevices of the rocky zone.

Beyond 10 m depth, small, pale coloured haplochromines (mainly *Haplochromis sheffersi* and *Haplochromis gracilior*) swam in small groups close to the light brown substratum from which they fed. The breeding territories of these fishes were never observed on this soft humic surface, but rather closer towards the coast between 8 and 10 m deep. Within this small depth range brightly coloured haplochromine males protected their breeding sites which consisted of shallow hollows scraped into the substratum. Other species occasionally encountered beyond the 10 m isobath were tilapiine species and on two occasions a large (700 to 800 mm) white catfish. The latter was most likely an albino *Clarias gariepinus* (pers. comm. Snoeks). *Barbus altianalis* was observed once during a dive beyond 30 m in between the two northern extremities of eastern and western arms of the island.

Common birds of prey fishing in the coastal waters were the Pied Kingfisher, *Ceryle rudis*, two egret species, the Great White Egret, *Egretta alba* and the Little Egret, *Egretta garzetta* and two cormorant species, *Phalacrocorax carbo* and *Phalacrocorax africanus*. Other fish-eating birds such as the Fish Eagle, *Haliaeetus vocifer*, and the Black Kite, *Milvus migrans* were also seen occasionally and probably took fish from time to time. At night large flocks of the Hadada, *Bostrychia hagedash*, came to rest on the trees of the island.

IV. TAXONOMY

> *"It is self evident that until it is possible to identify an animal much of the value of any observations that may be made on it is lost" (Fryer and Isles, 1972).*

1. Introduction.

The taxonomy of the haplochromine flocks in the East African Rift Lakes is beset with many difficulties (Fryer and Isles, 1972; Barel et al, 1977; Greenwood, 1979; Ribbink et al., 1983; Snoeks, 1986a). The central problem lies in the fact that within a related group the differences in external morphology are often clustered within a very narrow range. Further, the haplochromine species demonstrate a relatively great intraspecific variation for most characters (Greenwood, 1974; Barel et al., 1977).

Before starting any ecological work it was decided that a sound basis of the taxonomy of the haplochromine fish of Lake Kivu was essential. Prior to this study some knowledge was built up on the diversity of the species flock by consulting the reference collection of De Vos (Gisenyi, Rwanda), and by using the keys established by Coenen (1979) and Snoeks (1985b) (Koninglijk Museum voor Midden Afrika, KMMA). Although the species flock of Lake Kivu is very small compared to those of Lake Victoria, Tanganyika or Malawi (Appendix B), its taxonomic status has been highly confused (Snoeks, 1986a; Thys van den Audenaerde et al., 1982). When this study was started the taxonomy of the Lake Kivu haplochromines was not sorted out yet, with many uncertainties about the true identity of some species and special care had to be taken in the choice of my species. Twice prior to this study, I started biological observations on a species which after a few months appeared to be a species complex, namely *H. kamiranzovu* (confirmed by pers. comm. De Vos) and *H. scheffersi* (confirmed by pers.comm. Snoeks).

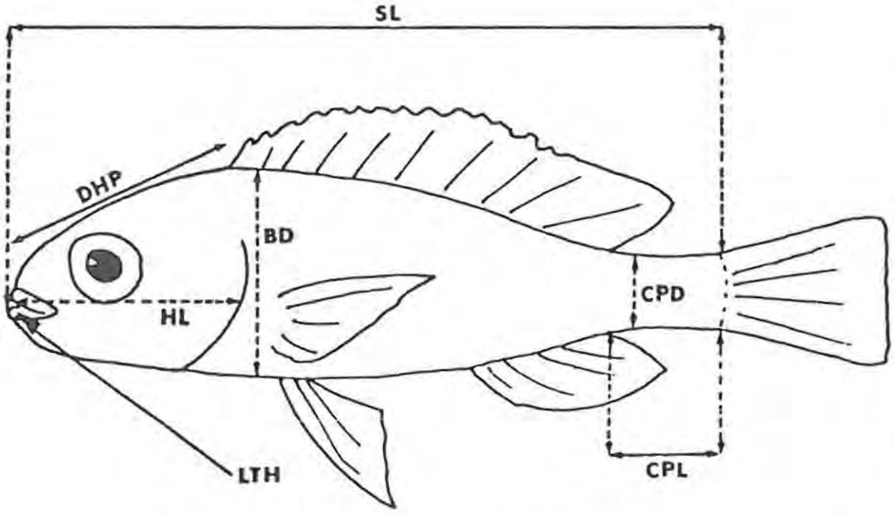
The criteria used for species distinction in this study are based on the Recognition Concept, which says that each species shares a common Specific Mate Recognition System (SMRS) (Paterson, 1978). The SMRS ensures effective syngamy between conspecific partners within their preferred habitat and involves anatomical, behavioural and ecological co-adaptations of a species. As mine is an ecological study, only those anatomical features which showed a significant difference and were readily recognized were selected. These involved dentition, general head and body shape and colour. Ecological data on breeding seasonality, preferred brooding and breeding sites and habitat preference confirmed the reproductive 'isolation' of each species.

On the basis of morphological characters, the species are classified according to Greenwood's 'genera' (Greenwood, 1979 & 1980). In this classification haplochromine species from lakes Victoria, Kioga, Nabugabo, Edward, George and Kivu are considered to belong to a superflock, comprising several lineages characterised by derived features unique to its members. Although incomplete (Greenwood, 1980), not generally accepted (Hoogerhoud et al., 1983; Witte, 1984; Verheyen, 1989) and considered not entirely satisfactory by the author himself, this classification has the advantage of relating the ill-defined haplochromine group which includes more than 300 species into monophyletic lineages which are delimited using a Hennigian approach. This classification has an evolutionary value as it allows characters to be recognized as being primitive (plesiomorphic) or derived (apomorphic) and allows relationships to be based only on shared derived characters (synapomorphies). By using this classification some knowledge can be obtained on the level of diversification achieved in the species studied and allows them to be compared with the haplochromines of the other East African Rift Lakes. As Greenwood's generic names are only used in an evolutionary context, they are placed between quotation marks; otherwise the pre-Greenwood concept of *Haplochromis* is retained.

2. Characters used in species' identification.

i. Body and head shape.

The generalized *haplochromis* body and head shape cloaks a wide variety of trophic specialisations (Greenwood, 1974). Nevertheless, body depth, dorsal head profile, head length, lip thickening, body elongation and compression and caudal peduncle length and depth as illustrated in figure 13 were found to be useful identification features (Barel et al., 1977).



BD = Body Depth
CPD = Caudal Peduncle Depth
CPL = Caudal Peduncle Length
DHP = Dorsal Head Profile
HL = Head Length
LTH = Lip Thickening
SL = Standard Length

Figure 13: Characteristics of body and head shape used to differentiate the various species. They can be observed without measurements to be taken and enable quick identification of the species in the field (from Barel et al., 1977).

ii. Dentition.

"It is in the head and dentition that the real diversity of these [haplochromine] species becomes apparent, and in which lies the evolutionary success of the Haplochromis species flock" (Greenwood, 1974). Trophic radiation, so characteristic to all cichlids, has been achieved by diversification of a basic and generalized dentition found in ancestral fluviatile species. The greater the change from this basic dentition, the greater the degree of diversification. Tooth examination has therefore an important evolutionary significance. It also has an important taxonomic value as tooth morphology is a species specific character (Barel et al., 1977) enabling fast and reliable identification of the species.

Teeth are borne on the upper and lower jaw (premaxilla and dentary bones) and on the upper and lower pharyngeal bone. However, only the oral dentition was used in species identification. The pharyngeal bone and its teeth were decided to be unreliable diagnostic features as intraspecific differences were often found to be larger than between the species, depending on the size of the fish. Also, dissecting out the bone involved too much time in order to be used as a key element in identification.

Although the range in tooth structure is very great in the cichlids, teeth are basically of three types: unicuspid (or conical), bicuspid and tricuspid (Barel et al., 1977)(figure 14a). Tooth form is described using a binocular microscope and tooth nomenclature is given in figure 14b.

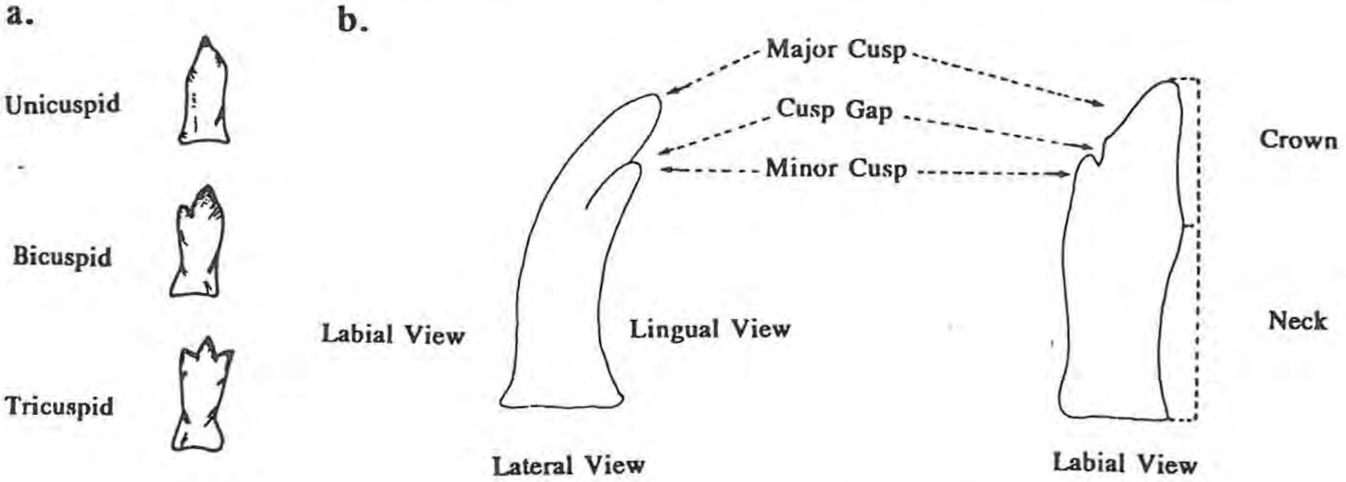


Figure 14: (a) The three basic types of tooth observed in the haplochromines and (b) tooth nomenclature (from Barel et al.,1977)

On the jaws, teeth are set in a single outer row of large teeth, and one or several inner rows of much smaller teeth (figure 15). Teeth in the outer row show a greater variety in shape and size than those of the inner series. The latter main contributions to dental diversity are their number and patterns of the rows present (Greenwood, 1974).

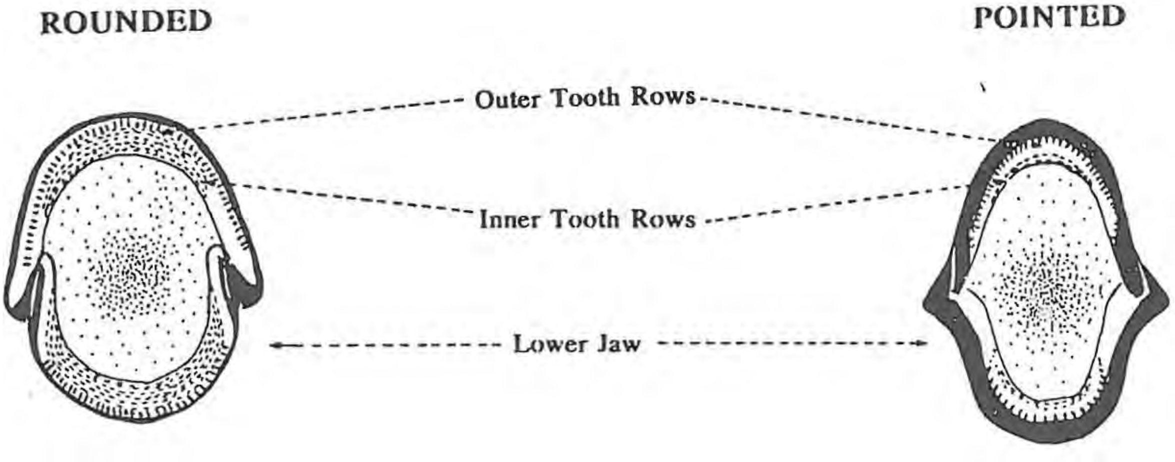


Figure 15: Shape of the tooth band illustrating the position of the outer and inner rows of teeth (from Barel et al., 1977).

By analogy with teeth of the generalized riverine *Haplochromis bloyeti*, unequally bicuspid teeth backed by two to three rows of smaller tricuspid teeth is taken to be the plesiomorphic oral dentition (Greenwood, 1974). Bicuspid teeth in which there is a differential growth of one cusp (usually the larger one) or equal development of both cusps are considered to be derived features, as are unicuspid teeth. In the inner tooth row, small tricuspid teeth represent the primitive condition. The presence of inner teeth other than tricuspid is a derived condition. The number of inner tooth rows varies, two to three rows being the plesiomorphic condition. Any increase or decrease indicates an apomorph condition (Greenwood, 1979).

iii. Colours and markings.

Colours and markings are species specific characters of live fishes and often allow immediate identification without reference to other morphological features (Baerends and Baerends-van Room, 1950; Greenwood, 1965 & 1974; Fryer and Iles, 1972; Fryer 1977). Colour in cichlids, especially in the dominant breeding males, plays an important role in the Specific Mate Recognition System (SMRS) (Paterson, 1980 & 1985; Ribbink et al., 1983; Greenwood, 1991). Subordinate males and females display dull uniform colours but the distribution of certain markings, the colour of small patches on the chest and flanks and particularly the fin coloration can play a role in the identification of species (Barel et al., 1977).

The coloured markings on the anal fin in males, in the form of spots or ocelli, call for some special attention. Coloured spots show a contrasting border, whereas the ocelli display a white and translucent surround (Greenwood, 1979). Wickler (1962) named the ocelli "eggdummies" on the assumption that the female during the spawning process mistakes these spots for eggs. When trying to grab the eggdummies the sperm is sucked up and fertilises eggs in the mouth of the female. Greenwood (1979) assumed that both the spots and ocelli were derived from coloured streaks and spots on the dorsal fins of the cichlids. The true ocellar eggdummies seem to be the end point of the differentiation process and represent the apomorphic condition. Coloured spots on the anal fin occur also in the females but they are less brightly coloured and never bordered by a translucent margin and are usually smaller.

3. Diagnostic features of the species studied.

In the species' descriptions which follow the aim is to introduce the reader to the studied haplochromines in the way I identified them; they are not to be considered as a full taxonomic description. Only mature individuals are described as juveniles were often difficult to recognize, displaying different morphological features from their parents. Voucher specimens of the studied species are available with RUSI for any future taxonomic studies.

Haplochromis astatodon (Regan, 1921).

1. Taxonomy.

Greenwood (1979) discovered that the first descriptions of *H. astatodon* (Regan, 1921; Pellegrin, 1928 & 1935; Poll, 1932 & 1939; David and Poll, 1937) included two distinct species on the basis of their dentition: one with movably implanted obliquely cusped teeth and one with fixed acutely cusped teeth. Greenwood (1979) retained the name of *H. astatodon* for those syntypes with obliquely cusped teeth. The group with fixed, straight implanted teeth is described on page 31.

2. Species' identification.

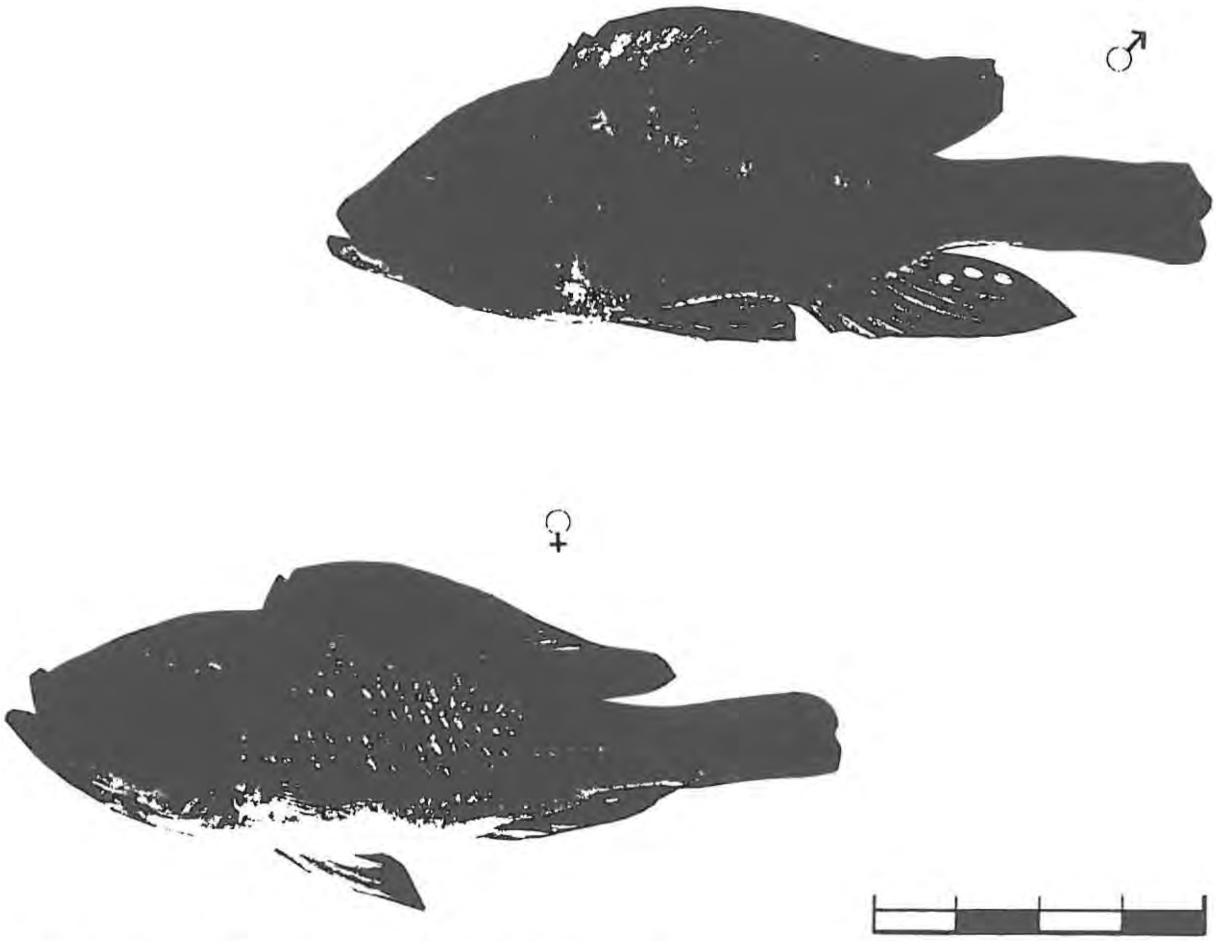


Figure 16: Sexually mature male and female *H. astatodon*.

i. Body and head shape.

Males have a moderately compact, deep body with a fairly slender caudal peduncle (figure 16). In females the body depth appears less deep and the caudal peduncle relatively less slender (figure 16). The head profile in both males and females is convex, but in females it is smooth and only slightly curved whereas in the males it is moderately curved, with a concavity above the eye which becomes more apparent in the larger specimens (figure 17).

Figure 17: Head shape of female and male *H. astatodon*.

ii. Oral teeth.

Dental arcade is moderately rounded; the upper and lower jaw carry an outer series of teeth and 4-5/3-5 inner series of teeth. The inner rows consist of small tricuspid teeth. Teeth in the outer row are closely and regularly set. The morphology of those teeth are very different from any other haplochromine of Lake Kivu and have the shape of an inverted hoof of a horse (figure 18).

- **the neck is slender and moderately elongated**
- **the crown is expanded and slightly recurved**
- **the major cusp is obliquely truncated and the secondary cusp is small.**
- **the cusp gap is narrow.**

Figure 18: Outer tooth description of *H. astatodon*.

iii. COLOUR AND MARKINGS.

Dominant males.

The overall body colour is bluish-black to pitch-black. In the aquaria (figure 16), however, dominant breeding males never became as black as observed during scuba diving at Tshegera Island (figure 58). The dominant colours are described from freshly caught specimens in the field.

The dorsal fin has an overall black translucent background. On the lappets small spots grading from orange-yellow anteriorly to yellow-orange posteriorly are commonly present. Within the fin streaks and maculae show also a gradual change in colour from red-orange anteriorly to almost orange posteriorly (figure 19a). The caudal fin is translucent black; further posteriorly (about 2/3 away from the caudal peduncle) it grades from uniform proximally orange-red to red-orange colour. Note that on the ventral side of the caudal fin, the red-orange colour extends further anteriorly towards the caudal peduncle (figure 19b). The anal fin displays colours as illustrated in figure 19c. The pelvic fin is black; the pectoral fin is transparent bluish-black.

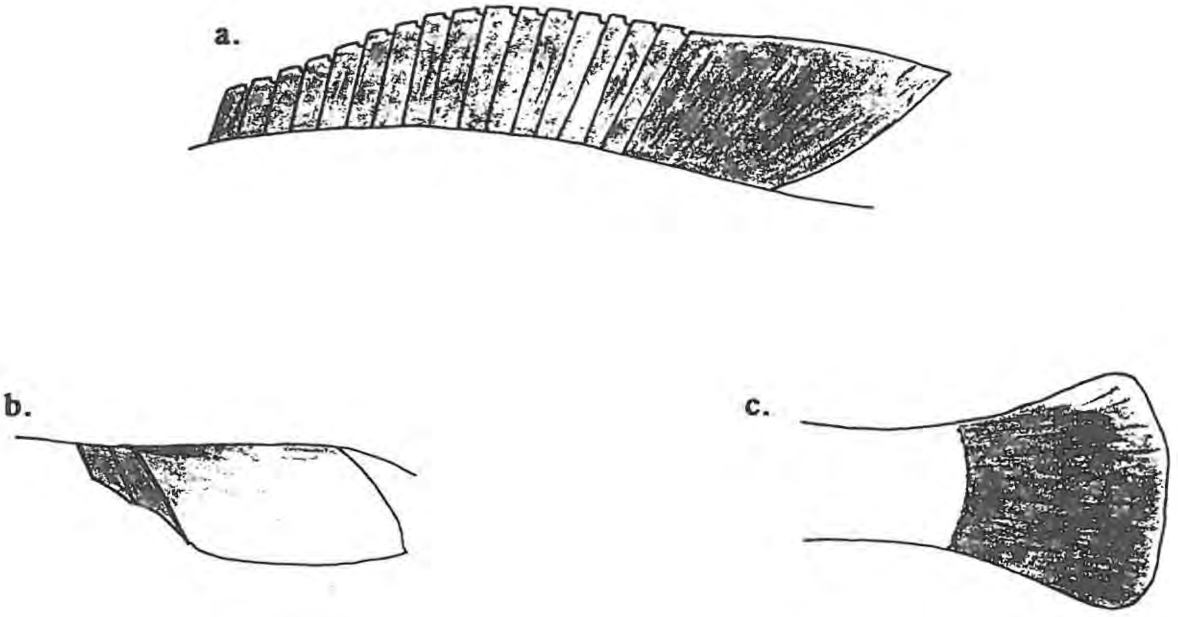


Figure 19: Colours displayed in (a) the dorsal, (b) caudal and (c) anal fins of dominant *H. astatodon* males.

Subordinate males.

These males have the same overall body colours as the females (discussed below). The fins, however, can show in different degrees of intensity the same yellow-orange to orange to red-orange colours as observed in the dominant males (but never as intense).

Females.

Head and body display a yellowish-brown colour with a goldish reflection (figure 16). On the body six to eight ventral stripes, sometimes a dorsal lateral band and a mid-lateral band are present in form of a pale greyish-brown colour. On the anal fin one to three pale yellowish-brown spots are present.

3. Relation between form and function.

The deep short body of this species suggests a sedentary mode of life. According to Verbeke (1957b) *H. astatodon* is a species typical of exposed rocky shores in the presence of a *Cladophera* carpet. Hulot (1956) mentions that this species rarely occurs on sandy substrata covered by macrophytes. However, one cannot be sure to which species the authors referred, i.e. the one with fixed acutely cusped teeth or the one with movably implanted obliquely cusped teeth.

Mees (1980), on the basis of stomach content analysis on *H. astatodon*, came to the conclusion that this species is a detritus feeder. Within the sediment on which the fish is presumed to feed *unselectively* (own italics), mud, mica, diatoms, algae, bits of higher vegetation and parts of insects become ingested. Mees suggested that, occasionally, the fish might also feed on the *Cladophera* carpet of the rocky shore.

The question one should ask here is why a generalised "bottom grubber" should have evolved obliquely truncated teeth? The fairly high number of small closely-set tricuspid teeth in the inner rows, together with the unusual type of outer teeth would suggest an epiphytic or epilithic type of feeding (Fryer and Isles, 1972; Greenwood, 1979). The obliquely truncated teeth could be compared with those of *Cyathochromis obliquidens* (Trewavas, 1935), a cichlid of Lake Malawi, which is known to graze using this type of dentition on both plants and rocks (Fryer, 1959).

At the University of Leuven (Belgium) I had the opportunity to analyze six stomachs of *H. astatodon* caught at Tshegera Island during the fieldtrips. In none were sand, mud, or mica observed (Patho Ulyel agreed that the latter were absent), but a large quantity of mucus, numerous diatoms and a few bits of vegetation appeared to be the most common food items.

Catch data at Tshegera Island demonstrated unambiguously that this species almost exclusively occurred within the vegetation zone. This was further confirmed by diving observations. The bottom surface of this habitat is covered with fine sand, mud and debris material and one can only wonder, if this species is a detritus feeder, why sand, mud or mica are totally absent from the six stomachs? The fact that this species lives at Tshegera Island within the vegetation zone, strongly suggests that it finds its primary food items within this area. If they were detritus feeders, they would be expected to occur offshore away from the vegetation and to feed in a similar way as *H. sheffersi*.

From the few stomachs analyzed I would tentatively suggest that this species scrapes diatoms attached to vegetation, pebbles or dead trunks, etc. and swallows them in a similar way as *Oreochromis esculentus* as described by Greenwood (1953): i.e. small quantities of food of a small size are brought into the mouth and become entangled by mucus secreted from glands within the mouth after which it moves further down the gut. In the stomach, diatoms are readily digested by enzymes which penetrate the minute pores of the silica walls (Fish, 1952).

4. Phyletic classification.

H. astatodon is classified in the genus '*Haplochromis*' together with four other species (figure 20). The members of this group are grazers on eplithic and epiphytic algae, and despite their generally unspecialized level of organisation, the dentition is derived and the gut specialized (pers. comm. Greenwood).

The genus is characterized by an increased number of rows of inner teeth and displays a morphocline based on the dentition of the outer row from the primitive bicuspid type observed in '*H*' *limax* and '*H*' *lividus* to the *obliquidens* type (figure 20). So, '*H*' *astatodon* together with '*H*' *obliquidens* display the most derived teeth within '*Haplochromis*'.

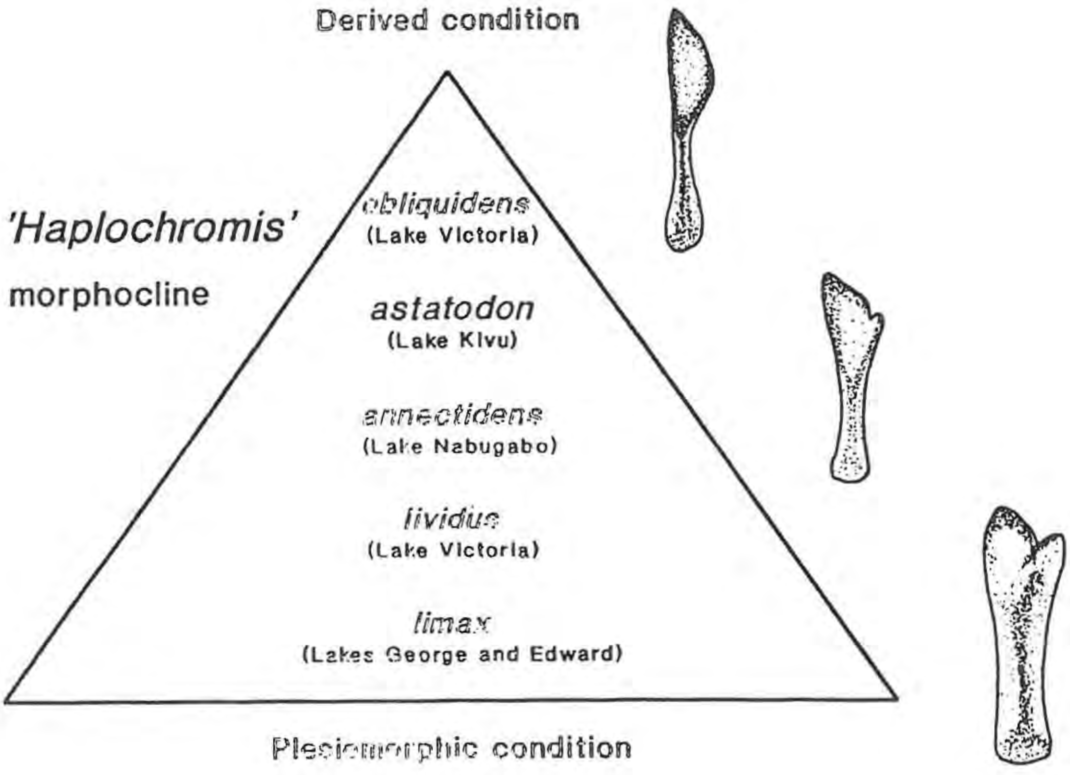


Figure 20: *H. astatodon* is classified in the genus *'Haplochromis'* (Greenwood, 1979) and displays the most derived condition based on dentition within the morphocline together with *H. obliquidens*.

Haplochromis olivaceus (Snoeks et al., 1990)

and

Haplochromis crebridens (Snoeks et al., 1990)

1. Taxonomy.

The specimens of *H. astatodon* type series with fixed, acutely cuspid teeth as mentioned on page 26 are now included in two new species: *H. olivaceus* (Snoeks et al., 1990) and *H. crebridens* (Snoeks et al., 1990).

2. Species' identification.

Haplochromis olivaceus.

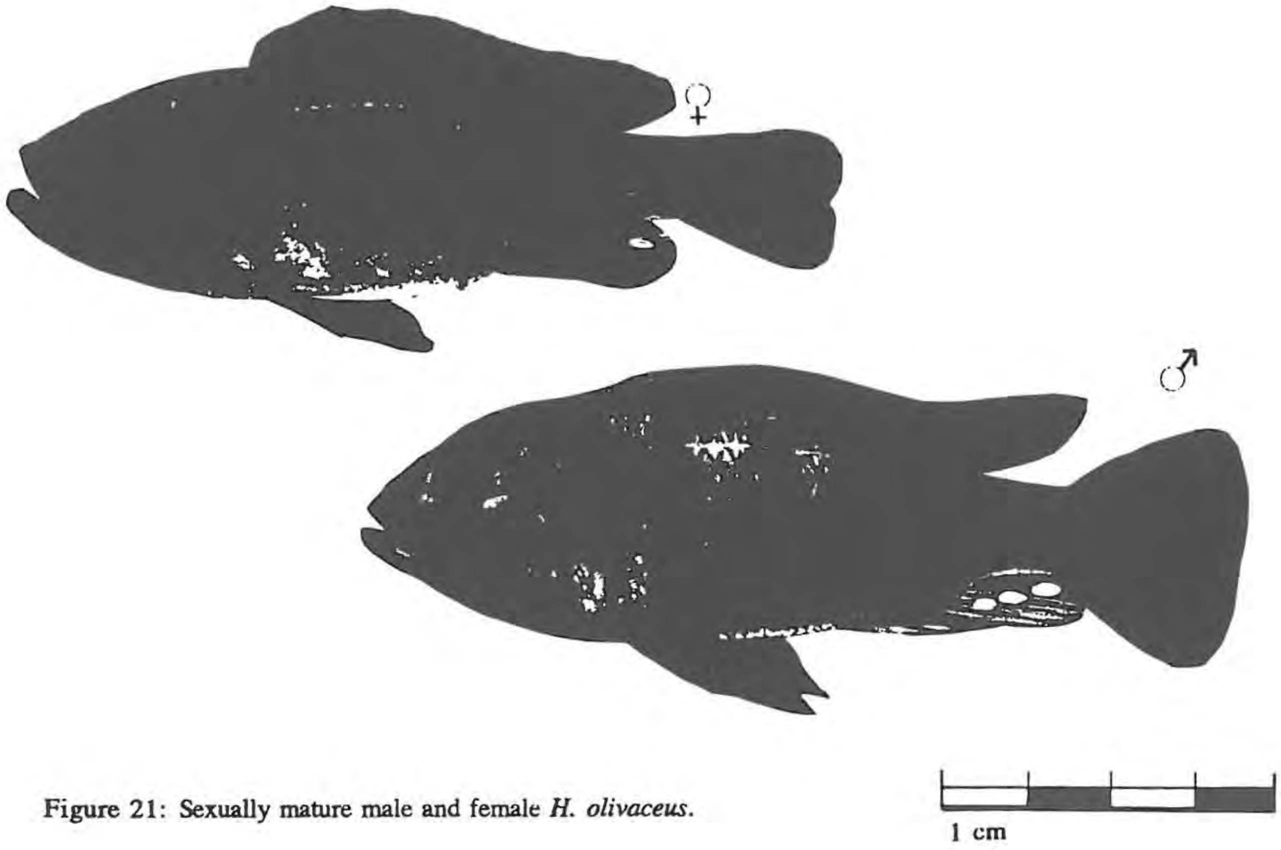


Figure 21: Sexually mature male and female *H. olivaceus*.

i. Body and head shape.

Males have a deep and compact body (figure 21), a strongly convex head profile and an obtuse snout which becomes more pronounced in larger specimens (figure 22). The eyes are moderately large and the lips moderately thick. Females have a more elongated body form (figure 21) and their dorsal head profile is less convex (figure 22). Eyes are large and lips are thin.

In males the posterior end of the dorsal and anal fins reach at least as far as the origin of the caudal fin; in most cases it extends beyond it. In females the dorsal and anal fins never reach as far (figure 21).

Figure 22: Head shape of female and male *H. olivaceus*

ii. Oral Teeth.

The dental arcade is broadly rounded and upper and lower jaw support a broad band of teeth: both jaws have an outer row of large unequally bicuspid teeth and 4-8/ 4-8 inner rows of small tricuspid teeth (figure 23).

. the neck is stout and short, rounded and not compressed

. the crown is slightly expanded and moderately recurved

. the gap between the major and minor cusp is large

. the secondary cusp is blunt and about 1/2 the size of the major cusp

. the major cusp displays different forms depending on the degree of wear.

Figure 23: Outer tooth description of *H. olivaceus*.

iii. COLOUR AND MARKINGS.

Dominant males.

Head and body are pitch black. The anterior part of the dorsal fin is opaque pitch black with a bluish tint; its posterior part displays red spots on the lappets (figure 24a). The caudal fin is also black, but with a red fringe at its posterior end (figure 24b). The anterior part of the anal fin is pale to dark red; posteriorly the anal fin becomes greyish-black and carries one to four bright yellow ocelli (figure 24c).

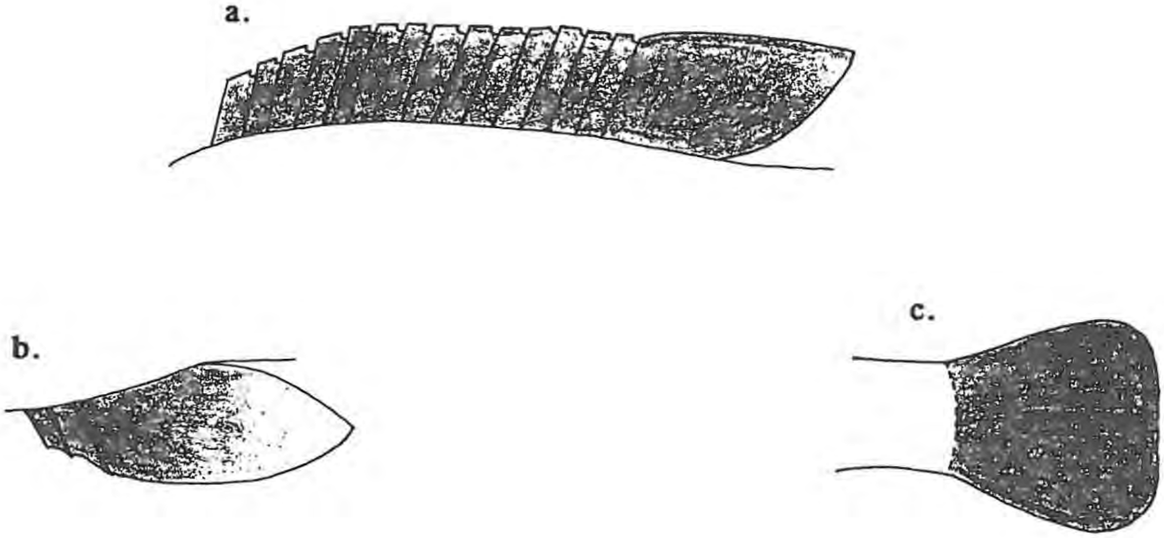


Figure 24: Colours displayed in (a) the dorsal, (b) caudal and (c) anal fins of dominant *H. olivaceus* males.

Subordinate males.

The body shows different degrees of yellow-green to olive-green. Some individuals display different degrees of light to dark grey (figure 21).

Dorsal, anal and ventral fins are greyish blended with the overall body colour. The dorsal fin, when not black, can display black spots on the posterior part of the lappets. Faint red colours in the fins, similar to those observed on the dominant males are sometimes present. The ocelli are usually bright yellow but might be faint or sometimes absent.

Some individuals display four to seven broad vertical stripes and a mid lateral band. A black blotch is sometimes present at the posterior part of the caudal peduncle. Very few individuals have an interorbital stripe and/or lachrymal stripe. All individuals have an opercular blotch.

Females.

They are more or less dull, uniform yellow in body colour (figure 21). Ventral and caudal fins are in most cases somewhat brighter yellow than those of the subordinate males. The dorsal fin is identical in colour to the overall body colour; the posterior part often displays brownish-black spots on the lappets. A black blotch on the posterior part of the caudal peduncle is sometimes observed. The spots on the anal fin are pale yellow or absent.

Individuals under stress, observed for example in the aquarium when chasing other fishes away from their fry, might become brownish-yellow. They then display very often five to seven vertical stripes, a mid lateral band and a vertical lachrymal stripe.

Haplochromis crebridens

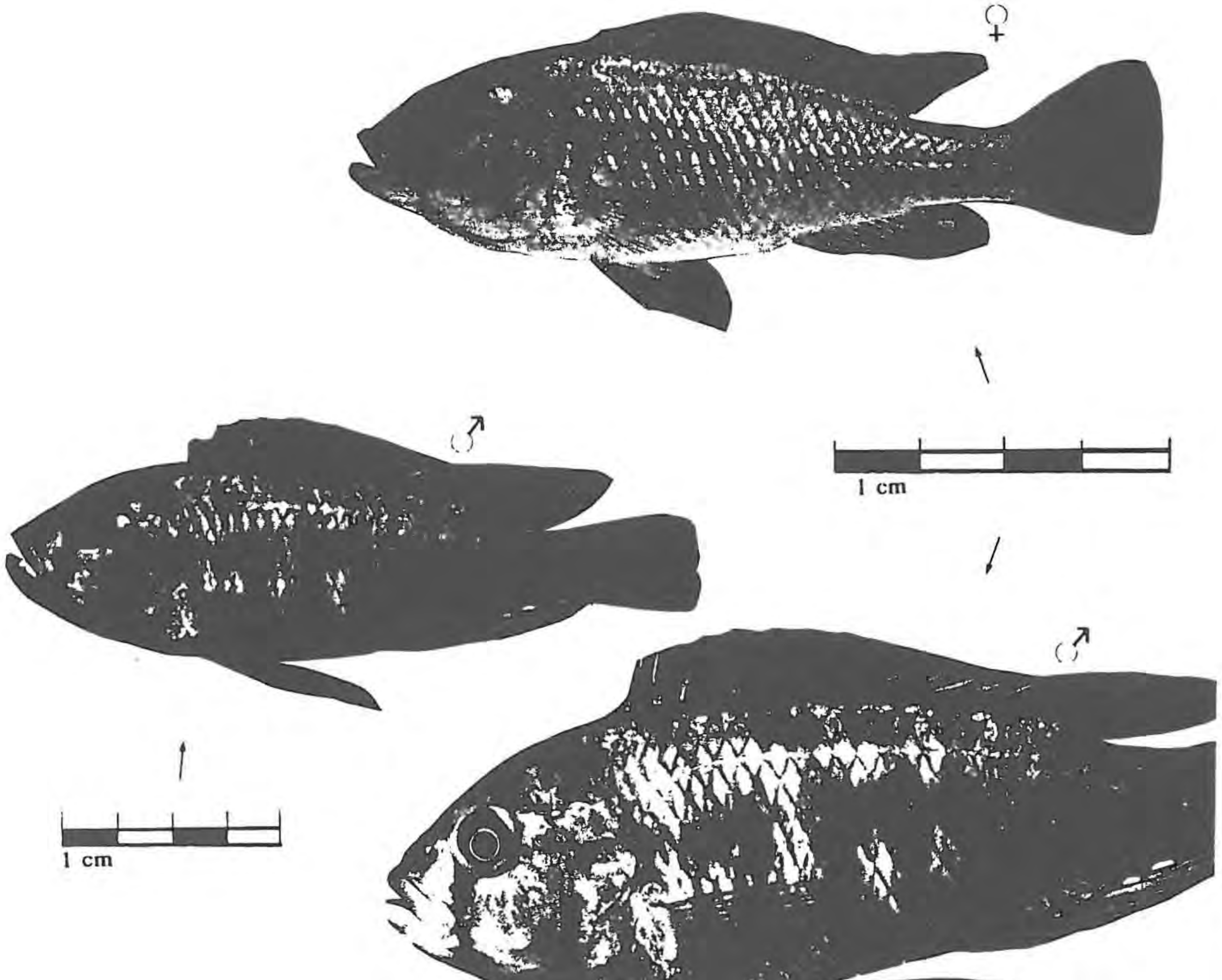


Figure 25: Sexually mature males and female *H. crebridens*.

i. Body and head shape.

Both males and females have a more elongated body form than *H. olivaceus* (figures 21 & 25). Their eyes are larger and their caudal peduncle and caudal fin are more elongated. Males have nevertheless a deeper body then the females. In females the dorsal and ventral fins never reach beyond the margin between the caudal peduncle and caudal fin, whereas in males it may reach further (figure 25). The dorsal head profile is moderately concave and smoothly curved in both males and females, but in males tends to be steeper (figure 26).

Figure 26: Head shape of female and male *H. crebridens.*

ii. Oral teeth.

The dental arcade and number of outer and inner rows of teeth are the same as in *H. olivaceus*. The morphology of the outer anterior teeth is also very similar to *H. olivaceus* and only small differences could be observed (figure 27). These differences in tooth morphology are too small to be reliable and were never used on their own as a distinguishing feature between the two species.

- **the neck slightly more elongated, less stout and less rounded**
- **the expansion of the crown less pronounced**
- **the gap between major and minor cusp smaller**
- **the minor cusp pointed in almost all specimens**
- **worn-off teeth seem to be less common and most teeth display pointed major cusps.**

Figure 27: Outer tooth description of *H. crebridens* comparatively to *H. olivaceus* (pp 32).

iii. COLOUR AND MARKINGS.

Dominant males.

The overall body colour displays a silverish reflection on a sky blue background (figure 25). The dorsum, venter and belly are dark whereas the flanks and head are silverish light blue to white. There are eight to ten vertical stripes which tend to be narrower compared with those observed in *H. olivaceus* and a faint mid lateral band is present.

The dorsal fin is translucent bluish-black anteriorly, becoming paler bluish-grey posteriorly (figure 28a). From about halfway posteriorly lappets have orange fringes; maculae, witch are orange anteriorly and reddish orange posteriorly, are also present. The caudal fin is bluish-black close to the caudal peduncle and translucent bluish-grey towards the centre (figure 28b). Orange maculae in the form of streaks are present in this central part. An orange coloured zone surrounds the caudal fin. Dorsally this surrounding zone is orange-red becoming red-orange towards the ventral side. The anal fin is red-orange anteriorly, translucent grey-orange towards the ventral posterior side and translucent orange towards the posterior tip of the fin (figure 28c). The ocelli are bright yellow-orange. The pectoral fin is pitch black.

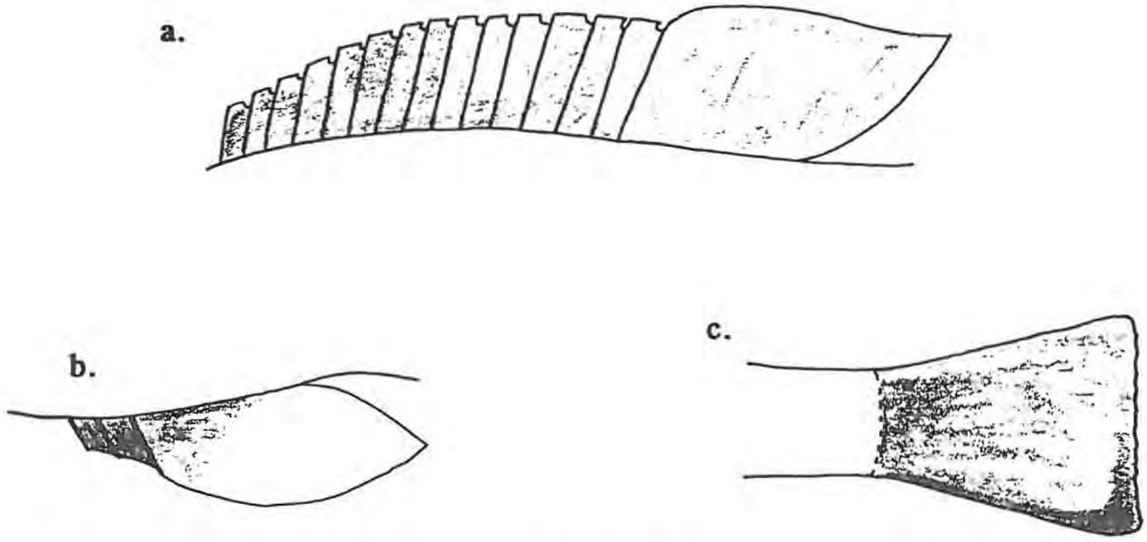


Figure 28: Colours displayed in (a) the dorsal, (b) caudal and (c) anal fins of dominant *H. crebridens* males.

Subordinate males.

The venter, belly, chest, cheek and operculum are white to grey-blue silver. Myomeres are clearly visible on the caudal peduncle, venter and belly. From the flanks upwards to the dorsum the amount of grey mixed with yellow and blue reflections increases. The base of the dorsal fin is brownish-black; so are the dorsal head surface and ethmoidal area. Fins are translucent grey. Posteriorly, the dorsal fin displays faint to very bright orange spots on the lappets and maculae within the fin. The outer margin of the caudal fin is orange-red and the ocelli on the anal fin are pale to bright yellow-orange.

Females.

The body colour is similar to that of the subordinate males, but tends to be more yellowish than greyish-blue (figure 25). The fins are also more yellowish and never display maculae. By naked eye or by microscope, orange-red spots on the lappets were observed posteriorly on the dorsal fin. This was a very helpful feature to differentiate the females from those of *H. olivaceus* when there was doubt. The anal spots are pale yellow to absent.

3. Relation between form and function.

Interspecific difference between the two species, in contrast to their anatomical similarity, is clearly expressed by body colour; this difference is most distinct in the beautifully coloured territorial males and less so in the more drably coloured females and subordinate males. In these species, as is also demonstrated in *H. heusinkveldi, H. pyrrhocephalus* and *H. laparogramma* of Lake Victoria (Goldschmidt and Witte, 1990), speciation might have occurred by divergence in reproductive characters, such as male breeding coloration, without preceding divergence in trophic morphology.

The overall body colour in the dominant breeding males appears to be related to an adaptation in being cryptic with respect to bird predation pressure. The predominantly silverish-blue colour of *H. crebridens* dissimulates its presence in shallow water above its breeding territory when seen from the surface; the predominant black colour of *H. olivaceus* breeding males corresponds to the dark basaltic rocks which constitute their normal habitat (Appendix E). On the other hand, the orange-yellow and red colours in the fins of *H. crebridens* and *H. olivaceus* respectively, might be an adaptation to make signalling most effective between partners within their normal habitat. As light properties vary with depth and locality, it might be that the dark red colours come out better on a dark background whereas orange colours in the shallow water within the water column.

From a morphological point of view, differences between the two species, although very small, are to be found in (1) the general body form, (2) eye size and (3) the tooth morphology in the outer row. On basis of the body shape one might only guess that *H. olivaceus*, with its short compact body, lives a sedentary life style close to the substratum. The more elongated body of *H. crebridens* suggests that this species moves more freely away from the substratum. Although few differences could be observed in the outer anterior teeth, the fact that those of *H. crebridens* tend to be slightly more elongated and pointed might suggest that this species also feeds on a slightly different food source.

The contents of six stomachs of each species caught at Tshegera were examined and although the food composition appeared to be very much the same in both species and consisted mainly of a green "broth" of algae, bits of insects, including mainly chironomid larvae, were also commonly present in the stomachs of *H. crebridens*. Chironomid larvae represent the floating stage of the insect and obviously suggests that the individuals which fed on them also moved away from the substratum.

This preliminary stomach content analysis suggests that the two species spend at least some time in different habitats. This is further confirmed by the catches and diving observations at Tshegera. During night dives *H. crebridens* was commonly seen swimming near the surface while *H. olivaceus* was always found resting on the substratum. Gillnet catches demonstrated that both species were bottom bound during the day, but that at night *H. crebridens* moved as well within the water column. De Vos et al., (1987) also mention that *H. crebridens* is readily caught at night in the surface nets. The larger eyes in *H. crebridens* might be related to its slightly different feeding behaviour compared to *H. olivaceus*.

4. Phyletic classification.

H. crebridens and *H. olivaceus* are similar to the phytophagous '*Xystichromis*' (Snoeks et al., 1990)(figure 29). Members of this taxon are epilithic algal grazers and retain a general unspecialized level of organization. No intralineage relationship can be determined within this genus (Greenwood, 1980). Dentition differs from the generalized bicuspid tooth in not having the crown distinctly broader than the neck. The crown is also somewhat more compressed than the generalized bicuspid tooth (Greenwood, 1980) (figure 29). On the basis of the dentition this group might represent a link between the generalized insectivores and specialized rockscrapers, such as those comprised in '*Neochromis*' (pers. comm. Greenwood).

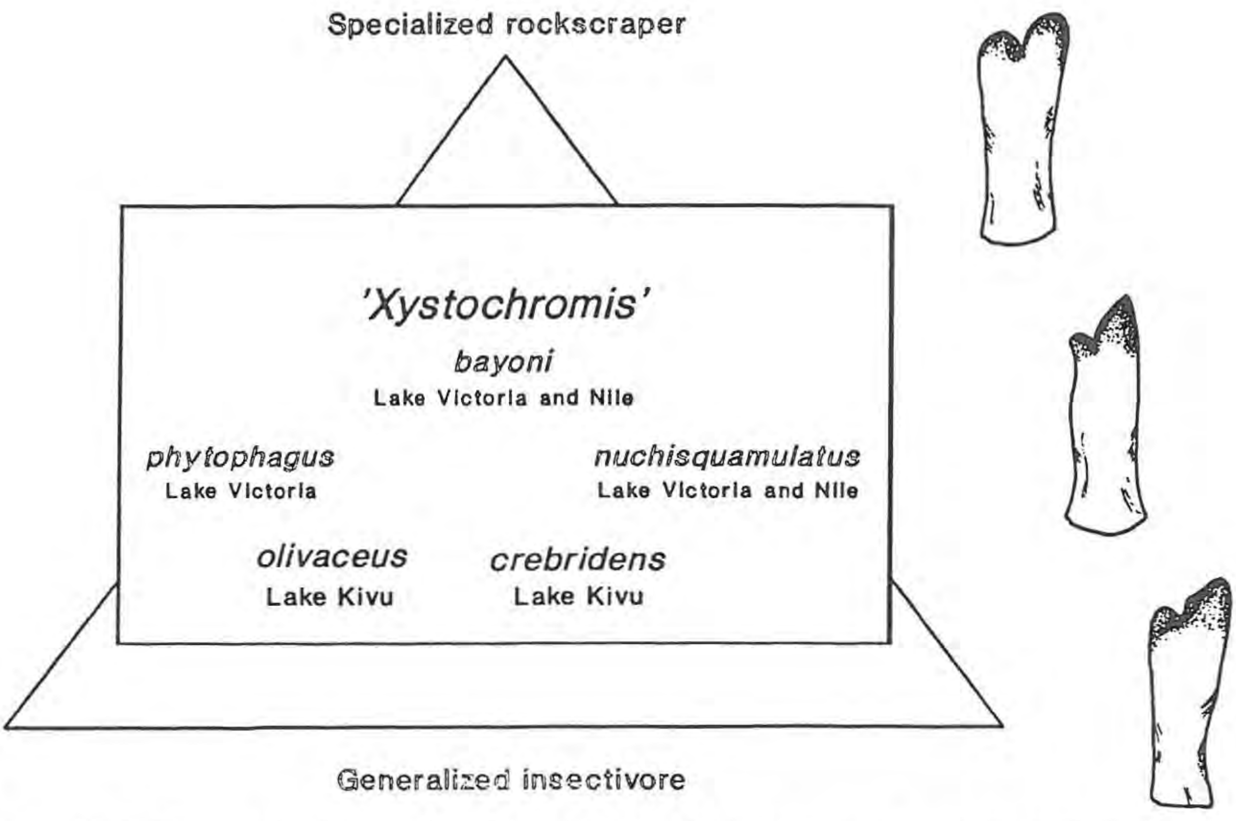


Figure 29: *H. olivaceus* and *H. crebridens* are together classified in the genus '*Xystochromis*'(Greenwood, 1979). No intralineage relationship can be determined. The dentition in this taxon is more derived than the generalized insectivores (such as *H. macrops*) and less derived than the specialized rockscrapers (such as *H. nigricans*).

Haplochromis paucidens (Regan, 1921).

1. Taxonomy.

H. schoutedeni (Poll, 1932) and *H. wittei* (Poll, 1939) are synonymies of *H. paucidens* and have been included in the species *H. paucidens* by Snoeks (1988).

2. Species' identification.

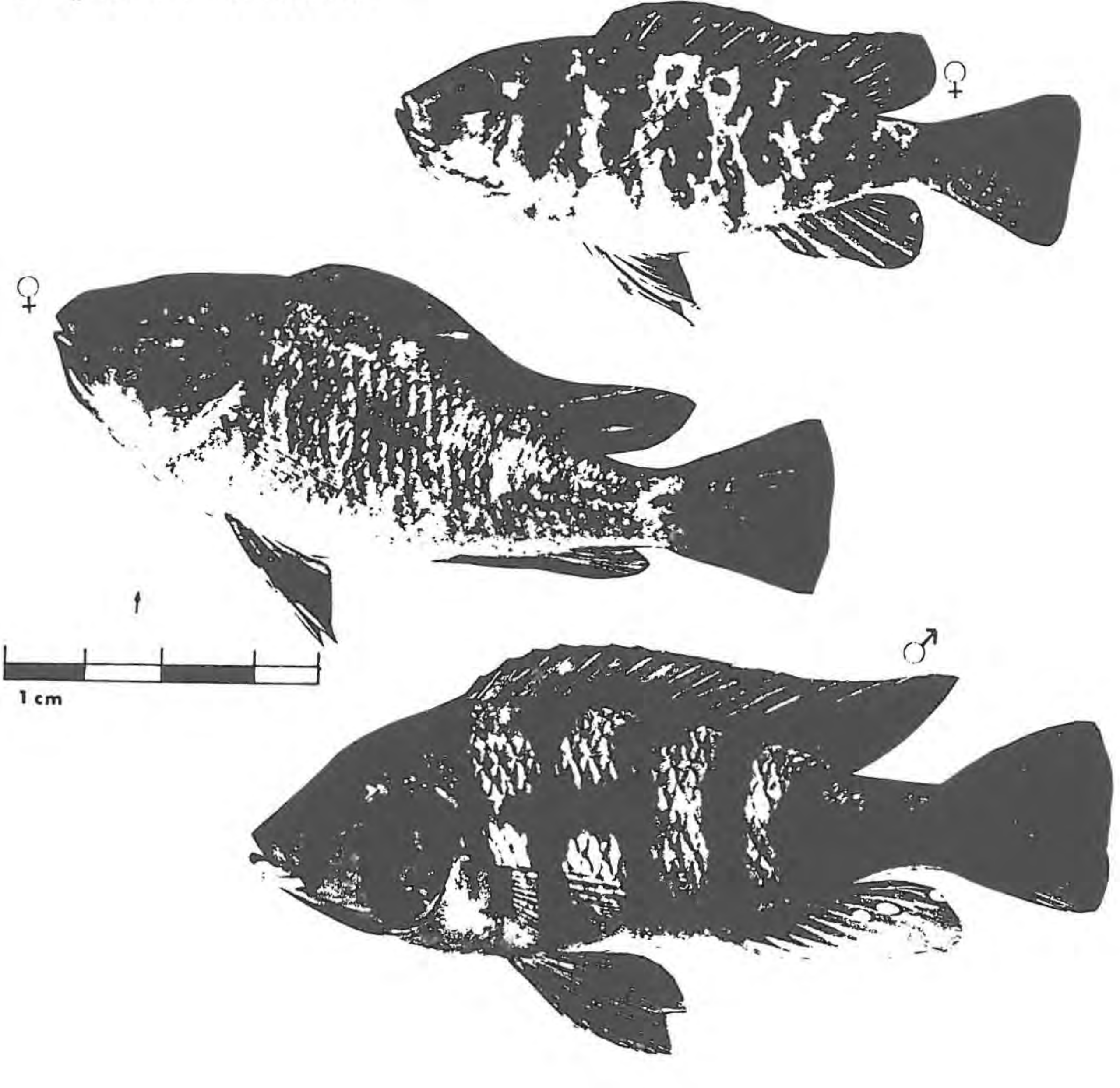


Figure 30: Mature male and females *H. paucidens*.

i. Body and head form.

The body is deep and moderately short (figure 30), especially in the larger specimens. The head is slightly convex in the females and smaller males, but is more strongly convex in larger males where a slight concavity might be present above the eye (figure 31). The snout is obtuse (most pronounced in females), the lips are thick and the mouth small.

Figure 31: Head shape of female and male *H. paucidens*.

ii. Oral Teeth.

The dental arcade is broad and rounded. The curve of the outer tooth row in the lower jaw displays a typical U-form. In the Lake Kivu haplochromines, in general, this dental arcade is posteriorly more separated and displays a V-form (Snoeks, 1988). The anterior teeth of the outer row are either weakly bicuspid or worn-off, blunt unicuspid (figure 32). The outer tooth row is backed by 2-3/2-4 inner teeth rows. Teeth in the inner rows are small and tricuspid, but those situated anteriorly might be more robust.

. the neck rounded, strong and stout

. the crown not expanded

. the gap between the major and minor cusp small

. the secondary cusp small and obtuse

. major and minor cusp can be worn-off, resulting in a blunt unicuspid tooth.

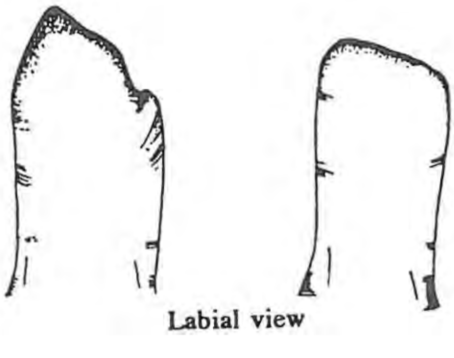


Figure 32: Outer tooth description of *H. paucidens*.

iii. Colour and markings.

H. paucidens is trimorphic: it displays normal, piebald and greyish colours (figure 30).

a. normal colour.

Dominant males.

The overall body colour is bluish-green, the degree of blue increasing with dominance (figure 34). The flanks are yellowish. Four to seven vertical stripes of variable intensity are observed in all dominant males. The anterior part of the dorsal fin displays almost the same colour as the overall body colour; posteriorly the fin becomes darker. Lappets have orange-yellow fringes; orange-red maculae are present within the fin (figure 33a). The central part of the caudal fin is dark grey to black with orange-red streaks. The posterior dorsal and ventral edges and the posterior margin are orange-yellow (figure 33b). The anal fin is black anteriorly becoming pale grey posteriorly. A maximum of four yellow ocelli are present (figure 33c). The pectorals are almost translucent and the pelvic fins are black.

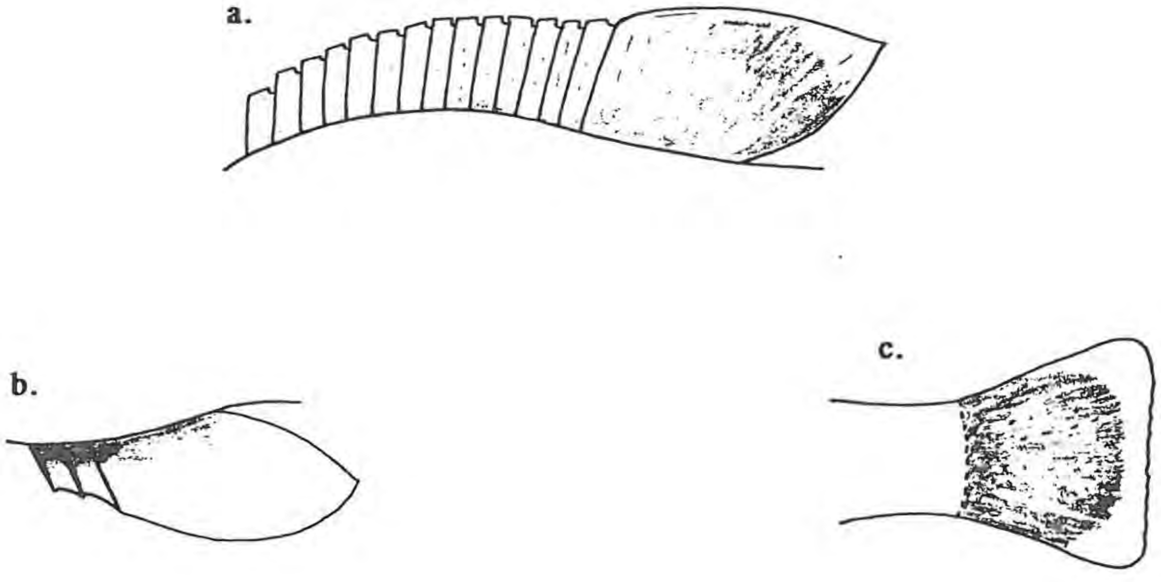


Figure 33: Colours displayed in (a) the dorsal, (b) caudal and (c) anal fins of dominant *H. paucidens* males.

Subordinate males.

Overall body-colour is yellow to yellowish-green. In addition to the ventral stripes observed in the dominant males, a mid lateral band is sometimes present (figure 30). Orange maculae on the dorsal and caudal fins are less intense. Pectoral fins are translucent and pelvic fins greyish.

Females.

Overall body colour is silverish grey with a green goldish shine and with four to seven vertical stripes and sometimes a mid lateral band. The dorsum is somewhat darker in colour and the belly is white with a silverish shine. Fins are the same colour as the body with dark maculae on the posterior part of the dorsal fin and anterior part of the caudal fin. Very small, almost transparent yellowish ocelli are sometimes visible on the anal fin.

b. PIEBALD COLOUR.

This type of colour is common in females, but extremely rare in males. Only one piebald male was caught which displayed the same colour as the piebald females. The overall background colour is yellowish-white and is covered by randomly dispersed black blotches on the body, head and fins (figure 30).

c. GREYISH COLOUR.

This was only observed in the females and is rare. The greyish pigmentation is not uniformly distributed and the intensity of greyish coloration varies irregularly over the body. The belly is silverish grey (figure 30).

Figure 34: Two dominant *H. paucidens* males chasing each other.

3. Relation between form and function.

The moderately thickened lips, dentition and dental arcade are typical of insectivorous cichlids. It has a short intestine and small stomach and feeds mainly on benthic insect larvae (Meysman, 1980). Breeding males and females appear tied to the *Cladophera* carpet, whereas their non-breeding counterparts are seemingly equally distributed on the *Cladophera* carpet, sandy benthos and within the water column (Meysman, 1980).

4. Phyletic classification.

H. paucidens is contained in the insectivorous group '*Paralabidochromis*' (figure 35). Within this genus the apomorph conditions are hypertrophied and lobate lips and a specialized dentition with outer teeth being stout unicuspid and forceps-like (Greenwood, 1980). Within this lineage '*P*'. *paucidens*, together with '*P*'. *beadlei* and '*P*'. *labiatus* display the least derived condition, with the most generalized dentition which departs only little from the *Astatotilapia* type (Greenwood, 1980).

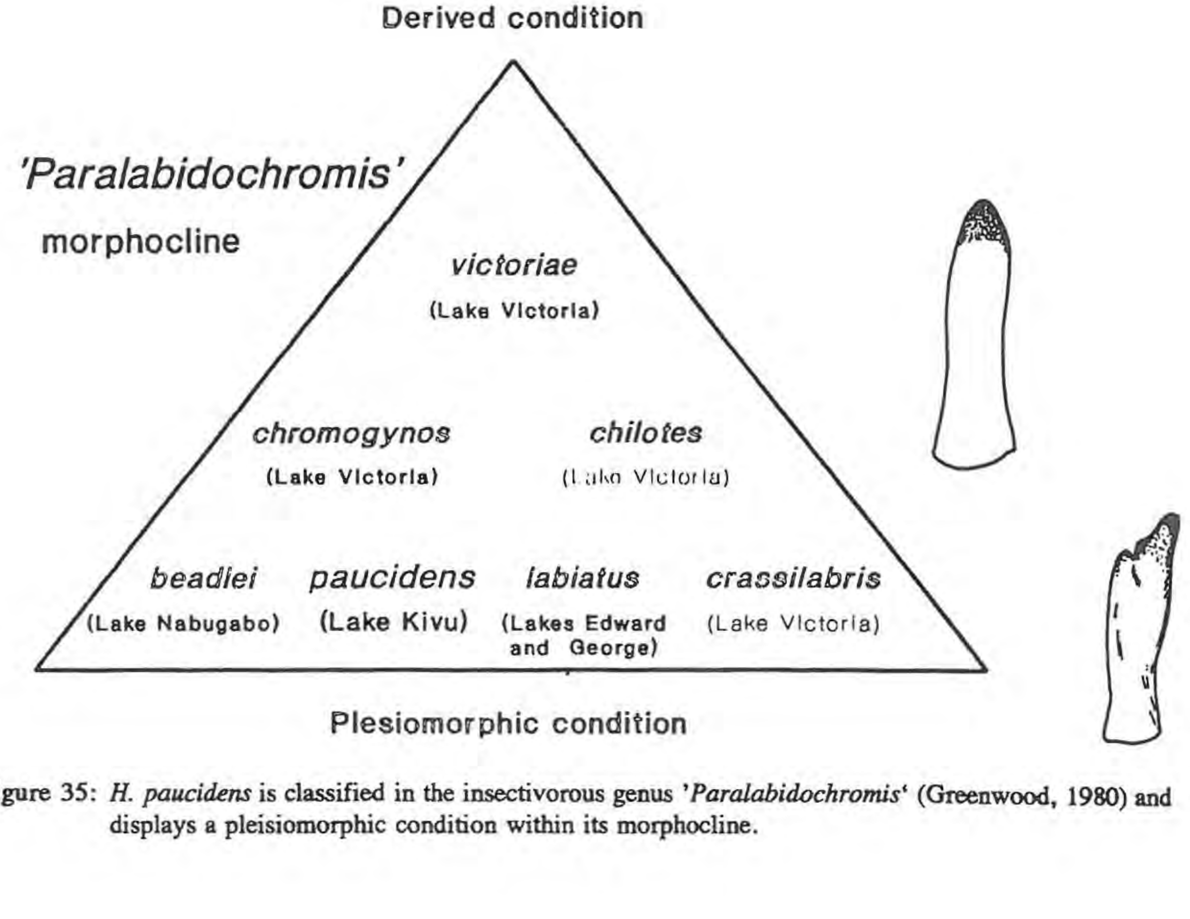


Figure 35: *H. paucidens* is classified in the insectivorous genus '*Paralabidochromis*' (Greenwood, 1980) and displays a pleisiomorphic condition within its morphocline.

V. Breeding Biology.

1. Introduction.

The predominant breeding system in the African cichlids, including the haplochromines of Lake Kivu (own observations), is maternal mouthbrooding with polygamy (Lowe-McConnell, 1975; Kuwamura, 1986). Mouthbrooders belong to the specialized reproductive guild of the bearers which is characterized by intense parental care, low fecundity but large yolked ova and large energy investment in each of a small number of young (Bruton, 1989).

Throughout the African cichlids, courtship and spawning behaviour are much the same (Ribbink et al., 1983). Although highly complex and including lateral-display, tail-beating, frontal-display, nudging, mouth-fighting, side-shake, follow-shake, lead-swim and spawning partners (Baerends and Baerends van Room, 1950), the difference in the behaviourial components and the sequence in which they are performed are essentially similar (figure 36)(Ribbink et al., 1983). This is consistent with a basic principle of the Recognition Concept (Paterson, 1978), which stresses the resistance of co-adapted SMRS to selection pressures in large populations. In this study, therefore, no attention has been given to the latter aspects of breeding behaviour, as they are only of little value in species distinction and are irrelevant in relation to the main hypothesis.

Other essential components of the SMRS are ecological co-adaptations of partners including selection for identical preferred habitats (Paterson, 1978). From diving observations the haplochromines studied are known to show a pronounced divergence in this regard, and displayed a microdistribution within the littoral with respect to preferred breeding territories (Appendix E). The mating stations within the territories consisted of particular small cleaned areas on the substratum, but never included any special structure.

In this chapter several reproductive traits, which contribute to the totality of the SMRS are considered and involve timing of breeding, size at first maturity, fecundity, egg sizes and condition factors. It confirms that despite the overall similarity in anatomy and behavioural aspects, each species has its own set of characters, holding the members of the species together and allowing effective syngamy between conspecific partners in the environment in which they evolve.

Figure 36: A male *H. paucidens* nudging its partner. This behaviour is believed to serve as to stimulate spawning in the female (Ribbink, 1975).

2. Material and methods.

a. Monthly sampling.

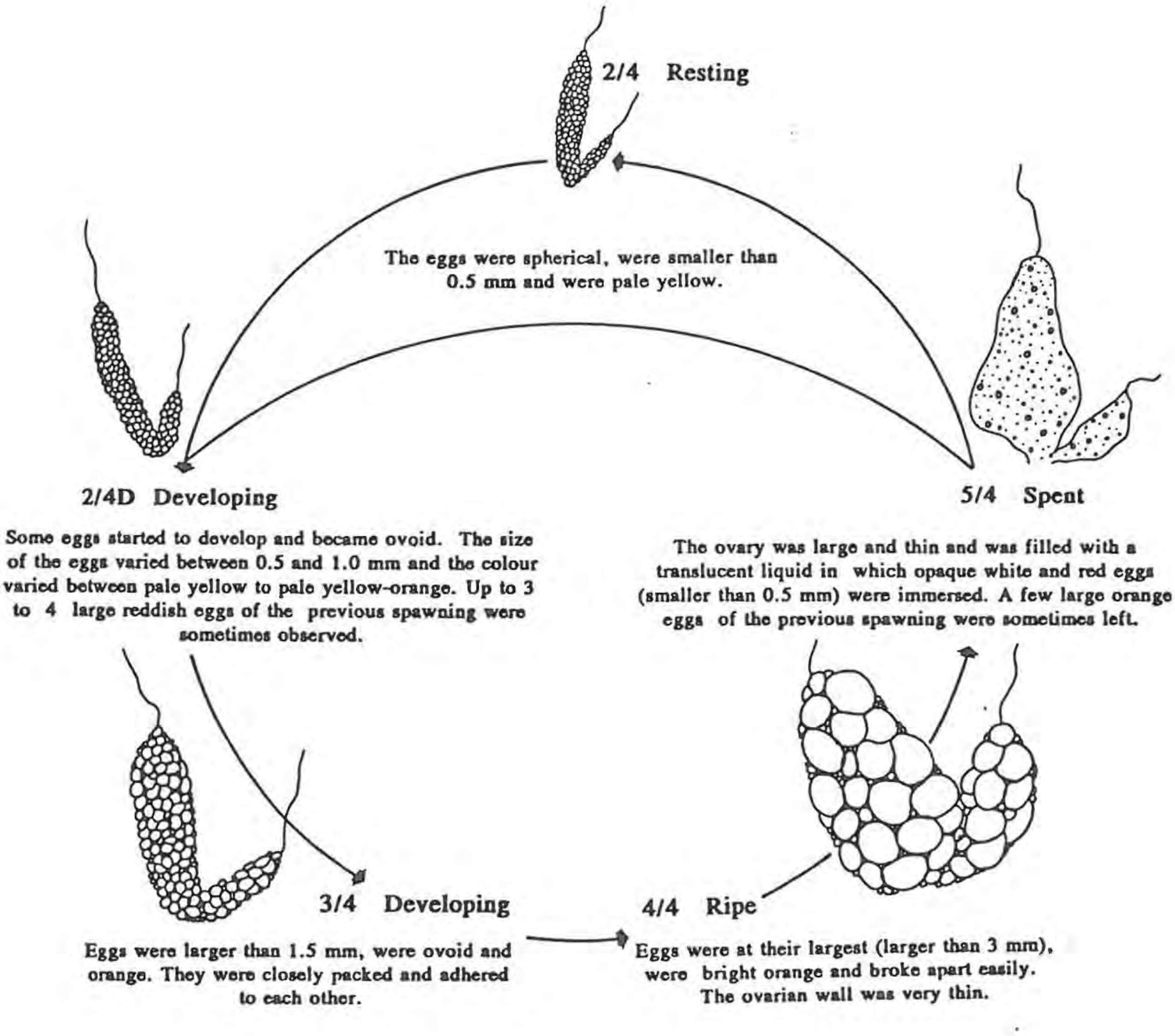
Monofilament gillnets with stretched mesh sizes of 8, 10, 12, 15, 20 and 24 mm were used. The 8 and the 10 mm nets were top set nets while all the other mesh sizes included both top and bottom set nets. Each net was 25 m long and 1.5 m deep.

Nets were set parallel to the coastline inside the crater either in front of the vegetated or the rocky zone between three and seven meters deep (figure 37). Nets of the same mesh size were never set out twice at the same place within the same month. To observe seasonal changes in breeding activity and body condition it was attempted to catch at least a minimum of 30 individuals per species per month.

Figure 37: Two nets set parallel to the coastline in front of the vegetated zone at Tshegera Island.
(□ buoys of the nets).

As soon as the nets were hauled, fish were immediately removed (unless weather conditions prevented it), injected with 5% formalin and kept in separate labelled buckets for each net. On return to the laboratory, fish were identified, labelled with a number and transferred to 5% formalin. For each fish, the date, time of capture, mesh size, net type and fishing site were recorded. Fish were preserved for four months in formalin before being dissected.

In addition to the gillnets, fish were caught at night using scuba and home made handnets, torches and "practice". The technique had the advantage that individual fish could be selected on the basis of species, size and sex. This was valuable in selecting specific fish for aquaria and for completing the monthly samples.



2/4 Resting

The eggs were spherical, were smaller than 0.5 mm and were pale yellow.

2/4D Developing

Some eggs started to develop and became ovoid. The size of the eggs varied between 0.5 and 1.0 mm and the colour varied between pale yellow to pale yellow-orange. Up to 3 to 4 large reddish eggs of the previous spawning were sometimes observed.

5/4 Spent

The ovary was large and thin and was filled with a translucent liquid in which opaque white and red eggs (smaller than 0.5 mm) were immersed. A few large orange eggs of the previous spawning were sometimes left.

3/4 Developing

Eggs were larger than 1.5 mm, were ovoid and orange. They were closely packed and adhered to each other.

4/4 Ripe

Eggs were at their largest (larger than 3 mm), were bright orange and broke apart easily. The ovarian wall was very thin.

Figure 38: The reproductive stages during the female gonadal development. After spawing gonads either go through a resting phase (2/4 stage) or immediately enter a new developmental cycle (2/4D stage).

b. Reproductive seasonality.

The reproductive seasonality of each species was analyzed by assessing reproductive stages of gonadal development in the females and by calculating their gonadosomatic indices.

The reproductive stages of gonadal development in the females were divided into five categories, as illustrated in figure 38. This division was established on the basis of the descriptions of Marsh et al., (1986) and my own experience. Undeveloped eggs were present throughout the complete developmental cycle. The various stages were therefore assessed by considering only the largest egg class. In relation to oocyte growth, as described by Jalabert and Zohar (1982), the 2/4D stage corresponds to the pre-vitellogenic phase, which involves a slow increase in egg size, and the 3/4 and 4/4 stages to the vitellogenic phase, which represents a fast increase in weight. To obtain an estimate of resting females in the total samples of each species the percentage of females with gonads in 2/4 stage in relation to those in the 2/4D, 3/4, 4/4 and 5/4 stages was calculated.

The reproductive stage of each female was evaluated and the percentage frequency of breeding individuals per month was calculated. Breeding individuals included the females with oocytes in the vitellogenic phase (i.e. 3/4 and 4/4 stages) and spent gonads (figure 38).

The gonadosomatic index (GSI) was calculated as follows:

$$\text{GSI} = (\text{gonad weight} / \text{body weight}) \times 100$$

and the mean values per month were estimated. Gonad weight was measured to the nearest 0.01 gm and body weight to the nearest 0.1 gm using an OHAUS balance (0.01 gm).

The smallest female with gonads in a 4/4 stage was considered to be the minimal size at which sexual maturity was reached whereas in the males it was the appearance of first breeding colours which were regarded as indicating first sexual maturity.

c. Fecundity.

The fecundity of fish is defined as the number of ripening eggs in the female prior to the next spawning period (Bagenal and Braum, 1978). The number of eggs were counted in all 3/4 and 4/4 stages and the mean, maximum and minimum number of eggs calculated. Egg height and width were measured using a vernier calliper, to the nearest 0.02 mm, for 10 eggs in all females with gonads in a 4/4 stage.

The relationship between ovarian egg production to length is expressed by the equation:

$$\text{fecundity} = a\ (\text{standard length})^{b} \quad \text{(Welcomme, 1967)}$$

In order to define the a and b values, the following logarithmic transformation was applied:

$$\log \text{fecundity} = \log a + b \log \text{standard length}$$

This relationship was further analyzed by applying multiple box and whisker plots (figure 39). This graphic representation detects outliers and dispersion behaviour within each grouping, since the plot divides the data into four areas of equal frequency (Statgraphics, 1986).

In addition to the absolute fecundities, relative fecundities (r) were calculated for each specimen with:

r = number of eggs / (mass of fish - mass of ovaries) (Bagenal, 1973).

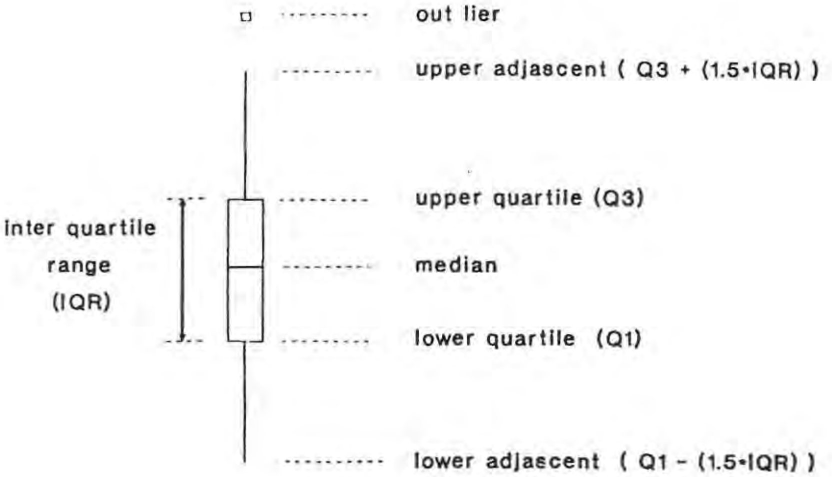


Figure 39: Multiple box and whisker plot.

d. Condition factor.

The study of condition is usually based on an analysis of length-weight data and assumes that heavier fish of a given length are in better condition (Bolger et al., 1989). It is believed to be a good indicator of the general well-being or fitness of the population under consideration. Changes in condition reflect normal seasonal fluctuations in metabolic balance and patterns of maturation (Wheatherly, 1972).

As condition factor, Rickers' condition factor K was used with:

$$K = [\text{body weight} / (\text{standard length})]^{b} \times 100$$

K assumes allometric growth and relates the actual weight which would be expected under "standard" conditions. The b-value is calculated from the standard length - body weight relationship which is expressed by the equation:

$$\text{body weight} = a\,(\text{standard length})^{b} \text{ (Pauly, 1984)}$$

The values of a and b are estimated by means of the linear regression:

$$\log \text{body weight} = \log a + b \log \text{standard length}$$

The value a represents the intercept on the X-axis and b the value of the slope. When growth is isometric, i.e. when growth proceeds in the same dimension as the cube of the length, the b-value lies close to 3 (Pauly, 1984).

Mean condition factor, and condition factor related to standard length grouped in 50 mm size classes and to time expressed in months were calculated for males and females separately. Finally, condition of the females was related to their stages of gonadal development.

3. Results.

a. Monthly sampling.

When sampling was started in January 1988 all nets were tried out and by the end of February it was established that whenever fishing took place, the bottom nets with mesh sizes of 12 and 15 mm caught the largest number of adult individuals of the species studied (figure 40). The smaller mesh sizes caught haplochromine juveniles which were difficult to identify and small *Barbus* species. The larger mesh sizes caught only occasionally large dominant haplochromine males and small *Tilapia*. From April onwards the most efficient nets (12 and 15 mm mesh sizes) were used during the monthly sampling program (Appendix D).

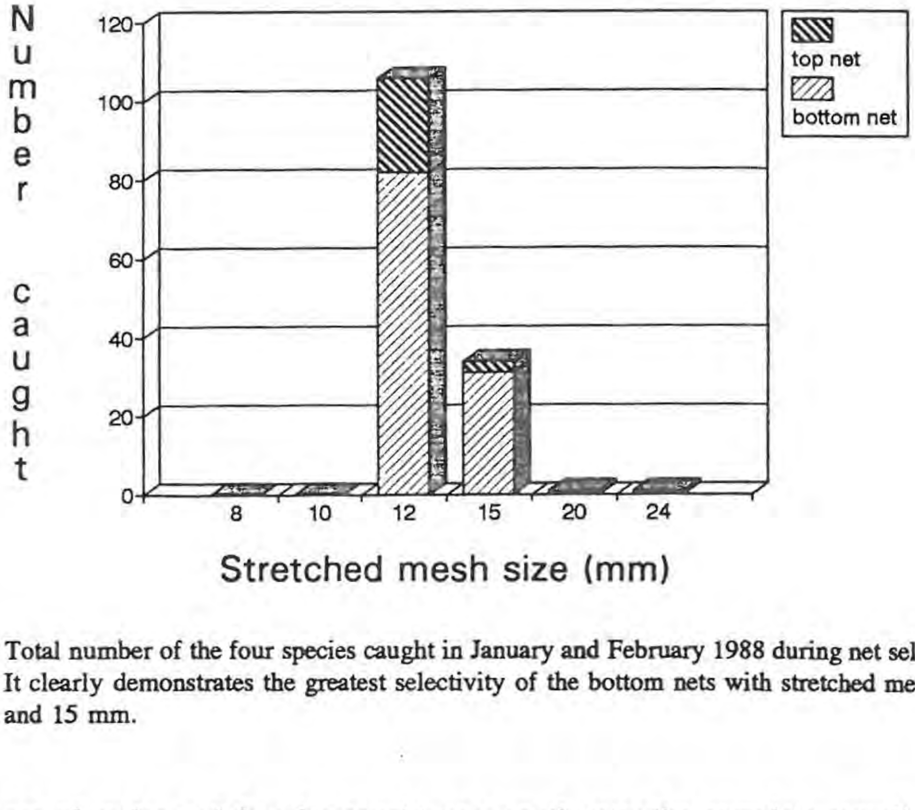


Figure 40: Total number of the four species caught in January and February 1988 during net selectivity trials. It clearly demonstrates the greatest selectivity of the bottom nets with stretched mesh sizes of 12 and 15 mm.

The numbers of males and females caught per month over the complete sampling period is summarised in figure 41. From April 1988 onwards a minimum of 30 individuals per month of *H. astatodon* and *H. crebridens* were caught. *H. paucidens*, because of its wide distribution both in shallow and deeper water, was caught in low numbers within the specified fishing zone; every month additional specimens had to be caught using scuba and handnets (table 4). Even using scuba, 30 individuals of *H. paucidens* per month were not caught. In September the catch of *H. paucidens* obtained by scuba was lost during the field trip and only seven specimens were available for that month (table 4; figure 41). Nevertheless, in spite of the low numbers, trends were discerned and could be compared with those observed in the three other species. In August only 22 *H. olivaceus* were caught (figure 41). If the nets would have been set within the rocky zone more specimens would most likely have been caught. This was not accomplished because of outboard engine trouble.

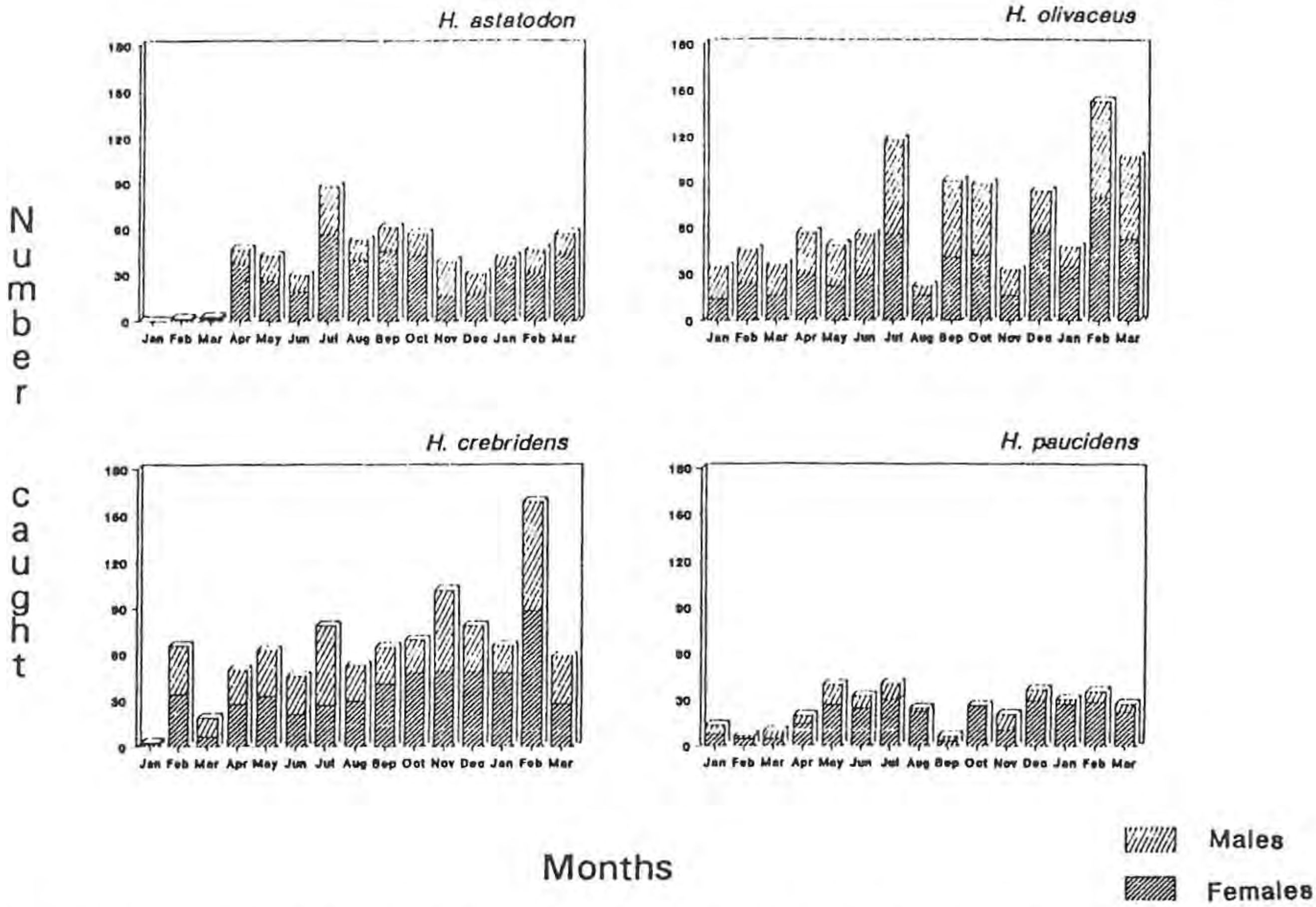


Figure 41: Number of males and females caught per month for each of the four species studied.

Table 4: Total numbers of *H. paucidens* caught per month using gill nets and scuba.

Year	1988												1989		
Month	Ja	Fe	Ma	Ap	Ma	Ju	Ju	Au	Se	Oc	No	De	Ja	Fe	Ma
Nets	14	7	10	12	26	19	27	2	7	6	13	15	8	18	10
Scuba	0	0	0	8	14	14	14	23	-	21	8	22	23	18	18
Total	14	7	10	20	40	33	41	25	7	27	21	37	31	36	28

The total number of males and females caught and sex ratios for each species is summarized in table 5. The sex ratio of *H. paucidens* is influenced by the fact that mainly large mature spotted females were collected during scuba. It is therefore not representative of the true relationship between the number of males and females present within the fishing site. The 1:2 sex ratio of the total sample of *H. astatodon* is believed to be related to the fact that the vegetation zone represented the breeding grounds of this species where females outnumbered males on the breeding arenas. Scuba observations confirmed this, as territorial *H. astatodon* were exclusively observed within the dense vegetation zone of Tshegera Island (figure 58).

Table 5: Total catches and sex ratios for each of the four species studied.

Species	Males	Females	Total	Sex ratio
H. astatodon	180	418	598	1:2
H. olivaceus	481	533	1014	1:1
H. crebridens	445	534	979	1:1
H. paucidens	86	291	377	1:3

The size distribution of the total catch in each species lay mostly within the range 55 to 80 mm (figure 42). The largest sizes were recorded in *H. crebridens* and *H. paucidens* which grew up to 105 mm and 110 mm respectively.

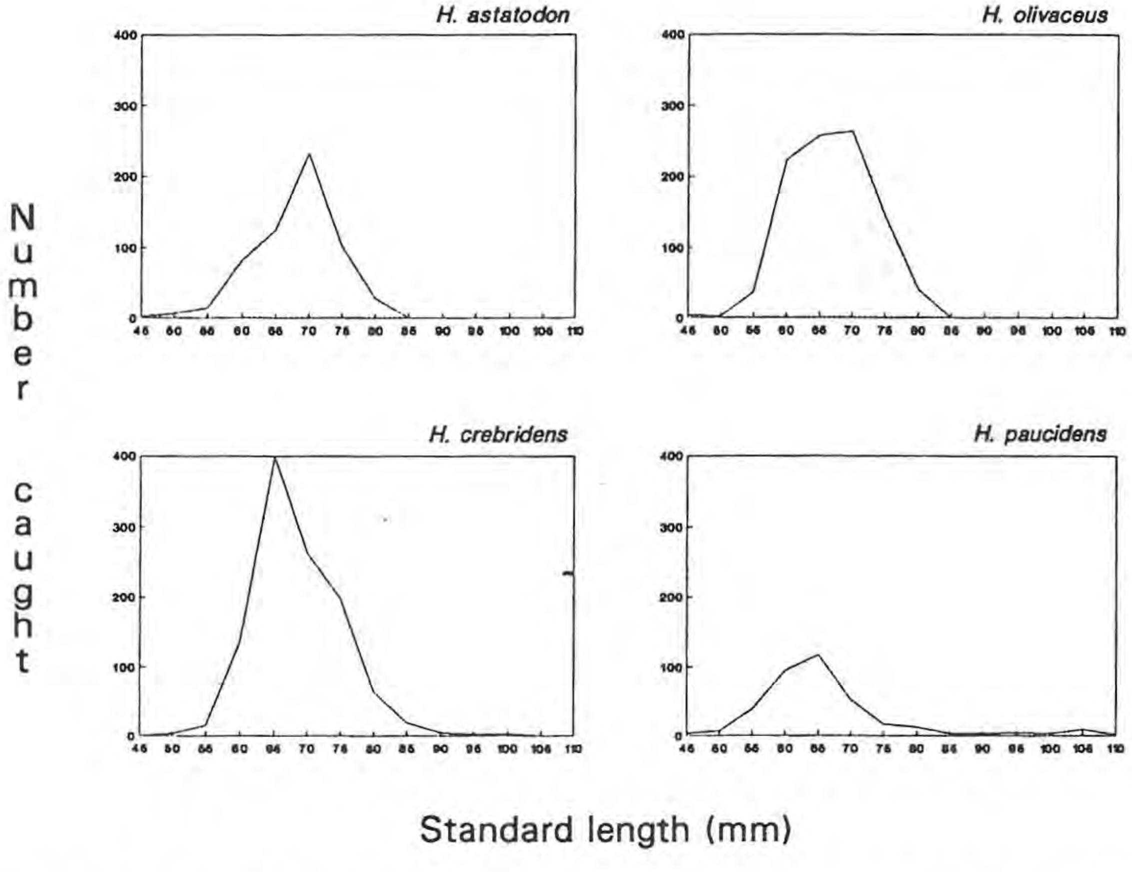


Figure 42: Size distribution of both sexes combined for the total catches for each of the four species studied.

The sex ratio varied according to the size of the fish concerned (figure 43). Females exceeded males in number between 55 and 70 mm standard length for *H. olivaceus*, and between 60 and 80 mm standard length for *H. astatodon* and *H. crebridens*. In *H. paucidens*, females were more abundant than the males in almost the complete size range, because, as already mentioned above, they were visually selected during night dives. In all four species the largest fish were males.

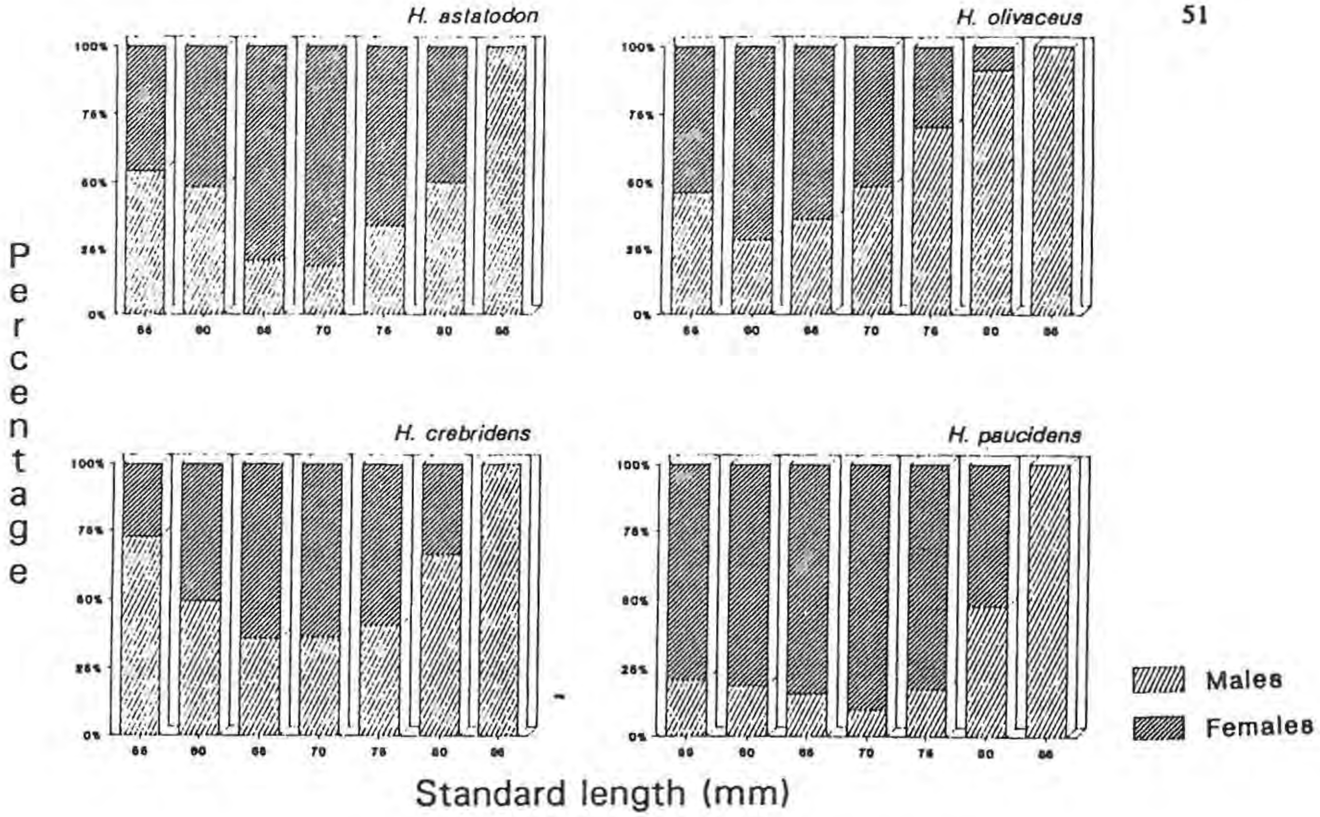


Figure 43: Percentage of males and females caught in 5 mm size classes for each of the four species studied.

b. Reproductive Seasonality.

Breeding of variable intensity went on throughout the year (figure 44a & b). In the total catches the percentage of resting females equals that of breeding females in *H. crebridens* and *H. paucidens*, whereas in *H. astatodon* and *H. olivaceus* resting females were less numerous (table 6).

Table 6: Percentage of resting females (with gonads in 2/4 stage) in the total samples for each of the four species studied.

Species	Percentage
H. astatodon	34
H. olivaceus	40
H. crebridens	52
H. paucidens	51

During the long dry season between June and September 1988, all four species showed an intensified breeding with a GSI peak in July (figure 44b). During the other seasons GSI peaks did not clearly correspond to one another and asynchronous breeding seemed to be the predominant phenomenon. Nevertheless, it appears that *H. astatodon*, (breeding peak in November, 1988), *H. olivaceus* (breeding peak in January and December 1988) and *H. paucidens* (breeding peak in January 1988 and December 1988) bred preferentially close to or during the short dry season. On the other hand, *H. crebridens* (breeding peaks in March 1988, 1989 and October 1988) spawned during both short and long rainy seasons. *H. olivaceus*, in addition to its intensified breeding periods during the two dry seasons, showed a breeding peak in March 1988 together with *H. crebridens*, but this peak was not repeated the following year.

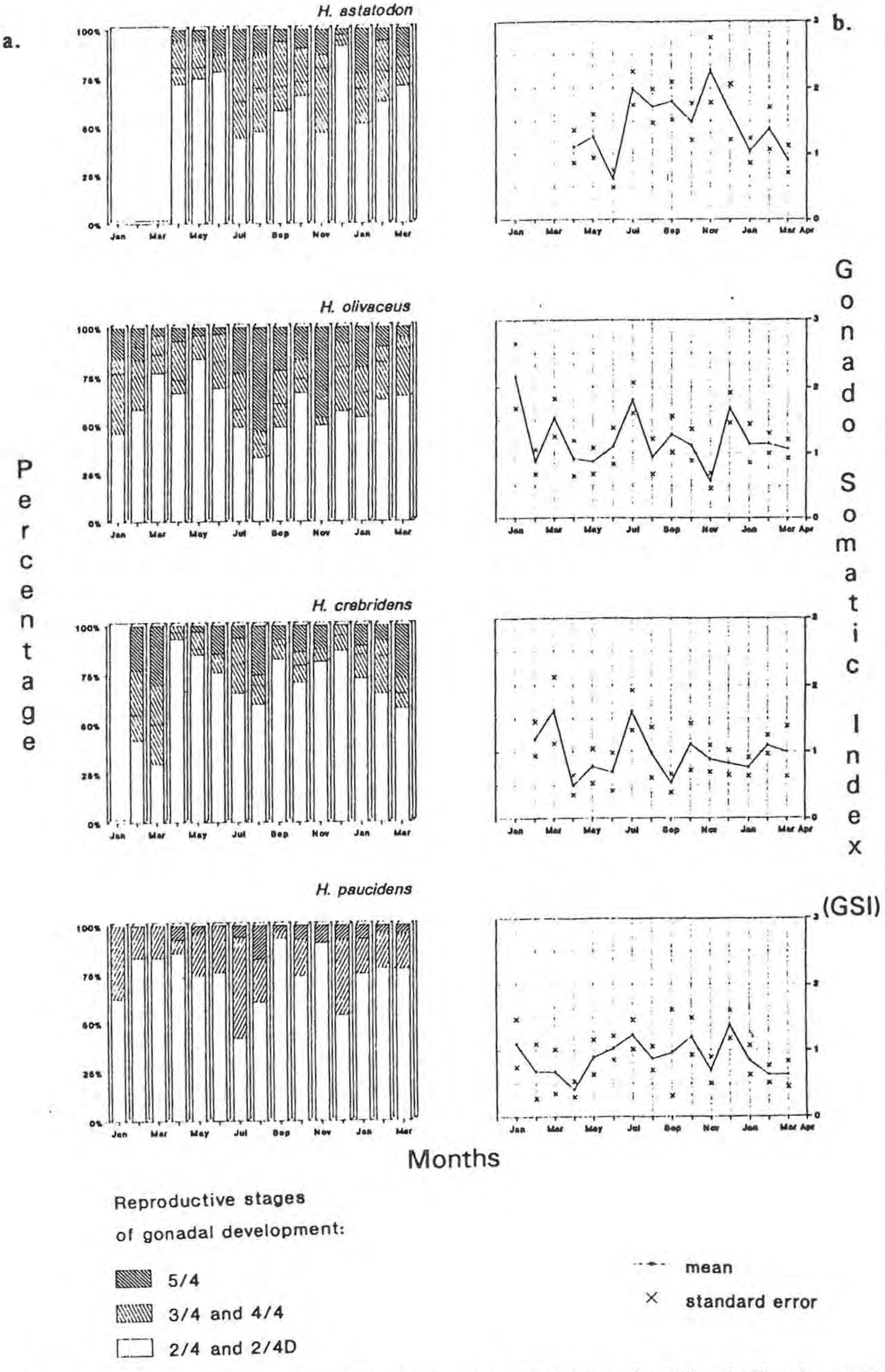


Figure 44: (a) Percentage of resting and developing (2/4 and 2/4D), breeding (3/4 and 4/4) and spent (5/4) females per month (n is the number caught); (b) mean GSI per month for each of the four species studied.

An interesting feature observed during assessment of the gonadal stages was that mouthbrooding females either had their gonads in stages 5/4 or 2/4 (as one would have expected them to be) or in a 2/4D stage (figure 38). This suggests that during a reproductive season females might go through a sequence of breeding sessions one after the other without recovery during a resting phase.

c. Fecundity.

The eggs were found to be unequally distributed between the two ovaries in each of the species, with the right ovary containing the largest number of eggs. The left ovary was much reduced and contained only about one third of the eggs contained in the right ovary (figure 38). Eggs were spherical in shape, but in the 4/4 stage they often became distorted because of compression.

All four species produced a low number of eggs per breeding cycle, the average ranging between 25 and 36 eggs per batch. The largest clutch size was counted in *H. crebridens* (59 eggs) and the smallest in *H. olivaceus* (9 eggs) (table 7).

Table 7: Relative fecundity (r), mean, maximum and minimum number of eggs produced in the ovaries for each of the four species studied (n is the number of females; ±std. is the standard deviation).

Species	n	r	±std.	Mean	±std.	Max.	Min.
H. astatodon	93	3.4	0.7	36	9	57	15
H. olivaceus	105	3.1	0.8	28	9	51	9
H. crebridens	71	3.0	0.8	31	9	59	13
H. paucidens	51	2.5	0.8	25	6	44	10

The size of the eggs was about the same in the four species with a mean egg height ranging between 3.5 and 3.7 mm and a mean width from 2.6 to 2.7 mm (table 8).

Table 8: Mean, maximum and minimum egg height, and egg width for each of the four species studied (n is the number of broods for which 10 eggs were measured).

		Egg height (mm)			Egg width (mm)		
Species	n	Mean	Max.	Min.	Mean	Max.	Min.
H. astatodon	16	3.5	3.9	2.9	2.6	3.0	2.3
H. olivaceus	18	3.7	4.3	3.2	2.7	3.1	2.1
H. crebridens	19	3.6	3.9	3.3	2.6	3.0	2.4
H. paucidens	10	3.6	4.0	3.2	2.6	3.0	2.3

Similar to the results obtained by Welcomme (1967) on mouthbrooding tilapiines, the relationship of ovarian egg production was found to be approximately equal to the square of the length (table 9). However, considering the r^2 values, this relationship has no meaning. By looking at the multiple box and whisker plots (figure 45) a trend of increase in egg number with standard length can be discerned as the medians increased as the fishes grew. The absence of any clear relation is likely to be explained by the small size range of the breeding females and the combined effect of low and high variable fecundity in relation to size, as illustrated by the widely overlapping interquartile ranges.

Table 9: Length (SL) - fecundity (F) relationship for each of the four species studied. The a, b, and r^2 values are from the regression as described in methods; n is the number of females.

Species	a	b	r^2	n
H. astatodon	0.50	2.20	0.20	93
H. olivaceus	0.53	2.10	0.29	105
H. crebridens	0.45	2.17	0.22	71
H. paucidens	0.73	1.83	0.38	51

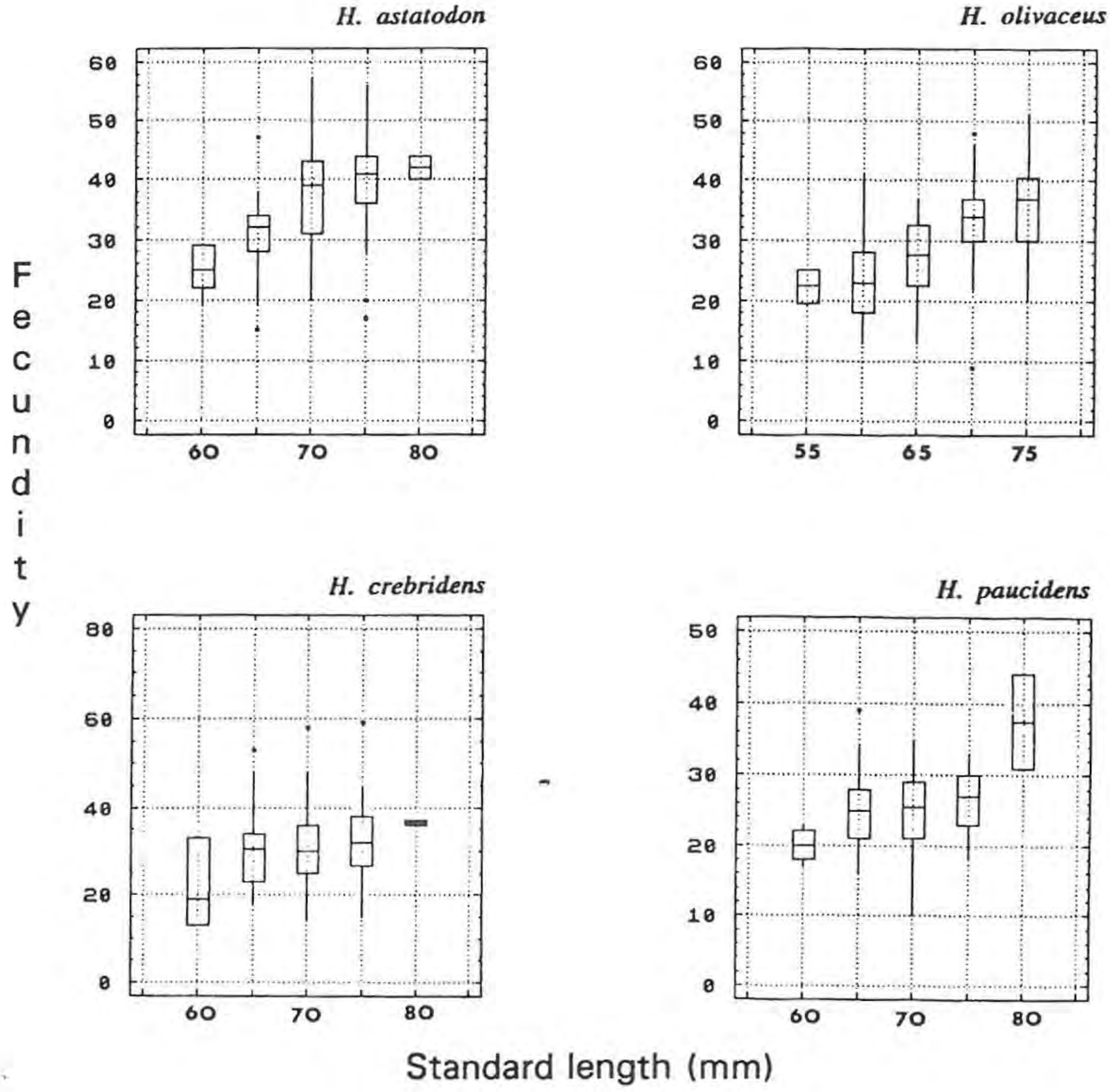


Figure 45: Relationship between standard length against fecundity for each of the four species studied.

d. Condition Factor.

Growth in weight was near isometric in all four species except for the females of *H. astatodon* and *H. olivaceus* which displayed allometric growth (figure 46; table 11). In the females and males of *H. crebridens* the b-value, and thus related growth rate, were the same; in the three other species males grew faster than females. Males grew to a larger size than females in each of the species and also reached sexual maturity at a larger size (table 10).

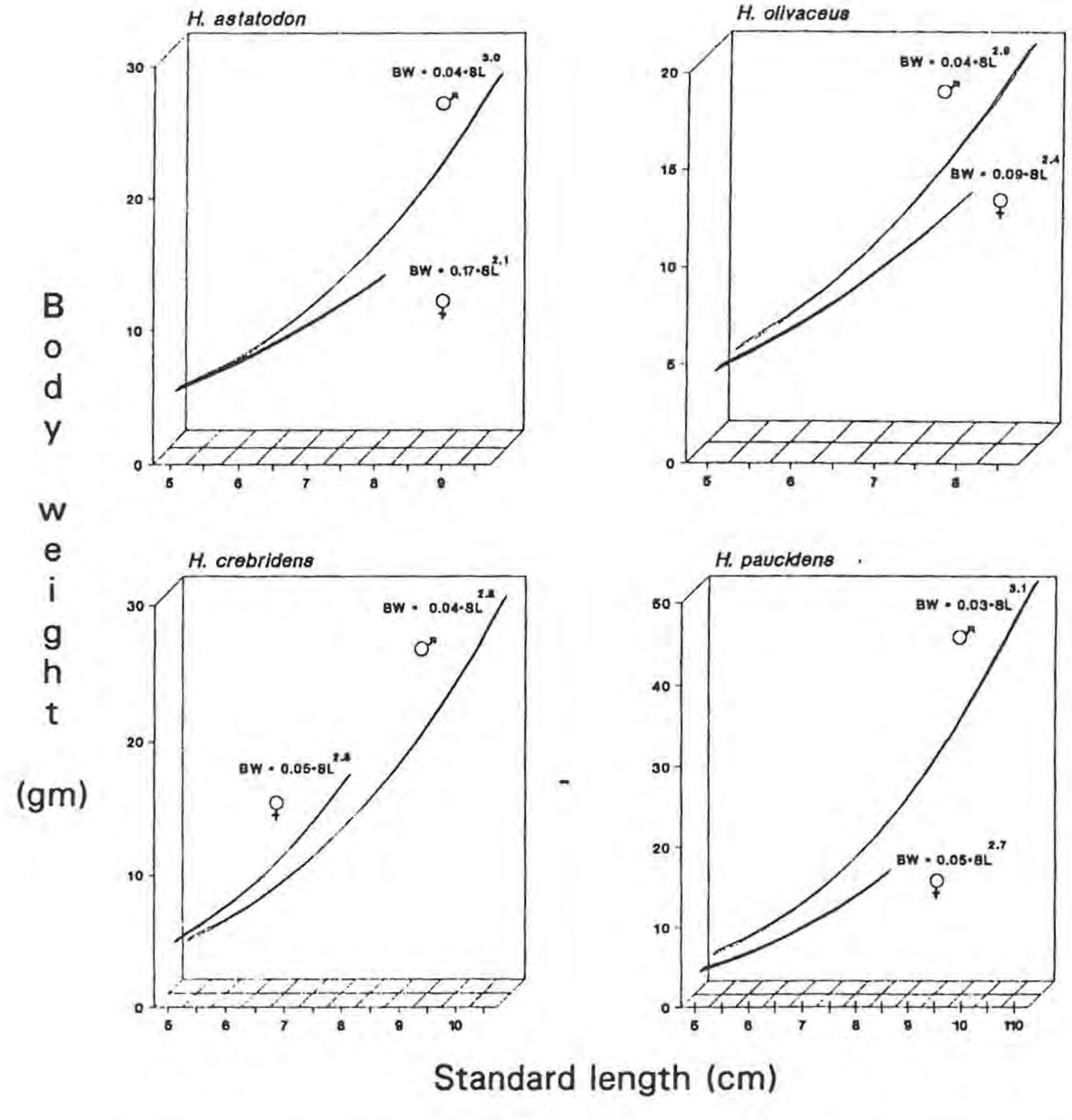


Figure 46: Length - weight relationship of males and females separately for each of the four species studied. (Standard length is expressed in cm and body weight in gm as recommended by Pauly, 1984)

In females of all four species *H. paucidens* attained the largest size (88 mm), the three other species reaching their greatest sizes at 81 to 82 mm (table 10). In males, *H. paucidens* also reached the largest size (109 mm), followed in descending order by *H. crebridens* (105 mm), *H. astatodon* (96 mm) and *H. olivaceus* (86mm). The latter showed the smallest intraspecific size difference compared with the females (table 10).

Table 10: Maximum size reached (standard length in mm), and size at first maturity for each of the four species studied (see methods).

	Maximum sizes		First maturity	
Species	Females	Males	Females	Males
H. astatodon	81	96	61	64
H. olivaceus	82	86	58	68
H. crebridens	82	105	60	79
H. paucidens	88	109	60	78

In *H. crebridens* the mean condition factor in the males and females was the same, whereas in the other three species it was greater in the females (table 11). The females of *H. astatodon* displayed the highest mean condition factor (18.2), followed in descending order by *H. olivaceus* (9.9), *H. paucidens* (5.4) and *H. crebridens* (4.4). In *H. astatodon* the mean condition factor of the females was more than four times higher compared to the males; in *H. olivaceus* and *H. paucidens* it was about twice as high.

Table 11: Length - weight relationship and mean condition factor (K) with standard deviation (±std.) for males and females for each of the four species studied; n is the number caught. Values of a, b and r^2 are from the regression as described in methods.

Species	n	Sex	a	b	r^2	K	±std.
H. astatodon	180	♂	-1.45	2.97	0.88	4.1	0.6
	418	♀	-0.76	2.12	0.66	18.2	3.2
H. olivaceus	481	♂	-1.34	2.86	0.87	4.1	0.5
	533	♀	-1.05	2.44	0.79	9.9	1.0
H. crebridens	445	♂	-1.40	2.83	0.92	4.4	0.5
	534	♀	-1.32	2.76	0.87	4.4	0.4
H. paucidens	86	♂	-1.58	3.06	0.84	2.4	0.4
	291	♀	-1.30	2.74	0.87	5.4	0.6

The condition factor of the males and females changed in relation to size (figure 47). In the females of *H. astatodon* and *H. olivaceus* condition factors increased up to 70 mm after which it decreased. *H. crebridens* displayed a bimodal pattern with the highest condition factors at 55 and 60 mm and at 70 and 75 mm. *H. paucidens* reached its optimal condition from 60 mm onwards. In contrast with the three other species, the condition factor of the latter did not decrease in the largest size class (figure 47). In the males of *H. astatodon* and *H. crebridens* the condition factor was lowest in the smaller size classes and increased rapidly in those fish between 85 and 100 mm (figure 47). Note that only low numbers were caught in the largest size classes where condition factors were optimal. In the males of *H. olivaceus* condition increased more gradually to the maximum value observed at 70 mm, after which it decreased. In this species largest numbers were caught in the size class with the highest condition factor. *H. paucidens* seems to display a similar trend as observed in *H. crebridens* and *H. astatodon* with optimal conditions in the biggest fish, but the number of males per size class was too small to draw any valid conclusions.

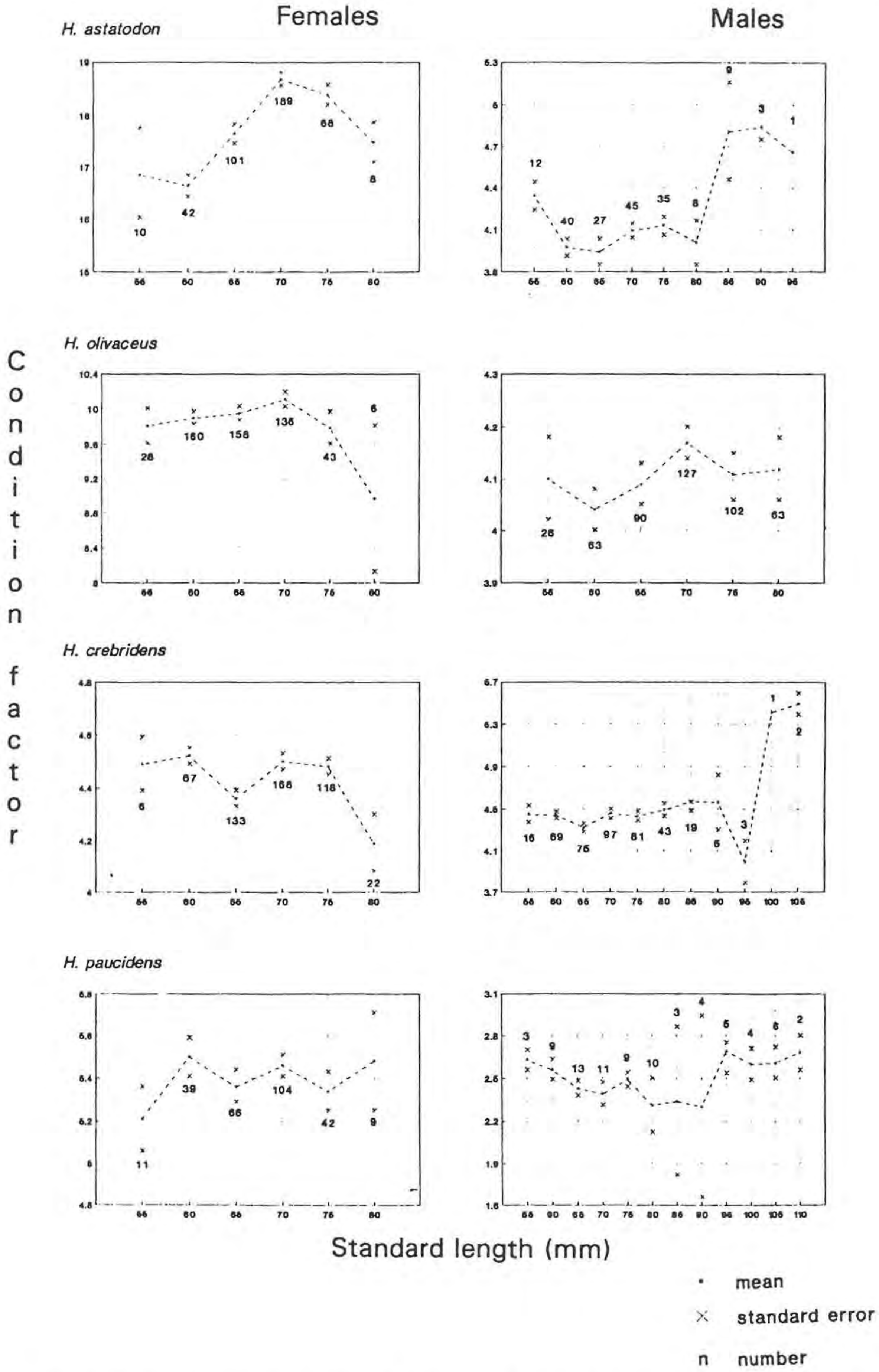
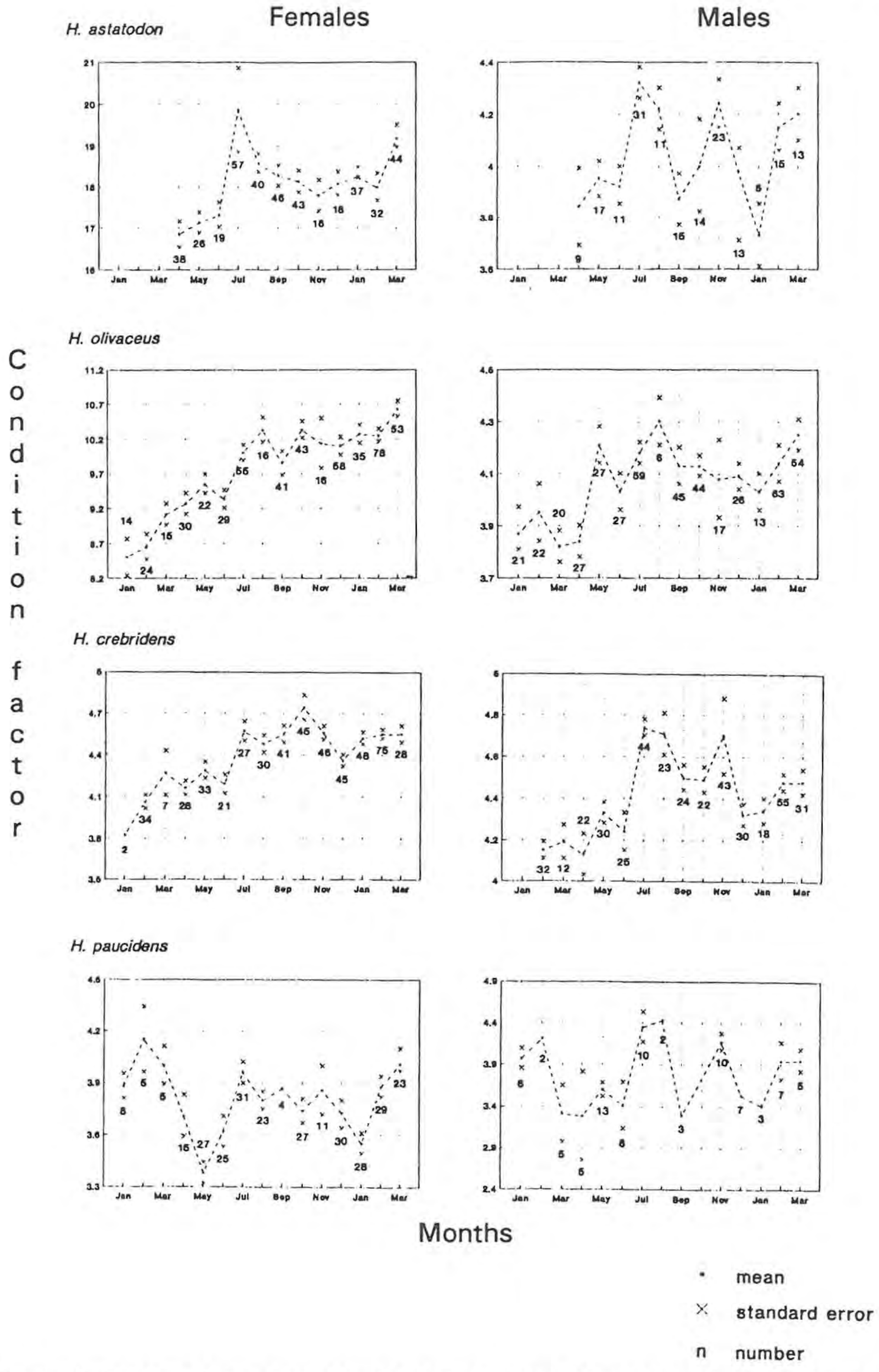


Figure 47: Relationship between standard length and condition factor for females and males separately for each of the four species studied.



Females

Males

H. astatodon

H. olivaceus

H. crebridens

H. paucidens

Figure 48: Relationship between time and condition factor for females and males separately for each of the four species studied.

The condition factors of the males and females also changed with time (figure 48). Over the sampling period condition factors of *H. astatodon*, *H. olivaceus* and *H. crebridens* gradually increased and in February-March, 1989 condition factors were higher compared with the previous year at the same time. The condition factor of *H. paucidens* did not display this general trend and was similar when sampling was started and ended.

All four species showed a peak in condition during the main dry season with *H. olivaceus* in August and the three other species in July (figure 48). At the end of the short rainy season (November, 1988) males of *H. crebridens*, *H. paucidens* and *H. astatodon* displayed high condition factors compared with the two previous months. In the females, only *H. crebridens* and *H. olivaceus* showed an increased condition factor between July 1988 and January-February 1989. In May, 1988 both males and females of *H. crebridens* and *H. olivaceus* showed a high condition factor.

In *H. astatodon* and *H. paucidens* condition was optimal when gonads were in the 3/4 and 4/4 stages, prior to spawning (figure 49). In *H. olivaceus* condition was optimal in the 2/4D stage and the 3/4 stage and in *H. crebridens* in the 3/4 stage. In all four species, condition dropped in the 5/4 stage to a level about equal to the 2/4 stage.

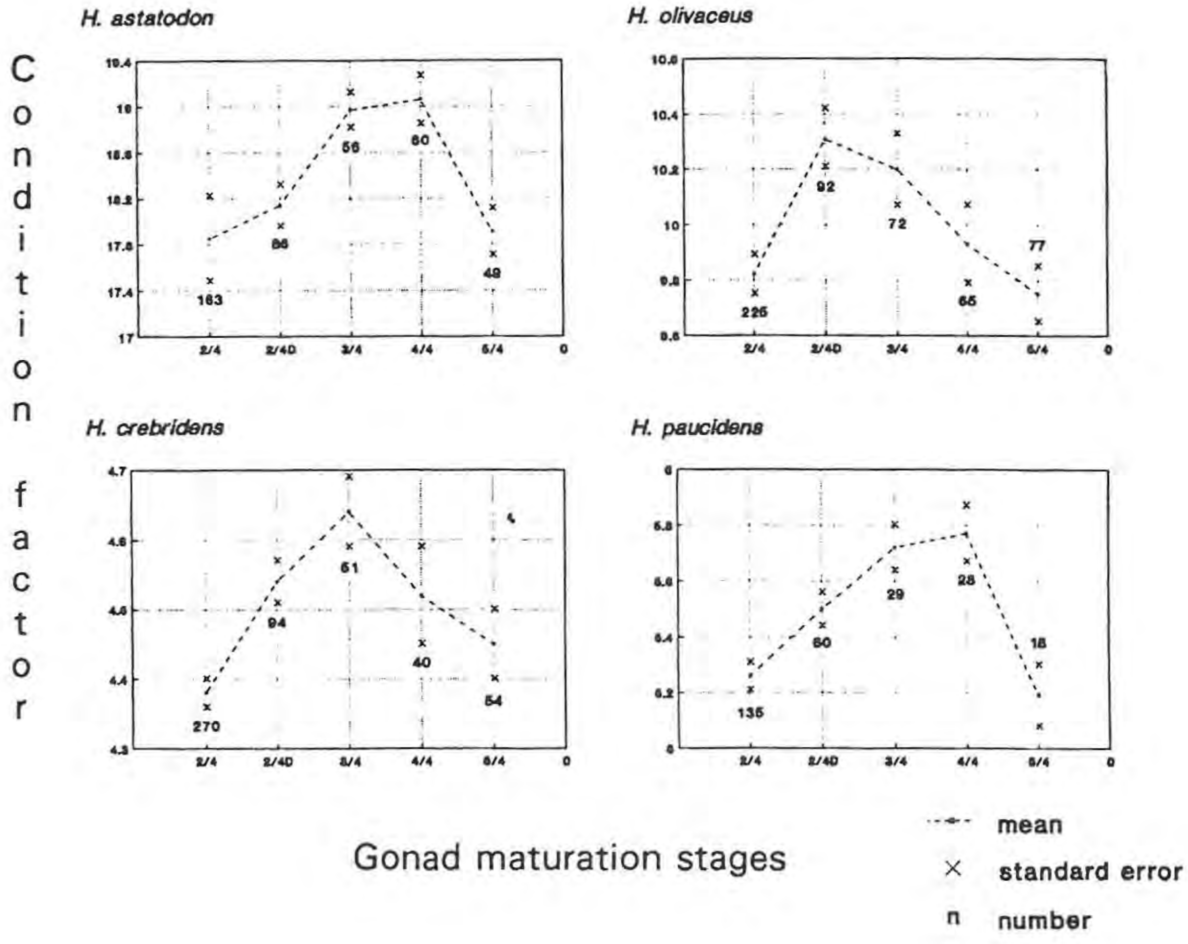


Figure 49: Relationship between gonad maturation stages in the females and condition factor for each of the four species studied.

3. Discussion.

Over the complete sampling period, overfishing of the species studied did apparently not take place as catches did not decrease in number or size. Even *H. paucidens*, with its low abundance within the fishing site, continued to be present throughout the sampling period.

The accumulation of males in the larger size classes is explained by males growing to a bigger size than females. Sexual dimorphism is a well known phenomenon in female mouthbrooders and has been described for cichlids of Lake Malawi (McKaye, 1984), Lake Victoria (Witte and Witte-Maas, 1987) and Lake Tanganyika (Kuwamura,1986). In most maternal mouthbrooders, large males establish territories which are essential for mating with visiting females (Kuwamura, 1986). Competition for optimal sites between the sexually mature males is high as their breeding success is entirely dependant on the ability to hold a territory (Chan, 1987). Behavioural studies on *Pseudocrenilabrus philander* (Chan, 1987), a small mouthbrooding cichlid endemic to southern Africa, clearly indicated that there was a general trend for large males to acquire breeding territories more easily. In territorial breeding males, the influence of size on dominance encounters has also been documented in *T. alcalica* (Coe, 1969), *Oreochromis esculentus* and *O. leucostictus* (Trewavas, 1983), *Cichlasoma nigrofasciatum* (Keenleyside et al., 1985) and many *Sarotherodon* species (Philippart and Ruwet, 1982).

Furthermore, in three of the four species studied, males grew faster in weight when compared with females and contributed additionally to males predominating in the largest size range. Faster growth in males relative to females has been observed in other cichlid fishes such as *Tilapia variabilis* (Fryer, 1961), *T. mossambica* (Bruton and Allanson, 1974) and *Sarotherodon mossambicus* (Hecht, 1980). Obviously, males in those species invest more in somatic growth, whereas females presumably in gonadal growth. Lowe-McConnell (1987) suggests that, in cichlids, discrepancy in size between sexes is a result of bioenergetic reasons, more weight being lost with egg than with sperm production and so retarding the growth of the females compared with that of the males. In *H. crebridens* males and females invested about equally in somatic growth and if the latter assumption holds, the females of this species would be expected to invest less in gonadal growth when compared with the females of the three other species studied. However, gonadal investment was highly similar in all four species and suggests that in this study the speed at which females increased in weight had no direct effect on gonadal growth.

Slow growth in weight came out to be related to a better condition factor and, hence, indicates that the slower growing females of the species studied accumulated larger body reserves when compared to the faster growing males. A better condition might be required in the females because of the interference of mouthbrooding, although this does again not hold for *H. crebridens*.

Interestingly, condition factor in the females of the species studied improved with the degree of specialisation. *H. astatodon*, an epiphytic algal grazer, displayed the most highly differentiated teeth and had a very high condition factor. *H. olivaceus*, the only typical aufwuchs feeder of the lake, comes next in order and *H. paucidens*, a more generalized insect feeder, displayed a low condition factor. One might take this line of reasoning further, for the level of specialization might in turn be related to food abundance. A more generalized feeder probably feeds on food items which are present in a wider habitat because of a eurytopic nature, whereas specialized species being stenotopic, limit themselves to a more and more specific feeding site and diet, exposing themselves to environmental fluctuations. Although lakes are known to be stable environments, variations in food abundance are known to fluctuate on a yearly basis. Improved body condition in order to cope with environmental instability might be an additional adaptation in the more specialized species and might allow females to produce offspring, even when environmental conditions are not optimal.

In the males, young individuals were in low condition most likely because of competition for fast growth in order to reach the size at which a breeding territory can be hold, at which condition factor improved slightly.

The dominance of females in the medium size range is more difficult to explain. Hodgkiss and Man (1978) obtained similar results in a biological study on *Sarotherodon mossambicus* and suggested that it might be the result from small males being less prone to capture or more prone to natural mortality than small females. In this study a higher natural mortality in the males might occur as indicated by the lower condition factors in the medium size ranges.

Most female mouthbrooders have a common reproductive strategy involving a lek-based mating system characterized by polygynous mating, weak or no pair-bonding, no parental care and localized areas where males and females congregate to mate (Fryer and Iles, 1972; Loiselle and Barlow, 1978). In the present study, males established stable mating stations (Appendix E), but concentrations of the territories was only apparent in *H. olivaceus*. In the other three species they were scattered over almost all the available habitat. Moreover, in all four species, the males usually fed within their territories.

In *H. olivaceus*, the concentrations of several male territory holders seemed to be related to a more intense aggressive behaviour when compared with the males of the three other species. During diving observations injured dominant *H. olivaceus'* males were occasionally observed hiding in rock crevices. In the aquaria territorial fights between dominant males of this species were so common that never more than one male was kept in a breeding tank. This strong aggressive behaviour is at least partly explained by the fact that the size difference between sexually competing males for territories is smaller compared to the males in the three other species. Aggression, namely, appears to occur more frequently between individuals that are closest in size (Barlow, 1974; Shulman, 1985).

The beginning of the main dry season was characterised by synchronous breeding as the four species showed both a peak in GSI and a peak of increased number of breeding individuals at that time of the year. Synchronous breeding often reflects a response to seasonal fluctuations in food availability (Lowe-McConnell, 1975, 1979 & 1987; Witte, 1981; McKaye, 1984; Marsh et al., 1986; Steward, 1988; Etim et al., 1989). Undoubtedly, the major reproductive phase between July and September takes place when environmental conditions for the offspring are optimal. The dry seasons correspond with major plankton blooms (figure 8)(Verbeke, 1957a; Kiss, 1966), the principal food item of the juveniles (pers. comm. Ulyel). The coincidence of fry abundance in cichlid species with periods of high plankton production is also mentioned by Lowe-McConnell (1987), Etim et al. (1989) and Goldschmidt (1989). For the mature individuals, however, food availability and feeding conditions are believed to be optimal before the major plankton bloom. The high transparency and quiet water conditions towards the end of the rainy season allow optimal epiphytic and epilithic algal growth (Van der Ben, 1959), a fundamental food component for most adult

Lake Kivu haplochromines (Verbeke, 1957b). During the dry season, increased wave action progressively destroys the *Cladophera* carpet (Van der Ben, 1959) limiting food availability for the adults. Similar results indicating breeding activity after a period of relative food abundance are described by Witte (1981) for haplochromine species in Lake Victoria. The major reproductive phase, therefore, takes place when food abundance for the reproducing individuals is scarce, but is optimal for the offspring. The adults, however, enter this major reproductive phase in optimal condition with reserves for breeding having been laid down previously.

A disadvantage of breeding during the dry season is that visibility at that time of the year is lowest. Current speed and turbidity are known to inhibit breeding behaviour in *Tilapia* species (Samarakoon, 1983). In Lake Victoria, Greenwood (1974) notes that despite the water turbidity, breeding activity in the haplochromines continues. Although haplochromines are known to be highly dependant on vision (Fryer and Iles, 1972), the importance of vision during breeding behaviour remains uncertain.

The other breeding peaks which were observed during the rest of the year were asynchronous. Asynchronous breeding is believed to be an important mechanism for maximizing limited food resources (Lowe-McConnell, 1987; Marsh et al., 1986).

The absence of a synchronous breeding peak during the short dry season might be explained by the fact that although this season corresponds to increased plankton blooms (figure 8), the intensity and regularity of these blooms are less pronounced compared with the main dry season (Verbeke, 1957a; Kiss, 1966; Van der Ben, 1959).

During the rainy seasons microclimates develop along the shore with sparse and localised phytoplankton blooms (Kiss, 1966) and irregular rainfall (Van der Ben, 1959). Breeding of local population in response to prevailing microclimatic conditions would be the rule during the rainy seasons resulting in a different reproductive activity for each species both spatially and temporally. The reproductive activity observed in the species studied during the rainy season is unlikely to be exactly the same in subsequent years as local microclimatic conditions vary from year to year. This is in contrast with the breeding activity displayed during the main dry season which is likely to take place on a more regular yearly basis in response to a lake wide environmental change.

In all four species, condition factor increased in the females as soon as gonads started to develop (2/4D stage). Therefore, at the onset of gonadal development both body weight and egg maturation were dependant on external food sources. In *H. olivaceus* and *H. crebridens*, condition factor dropped respectively in the 3/4 and 4/4 stages and suggests that part of the body reserves accumulated during the earlier stages of gonadal development are channelled in egg growth. In the two other species, *H. astatodon* and *H. paucidens*, egg growth was entirely dependant on energy tapped from the environment, as body condition continued to improve until eggs were ripe. In spent and mouthbreeding females, condition dropped to the same level as observed in individuals with resting gonads. The present observations, therefore, clearly indicate that only the amount of energy accumulated during gonadal maturation becomes consumed during mouthbrooding and suggests that although the energy turn-over during gonadal development might be high, the energy demand on the female is low. These findings concord with the work of Mrowka and Schierwater (1988) who state that mouthbrooding, in terms of energy metabolism, can be split in two extremely different periods: an investment phase and a consumption phase. The investment phase is characterised by intense food intake which contributes to maintenance, growth, new egg batches and energy storage for use during the subsequent spawning. The consumption phase corresponds with the mouthbrooding phase and is characterised by low energy turn-over capitalising on investment made previously. Therefore, it can be concluded, as stated by Mrowka and Schierwater (1988), that "*mouthbrooding is a low-cost strategy profiting from investment made during the preceding non-reproductive phase*".

Except for *H. paucidens*, the overall well being of the fishes increased gradually over the sampling period. Notably, the amplitude of change in condition with time was larger when compared to change in condition with intensified breeding, gonadal maturation or size. Findings in studies on the nutritional ecology of *Oreochromis mossambicus* populations in man-made lakes in Sri Lanka (De Silva, 1985) and on *Sarotherodon mossambicus* in Lake Sibaya, South Africa (Bowen, 1979) illustrated that, although within a population the condition may change with the reproductive status of the population, the overall condition of a population is determined by the nutritional value of the material ingested. Therefore, it is likely that in the species studied, the gradual increase in condition with time is related to a gradual improvement in the environment with respect to food availability and/or quality, and that nutritional constraints have a more important impact on the overall well being of the fishes rather than breeding. In *H. paucidens*, the more or less uniform condition factors observed over the sampling period might be related to its generalized insectivorous diet which is likely to be more uniformly available throughout the year.

Increase in fecundity with standard length is a common phenomenon in fish in general (Botros, 1969; Welcomme, 1967; Perrone, 1978; Lowe-McConnell, 1987; Kuwamura, 1986; Etim et al., 1989). Although in this study no correlation was found between fecundity and standard length, the multiple box and whisker plots clearly indicated an overall trend of increase in egg number with size of the adults. The poor correlation could be a result of successive breeding by the females. As mentioned earlier, females are believed to be able to breed several times without a resting phase between. At the beginning of a breeding cycle both small and large individuals produce their highest number of eggs with the highest fecundity in the largest specimens. As the breeding cycles succeed each other, the number of eggs produced decreases, giving rise to the poor correlation and wide range of eggs produced per size class as observed in the multiple box and whisker plots. Cases of successive spawning among African cichlids in one season with number of eggs diminishing at each spawning is also mentioned by Lowe-McConnell (1987). Jubb (1952) observed five broods in one breeding season in *Sarotherodon*. Successive waves of gametogenesis in cichlids has also been demonstrated for both males and females by Hyder (1970), Bruton and Boltt (1975) and Siddiqui (1979).

Successive breeding observed in the four haplochromines studied must nevertheless be distinguished from some tilapiine species, where at the beginning of the breeding season the egg sizes can be differentiated into a number of size classes corresponding to the number of broods within that same breeding season (as illustrated by *Tilapia zillii* in Lake Mariut; Botros, 1969). In the haplochromines studied, the gonads in the 4/4 stage display one size class, and eggs produced at each breeding session start from a batch of undeveloped eggs.

VI. Circadian Activity and Fish Distribution.

1. Introduction.

Organisms display particular distributions and activity patterns within their normal habitat (or preferred habitat). The normal habitat of a species refers to the habitat in which it originally evolved. It is viewed as a basic aspect of the recognition concept and is a characteristic of a species (Paterson, 1982).

Circadian rhythms, in general, are explained by diurnal changes in ecological parameters, such as light, temperature, oxygen and salinity (Mondshawsky, 1958), and food availability (Neveu, 1981). In fish, depending on the ecological requirements of each species, a variety of activity patterns have been found in relation to feeding behaviour (Sharp, 1981; McKaye, 1983; Ulyel, 1991), breeding behaviour (Ribbink, 1975; Sharp, 1981; McKaye, 1983) and physiological adaptations (Welcomme, 1964), such as for example optimal temperature selection for growth (Caulton, 1975 & 1978).

In the East African Rift Lakes the geographic distribution of the cichlids is known to be linked to the ecological requirements of each species. Most fishes are distributed according to water depth and nature of the substrate (Ribbink, 1991).

In order to obtain information on daily rhythms, depth distribution and substrate preference of the Lake Kivu ichthyofauna in general, and of the haplochromines studied in particular, 24-hour fishing periods in different biotopes at Tshegera Island were carried out (figure 50).

Figure 50: Fishing sites during the first, second and third 24-hour cycles at Tshegera.

2. Material and methods.

a. Circadian activity.

To investigate circadian fish activity, 24-hour fishing sequences were carried out. They were divided into six four-hour periods at which catches were removed.

The ichthyofauna at the island was subdivided into three groups including: (1) the 'species studied', (2) all the 'other haplochromines', and (3) all 'non-haplochromines' including the *Tilapia* species, *Limnothrissa miodon*, the *Barbus* species, *Clarias gariepinus* and *Opsaridium moorii*. Their daily activity was investigated in two different environments at the island: in August 1988 (dry season) and in November 1988 (wet season) nets were placed along the vegetated zone between 3 and 10 m deep and in April 1989 (wet season) they were set in between the two northern extremities of the eastern and western arms between 10 and 30 m deep (figure 50).

During the first two 24-hour cycles 10 nets were set separately and perpendicular to the coastline (figure 51a). To avoid a gradual selection of fish with respect to size from one end to the other end of the fishing area the mesh size sequence was varied as illustrated in figure 51a. The distance between the nets was 20 m. During the third 24-hour cycle the same nets were linked to each other and were set out as illustrated in figure 51b. The first 24-hour cycle started at 16h, the second at 4h and the third at 20h (weights and buoys were set out beforehand).

By placing the nets perpendicular to the coastline in the first two 24-hour cycles, differences in catches between them should not be due to difference in habitat or to depth preference as the slope and substratum are uniform (figure 12a & b), but rather to a difference in activity and density of the various species of different sizes within the same habitat.

Nets were lifted every four hours and were immediately returned into the water after removal of the catch. Caught fish were first injected with 5% formalin and numbers caught per net were counted; they were then transferred into a single bag referring to net setting, mesh size and fishing period. On return to the camping site the bags were placed in buckets for each fishing period separately and were preserved in 5% formalin. In the laboratory fish were then further identified and labelled as mentioned earlier.

During the first 24-hour cycle the weather during the day was sunny with almost no wind. At night the weather was quiet with short soft rain at midnight. When lifting the nets at the end of the final fishing period at 20h, a strong north-wind made rowing very difficult and the engine was used. The weather during the second 24-hour cycle was fine when nets were set out until about 16h when clouds and wind came up. Between 18h and 20h heavy rain poured down. At 20h dense clouds of Ephemeroptera flew close above the water surface. The moon came up at midnight. The weather during the third 24-hour cycle was quiet; at night there was little soft rain.

During the first two cycles fishing took place over 28 hours instead of 24 hours because in both the first fishing period appeared to represent an activity peak. To make sure that this peak was a true peak and not only due to a greater density of fish when fishing was started, nets were set out for one more period after the 24-hour cycle. Depending on the size of the

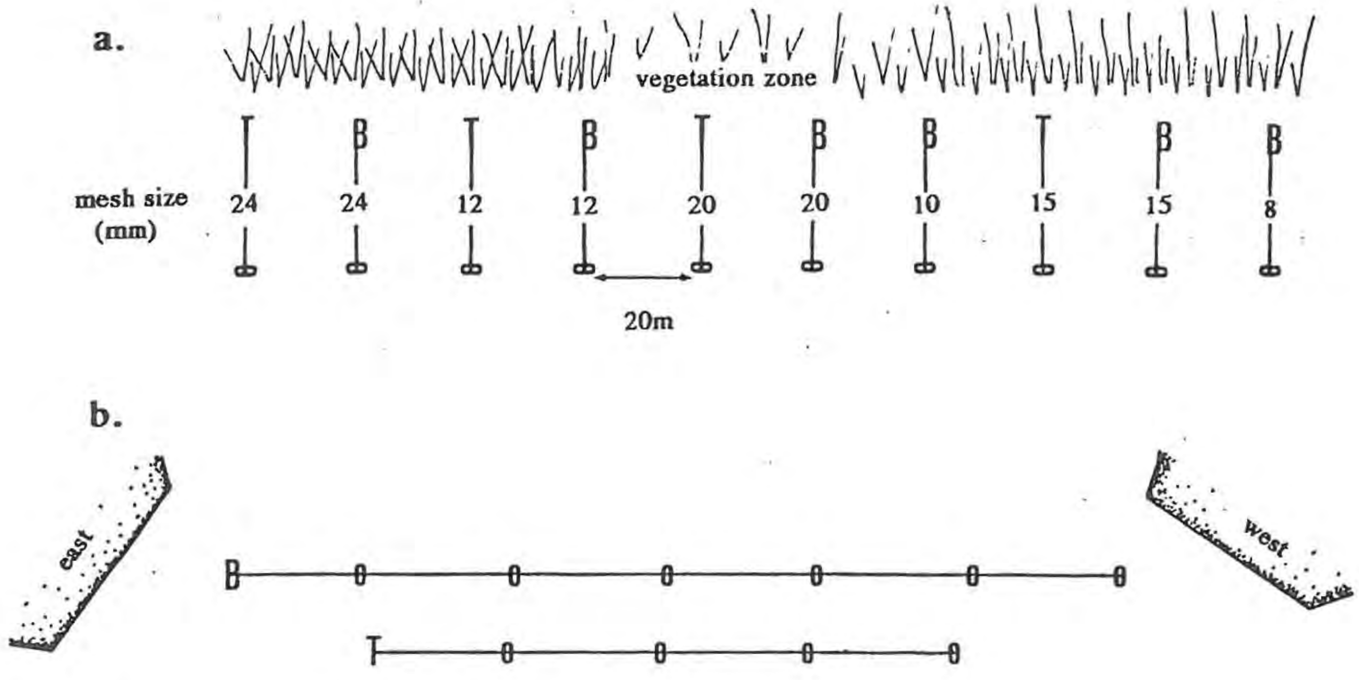


Figure 51: Net sequence and position during (a) the first and second 24-hour cycles and (b) during the third 24-hour cycle at Tshegera Island (T---O top nets; B---O bottom nets).

catch, the validity of the peak obtained during the first fishing period would be either confirmed or rejected.

Problems encountered during the 24-hour cycles were:

- During the activity peaks (where up to 370 fish were caught), the time between the removal of fish from the first net and the last one could be more than 1 hour.
- During the first 24-hour cycle, at the end of the first fishing period, the bottom net of 8 mm and of 24 mm were lost (these nets were found the following day using scuba). The net loss was due to (1) use of weights which were not heavy enough (between five and ten kg) and (2) "poor knots" in the ropes linking buoys and weights together.

The first problem could not be solved. The second one was solved by using weights of about 50 kg and by improving the knots, of course!

b. Activity peak analysis.

During the 24-hour cycles, increased activity took place during the early morning and evening. In order to establish the effect of change in light intensity on the activity of the species studied, each activity period was divided into three one-hour periods corresponding in the morning to: (1) before dawn (2) dawn/sunrise and (3) early morning and in the evening to: (1) dusk (2) sunset/twilight and (3) early evening.

Differences in timing of activity and species composition during the activity peaks were investigated in the vegetated and rocky environments of the island; all three morning and evening periods were repeated twice in each environment separately.

Only the meshes which caught the largest number of fishes during the 24-hour cycles, i.e. 12 and 15 mm top and bottom set nets were used. The nets were set out parallel to the coast line between three and seven meters deep and were immediately hauled in after a one hour period.

The difference in daylight between the main dry and wet seasons changed about 30 minutes in the morning and evening. During the dry season, days were about one hour shorter than during the rainy season. In the dry season the day began at about 6h00 and ended at about 18h00, whereas during the rainy season the day began at about 5h30 and ended at about 18h30. The days were shortest in July and longest in December.

As insufficient numbers of *H. paucidens* were caught in neither of the two environments using the gill nets, its activity during the activity peaks could not be analyzed.

3. Results.

a. Circadian activity.

The nets with mesh sizes 12 and 15 mm together caught at least 80 % of the four species (figure 52). The 15 mm net caught the largest number of fish during the dry season (first 24-hour cycle), whereas the 12 mm net during the wet season (second 24-hour cycle).

The loss of the nets with 8 and 24 mm mesh size during the first 24-hour cycle is believed not to have had any major consequence on the catch of the species studied. During the second 24-hour cycle no fish were caught in the 24 mm nets. Thys van den Audenaerde et al. (1982) mention that this mesh size only caught large *H. grauerie* and *H. vittatus* at greater depth close to the oxygen limit. This net, therefore, is of little use in the shallow water. The 8 mm net caught during the second 24-hour cycles a total catch of 160 fishes, of which 50% were represented by juvenile haplochromines. None of the four species could be recognized in this sample.

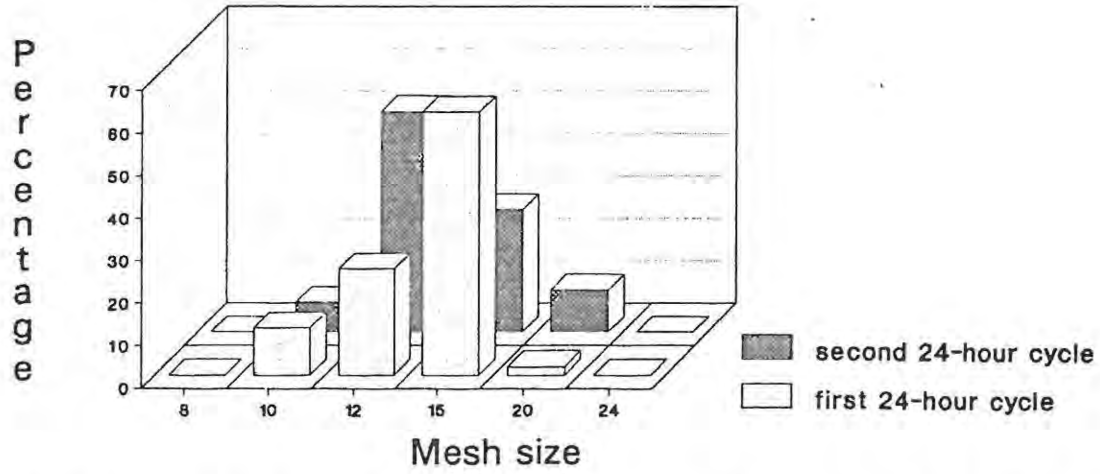
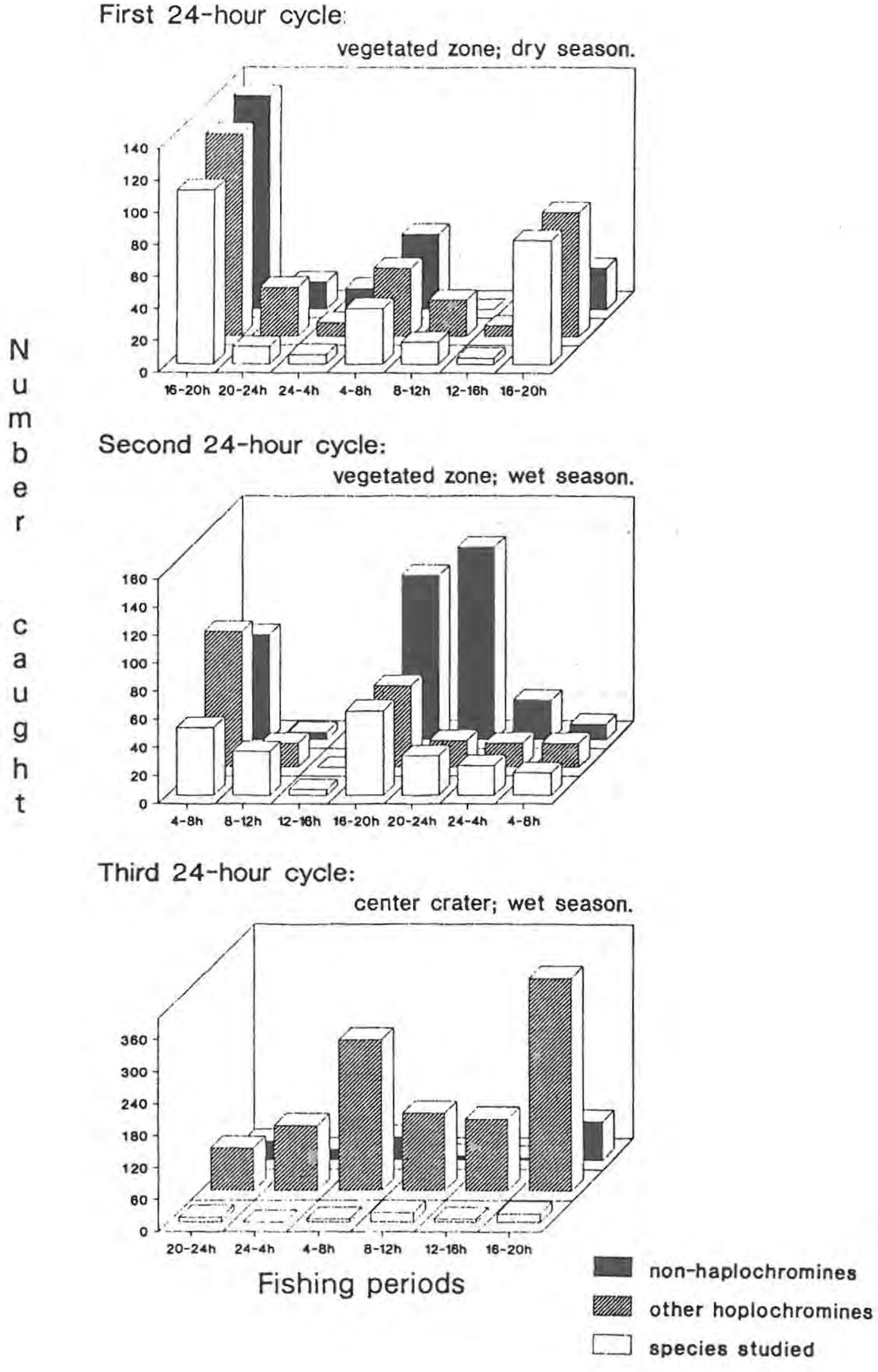


Figure 52: Percentage of the species studied caught in each mesh size during the first and second 24-hour cycles.

During the three 24-hour cycles, regardless of when fishing started, the largest numbers of fish were caught between 16h and 20h and between 4h and 8h (figure 53). In between those two activity peaks, fish activity was low. During the second 24-hour cycle after the evening activity peak, the non-haplochromines especially, continued to be active until midnight after which activity decreased (figure 53).

During the first 24-hour cycle the activity peak obtained in the early evening was repeated the following day, clearly confirming increased activity at that time of the day. This was not so for the second 24-hour cycle where increased fish activity observed during the early morning was not repeated on the next day. The absence of activity might be explained by the combined effect of overfishing and apparent lower activity compared with the evenings. In general, fish activity appeared less pronounced in the morning as at that time catches were always lower compared with the evenings independent when fishing was started. Nevertheless, fish clearly displayed increased activity in the early morning as its catch was always larger when compared with the two previous night fishing periods.


First 24-hour cycle:
vegetated zone; dry season.

Second 24-hour cycle:
vegetated zone; wet season.

Third 24-hour cycle:
center crater; wet season.

Figure 53: Number of the 'species studied', 'other haplochromines' and 'non-haplochromines' caught per four-hour fishing period during the first, second and third 24-hour cycles. Note that each cycle starts at a different time.

All four species were most commonly caught in the bottom set nets, except for *H. crebridens*, which during the night of the second 24-hour cycle displayed an activity within the watercolumn and near the surface (figure 54). Although *H. paucidens, H. olivaceus* and *H. astatodon* were occasionally caught in the top nets at night (figure 54), these individuals were always trapped at the bottom part of the nets in the shallow water close to the shoreline and most likely consisted of individuals frightened in their sleep. No fish were ever caught in the top nets during the day.

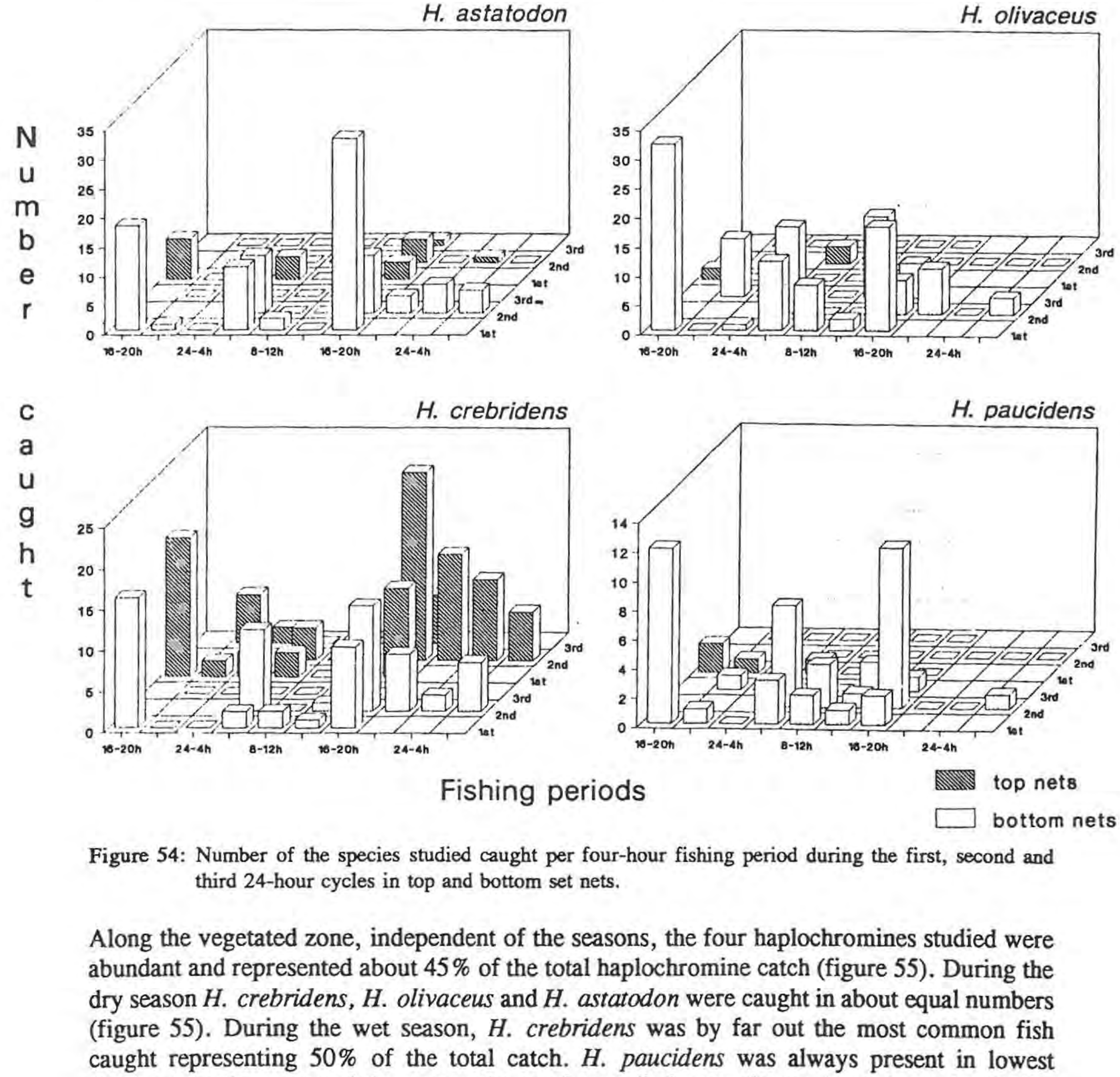
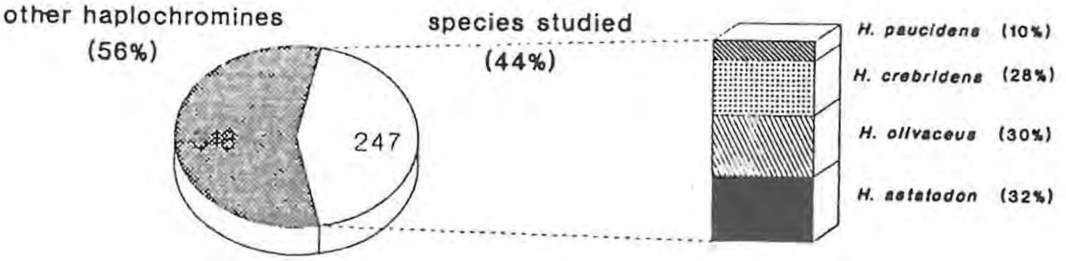


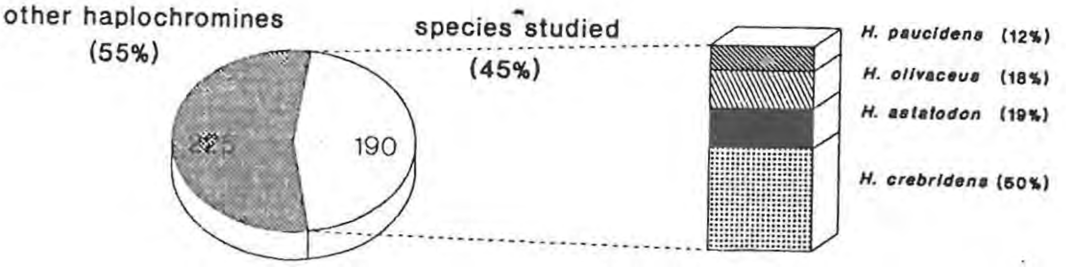
Figure 54: Number of the species studied caught per four-hour fishing period during the first, second and third 24-hour cycles in top and bottom set nets.

Along the vegetated zone, independent of the seasons, the four haplochromines studied were abundant and represented about 45% of the total haplochromine catch (figure 55). During the dry season *H. crebridens, H. olivaceus* and *H. astatodon* were caught in about equal numbers (figure 55). During the wet season, *H. crebridens* was by far out the most common fish caught representing 50% of the total catch. *H. paucidens* was always present in lowest numbers. In the centre of the crater, the species studied were almost absent from the fishing site whereas the 'other haplochromines' were caught in much larger numbers compared with the coastal fishing site (figure 55). Of the four species, *H. olivaceus* was the most common fish caught in the centre of the crater, followed in descending order by *H. crebridens, H. paucidens* and *H. astatodon* (figure 55).

First 24-hour cycle: vegetated zone; dry season.



Second 24-hour cycle: vegetated zone; wet season.



Third 24-hour cycle: center crater; wet season.

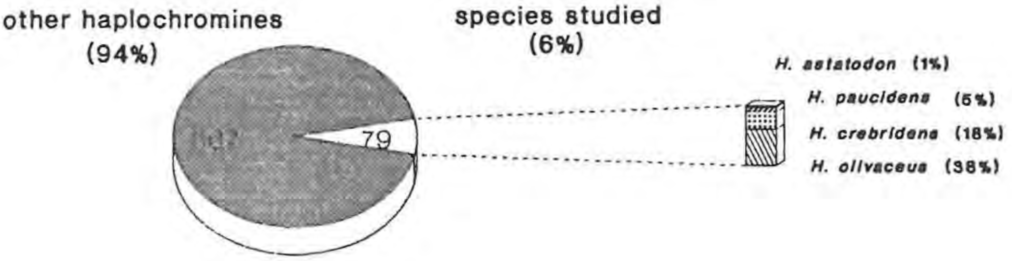


Figure 55: Percentage of the species studied relative to the total haplochromine catch and relative to one another for every 24-hour cycle.

b. Activity peak analysis.

Within each environment the percentage species composition between the early morning and evening activity peaks did not change. However, in the vegetated and rocky zones the percentage species composition during the activity peaks was different (figure 56). *H. crebridens* was commonly caught in both environments, *H. olivaceus* was more common within the rocky zone and *H. astatodon* was almost exclusively caught along the vegetated zone.

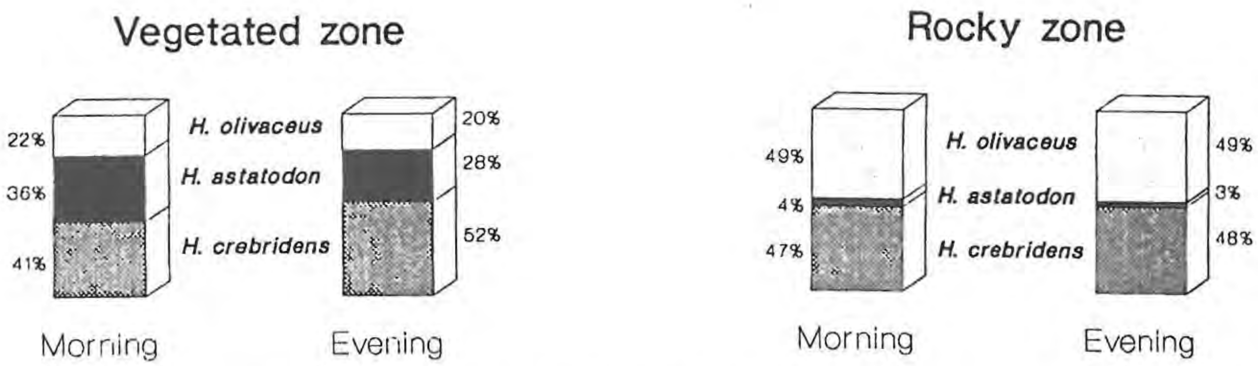


Figure 56: Percentage composition of the species studied in the early morning and evening along the vegetated and rocky zones.

In the morning, in both the vegetated and rocky zones, highest activity was observed during dawn, apart from *H. crebridens* which also showed increased activity before dawn in front of the rocky zone (figure 57). In the evening, all three species presented an increased activity during twilight in both environments. Activity dropped during the early evening, except for *H. astatodon* which once displayed a burst of activity in front of the vegetated zone.

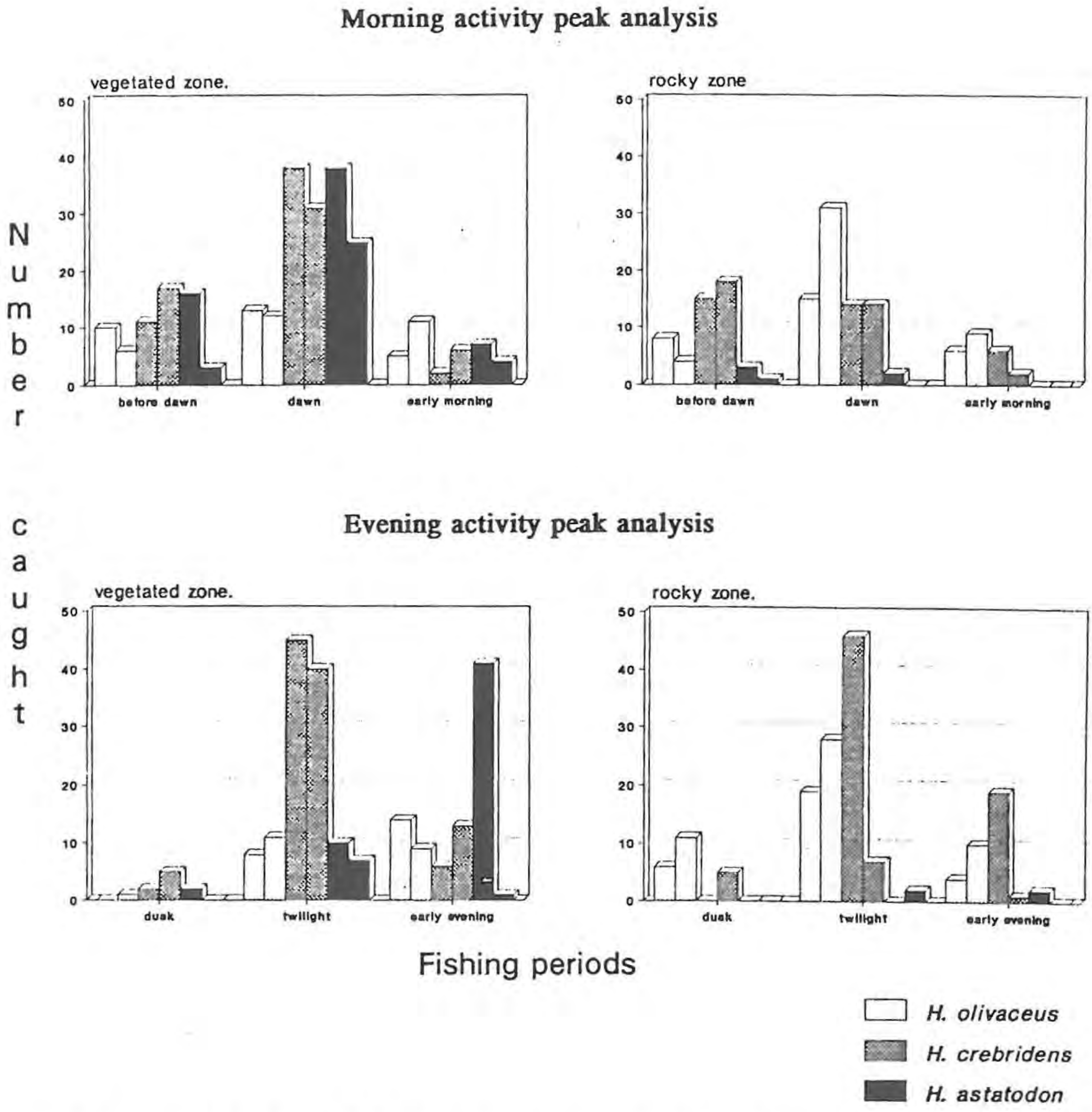


Figure 57: Analysis of the activity of the species studied in relation to change in light intensity in the early morning and evening along the vegetated and rocky zones.

3. Discussion.

The circadian activity of the haplochromines at Tshegera which was apparent regardless of site was characterised by two periods of synchronised activity: one in the early morning and another one in the early evening. These findings correspond to preliminary observations on circadian activity on the Lake Kivu haplochromines by De Vos et al. (1987), who experimented with the same gillnet sequence between 10 and 50 m deep in front of Gisenyi (Rwanda). The early morning and evening activity of the haplochromines, therefore, appears to be a lake wide phenomenon. It is likely to be stimulated by a common driving force and gives the impression that all haplochromines form a single unit.

This is in contrast to the observations made on habitat preference, where the individuality of each species within the haplochromine flock becomes more apparent. *H. olivaceus, crebridens* and *astatodon* not only are more common along the shore when compared to the haplochromine flock in general, but also show habitat preference within the narrow stretch of the coastline with respect to rocky, vegetated or midwater biotopes.

Daily rhythms of fish behaviour have been found to be related to increased territorial and foraging behaviour at specific times of the day as observed for example in *Pseudocrenilabrus philander* (Ribbink, 1975) or daily inshore and offshore movements by cichlid fishes into and away from shallow water in response to temperature preferences (Caulton, 1975 & 1978; Bruton and Boltt, 1975) or predator avoidance (Fryer, 1961; Jackson, 1961). In this study one must search for a common phenomenon causing synchronized circadian activity of all Lake Kivu haplochromines.

The analysis of the activity peaks seems to suggest that the impulse causing synchronized activity appears to be related to the change in light intensity at dawn and dusk. A common phenomenon shared by the Lake Kivu haplochromines is that they are active during the day and rest on the substratum overnight, except for a few species such as *H. crebridens* which occasionally was also active at night. From diving observations, lower catches in the bottom set gillnets between 8h and 16h appeared to be related to haplochromines dispersing away from the substratum. Consequently, the common morning and evening activity peaks are likely to be related to the haplochromines concentrating on the substratum overnight and dispersing again on the following morning. The circadian activity observed up to the present in the lake, therefore, is most likely only a glimpse of the full picture as activity has only been measured 1.50 m away from the water surface and the substratum, leaving the water column in between completely unexplored. The activity measured in this study is apparently only a reflection of the major resting and swimming periods of most haplochromines, but nothing is really known of possible greater or lower activity that might take place during the day itself.

The avoidance of the surface waters during the day by the entire ichthyofauna is believed to be related to bird predation pressure. Although bird predation has not been measured quantitatively, many indications support this hypothesis. One indication is the aggregation of cormorants, kingfishers, egrets and kites soon after dynamite fishing along the shore. Although these bird predators are usually present in low numbers, their sudden quick appearance when plenty of killed fish are stranded on the substrate, suggests that they are likely to effect fish distribution in the shallow transparent water. This is supported by diving observations. During the day in front of the vegetated zone, only those haplochromines (*H.*

sheffersi and *H. gracilior*) which mimic closely the colour of the pale yellow-brown substratum seem to be able to persist in this apparently unhostile biotope. This is further supported by the fact that the brightly coloured breeding males of these species (overall black body colour) defended their territories in water deeper than eight meters, most likely in avoidance of bird predation. The same holds for the more brightly coloured haplochromines on the rocky shore, which were never observed to venture over the uniform pale coloured substratum during the day. An interesting feature displayed by the haplochromines in general was that, with increasing depth fish moved away more freely from the substrate and gathered more easily in groups when compared to shallower water. This might again be under the influence of bird predation pressure in the littoral.

In contrast to bird predation pressure during the day, haplochromines are exposed to fish predation pressure at night. Adult *H. vittatus* in the aquaria fed on other haplochromine members only at night and usually hid behind rocks during the day. This behaviour was confirmed by diving observations, as adult *H. vittatus* only made their appearance at night in the coastal waters in search for their prey. The same holds for *Clarias gariepinus* which is known to feed on haplochromine species overnight, as for example in Lake Ihema, Rwanda (Plisnier et al., 1988) and in Lake Malawi (McKaye, 1983). But seeing the low numbers of both species (Thys van den Audenaerde et al., 1982), it is unlikely that these predators have any major consequence on fish behaviour.

VII. General Discussion.

1. Taxonomical and ecological aspects.

In accordance with the recognition concept, each of the four species studied comprises its own set of anatomical and ecological species specific characters, holding the members of the species together and allowing effective syngamy between conspecific mating partners within their normal habitat.

In this study, research has been directed with the aim to obtain an estimate of the level of specialisation of the Lake Kivu haplochromine flock, with an initial hint that the species flock is likely to be composed of generalised species. Applying the more recent punctuated model of evolution, which suggests that the main direction in evolution is towards increased specialisation in species specific characters (Vrba, 1980), it can be insinuated that the Lake Kivu haplochromines are likely to be in an early stage of diversification when compared with the highly evolved species flocks in the other East African Rift Lakes.

In classical taxonomy and evolution, specialization is equated with morphological specialization (Holm, 1985). Various degrees of morphological specializations are well illustrated in the haplochromines of East Africa, which show an overall trend of diversification from a generalized or plesiomorphic condition in the riverine ancestral environments to different levels of specialization and diversification (or derived conditions) in the East African Rift Lakes.

Viewing the Lake Kivu haplochromine flock in its integrity, the same basic trophic groups as recognized in the other East African haplochromine flocks can be identified (table 12).

Table 12: Trophic groups represented in Lake Kivu out of the 13 recognized in the African Great Lakes.

Trophic groups in African Great Lakes (from Fryer & Iles, 1972)	**Representatives in Lake Kivu** (from Ulyel, 1991 & own observations)
DEPOSIT FEEDERS	*H. scheffersi*
AUFWUCHS EATERS	*H. olivaceus / H. crebridens*
PERIPHYTON COLLECTORS	*H. astatodon*
MOLUSK FEEDERS	*H. adolphifrederichi*
FEEDERS ON INSECTS & OTHER BENTHIC ARTHROPODS	*H. paucidens / H. graueri*
ZOOPLANTON FEEDERS	*H. kamiranzovou*
PISCIVORUS SPECIES.	*H. vittatus*
EGG, EMBRYO & LARVAL FISH EATERS	*H. occultidens*
EYE BITERS	NOT REPRESENTED
PHYTOPLANKTON FEEDERS	
LEAF CHOPPERS	
SCALE EATERS	
FIN BITER	

However, the intragradation of contemporaneous forms within each trophic group from plesiomorphic to derived conditions, a phenomenon most clearly displayed in Lake Victoria (Greenwood, 1974), is absent. This aspect is clearly demonstrated in the species studied, where the plesiomorhic forms and/or intermediate forms leading to the derived condition within each lineage are missing.

Morphologically, according to Greenwood's classification the four studied species belong to taxa with a generalized level of organization. Synapomorphies within each lineage are mainly found in dentition indicating early trophic diversification. *'Paralabidochromis' paucidens* displays the least derived dentition within its taxon (figure 35) and has almost not evolved from the ancestral riverine species which are believed to display an insectivorous benthic feeding habit. *'Xystichromis' crebridens* and *'X' olivaceus* closely resemble *'X' nuchisquamulatus* (figure 29). This species is believed to represent the link between riverine insectivorous benthic feeding to algal scraping. *'Haplochromis' astatodon* is the only species which shows a highly derived condition within its taxon (figure 20).

In ecology, specialists (or stenotopes) are usually defined as species displaying narrow utilisation and tolerance of one or more environmental parameters, while generalists (eurytopes) are broadly adapted to the environment (Vrba, 1980). A characteristic of specialization is therefore comminution of the ecosystem (Bruton, 1989). As suggested by Holm (1985), before it is possible to consider the attributes of specialized and generalized species it must be stressed that we are only dealing with the opposite ends of a continuum and that most species vary within the eurytopic-stenotopic scale. Nonetheless, as stated by Eldredge (1979) in Vrba (1985), it is valid to distinguish between predominantly or "basically" eurytopic and stenotopic species. Each group of organisms, namely, has an inherited level of specialisation in which they can adopt various stages between eurytopy and stenotopy. A classical example of a eurytopic group is the cichlid genus *Tilapia*. Members of this group are characterized by marked ecological tolerance reflected by the distribution of particular species in a variety of environments (Fryer and Iles, 1969). By contrast, the genus *Haplochromis* exhibit a narrow utilisation and tolerance of the environment (Ribbink, 1991) and can be referred to as a "basically" stenotopic group of organisms. In similarity to their morphological specialisation mentioned above, the degree of habitat restriction in this group becomes also amplified with diversification from rivers into the lakes.

With respect to geographical distribution, the Lake Kivu haplochromines display a lake wide dispersion within the narrow stretch of coastline and show a wide range of depth preferences within the ML1 layer (figure 7). Investigations on the distribution patterns at Tshegera Island indicated that, at least in the species studied, haplochromine abundance is influenced by specific habitat or substrate criteria. *H. paucidens*, in spite of its more or less uniform distribution showed a preference for a sandy substrate; *H. olivaceus* and *H. crebridens* were confined predominantly, but not exclusively within the rocky zone; *H. astatodon* was the most selective species and occurred almost exclusively within the vegetated zone (figure 58).

From these observations on the species studied and on basis of more general diving observations it appears that the Lake Kivu haplochromines have invaded the major habitats available and have become adapted to live over sand, among rocks and within aquatic vegetation. Habitat restriction and comminution of the major habitats, however, is far from reaching the situation exhibited by the highly stenotopic and philopatric species of the Mbuna of Lake Malawi, which are characterised by a high regional endemicity within specific biotopes (Ribbink et al., 1983 and Ribbink, 1991).

However, in spite of the generalized nature *qua* geographic distribution, microhabitat became strongly expressed during breeding periods within the littoral, as was clearly demonstrated in the species studied (Appendix E). It is interesting to note that the specific habitat requirements for breeding territories in those species correspond with a general description of Ribbink (1988) with respect to the stenotopic habitat demands of haplochromines in Lake Malawi in general: " *Many species have specific substrate requirements, inhabiting areas composed of only large, small or medium sized rocks...* " (equivalent to breeding territory requirements in *H. olivaceus* and *H. crebridens*) ..."*Others occupy zones in which rocks are interspersed with sand*" (equivalent to the breeding territory requirements in *H. paucidens*; ..."*and for certain species the presence of macrophytes among rocks is a necessary habitat constituent*" (equivalent to the breeding territories requirements in *H. astatodon*, as illustrated in figure 58).

Figure 58: At Tshegera Island *H. astatodon* breeding males protected territories exclusively in the shallow vegetated zone (see also Appendix E).

With respect to the eco-ethological classification of fishes (Balon, 1975), the haplochromines belong to the reproductive guild of external bearers. Within this specialized reproductive guild of mouthbrooding cichlids, characterized by low fecundity and large yolked ova, the egg number and egg size vary fairly widely. Fecundity ranges between 6 and 4300 eggs per brood and egg sizes between less than 2.0 mm and 7.1 mm (table 13).

In general, taking into consideration that larger species have larger brood sizes, the decrease in egg number is often associated with an increase in egg size and virtual loss of the right ovary (Fryer and Iles, 1972; Kuwamura, 1986). This trend is explained by the fact that fishes, in general, are able to alter their life-history style within their reproductive guild by adopting either an altricial or a precocial state in order to fit the environment (figure 59).

Table 13: Average body sizes, brood sizes and egg sizes in female mouthbrooders (Cichlidae), illustrating their range in diversity.

SPECIES	MEAN		
	Standard length (mm)	Brood size	Egg size (mm)
Tilapia grahami (Coe, 1969)	-	-	< 2
Tilapia alcalica (Coe, 1969)	59	34	2.8
Gnatochromis pfefferi (Kuwamura, 1986)	75	52	3.1
Haplochromis heusinkveldi (Goldschmidt & Witte, 1990)	66	25	3.7
Petrotilapia spp. (March et al. 1986)	108	78	4.9
Tilapia linnelii (Fryer & Iles, 1972)	-	-	5.5
Petrochromis famula (Kuwamura, 1986)	92	17	6.4
Tilapia aurea (Fryer & Iles, 1972)	250	4300	-
Petrochromis polydon (Kuwamura, 1986)	134	12	7.1
Petrochromis trewavasae (Kuwamura, 1986)	143	6	-
Haplochromis astatodon	6.8	36	365
Haplochromis olivaceus	6.7	28	3.7
Haplochromis crebridens	6.9	31	3.6
Haplochromis paucidens	7.0	25	3.6

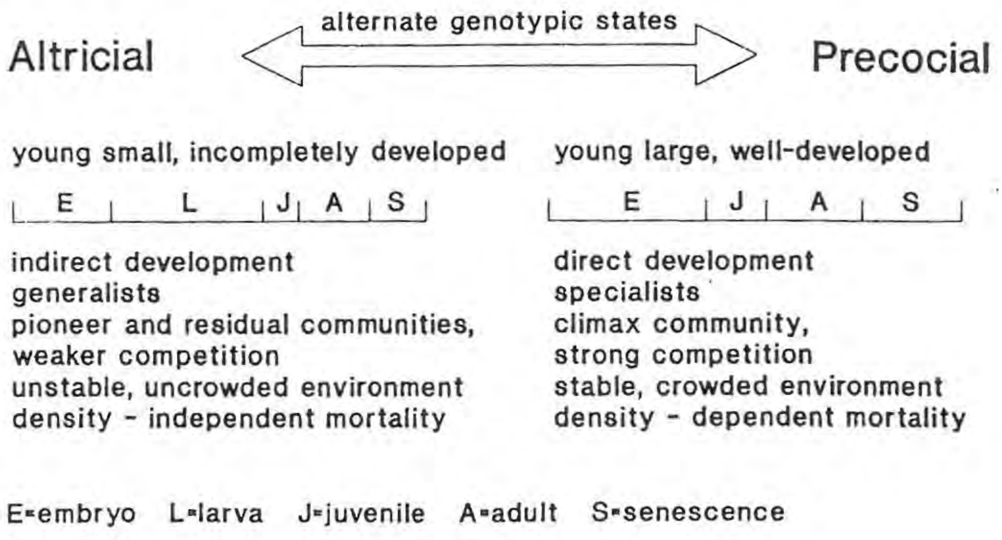


Figure 59: Diagrammatic representation of altricial and precocial alternative phenotypic states and their associated characters (from Bruton, 1989)

Based on the assumption that natural communities tend towards a more mature, diverse state through ecological succession, the general trend in evolution goes from altricial to more precocial forms (Bruton, 1989). The cichlids of the African Great Lakes, in their adaptation from unstable riverine conditions to stable lacustrine conditions, show a trend of specialisation from altricial to precocial. The degree of specialization depends on the degree of predictability of the environment and availability of evolutionary time (Balon, 1975).

When the egg sizes, body sizes and fecundity in the species studied are compared to those of the East African Cichlid community in general (table 13), it appears that from a reproductive point of view the four species studied tend to be more generalists on the continuum from the altricial to precocial.

In conclusion, the species studied are morphologically and ecologically predominantly generalized species (figure 60). Nevertheless, this does not withhold them to display different levels of specializations with respect to morphological criteria and habitat restriction. The level of specialization between the altricial and precocial scale with respect to egg sizes and fecundity, however, is very similar in the four species.

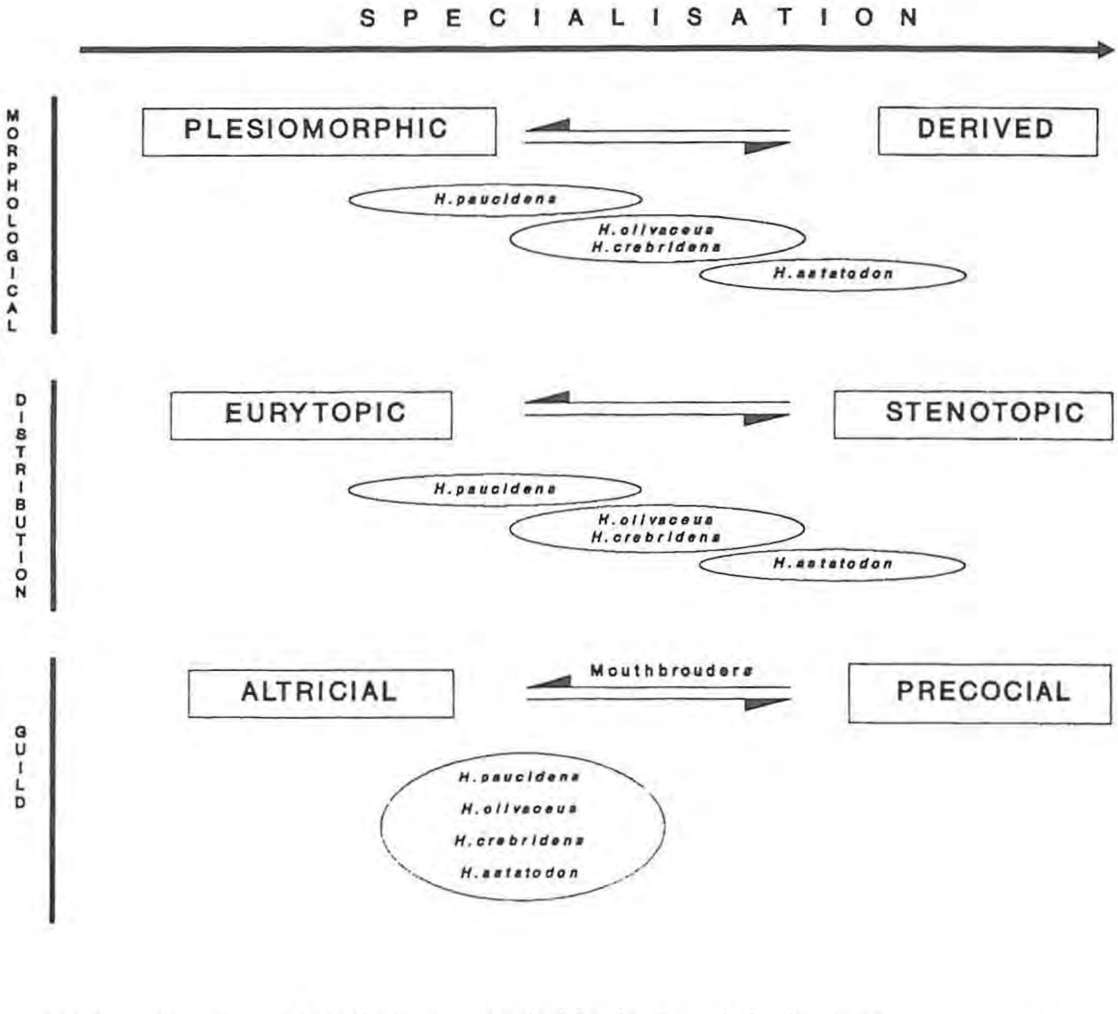


Figure 60: Overview of morphological and ecological levels of specialization in the species studied.

2. Evolutionary implications.

a. MODE OF SPECIATION IN THE GREAT AFRICAN LAKES.

Mode of speciation in the Great African Lakes is believed to be predominantly by allopatric speciation (Greenwood, 1965; Ribbink et al., 1983; Witte, 1984). Geographically isolated populations of a species diverge genetically, principally as a consequence of adaptation to their differing environments and also as a result of their genetic differences (Ribbink, 1988). The adaptive characters that are fixed in the original small isolate are subsequently fixed by stabilizing selection within the normal habitat of the species (Paterson, 1985).

In the highly diversified species flocks such as in Lake Tanganyika or Malawi, intralacustrine allopatric speciation is easy to envisage considering their stenotopic and highly philopatric mode of life. However, as the ancestral species were generalized and had a wide distribution pattern, the study of these highly diversified species flocks does not give any indication of how the specializations and philopatric tendencies arose originally?

The cradle of explosive diversification is to be found back in rivers, where the unpredictability of the environment favours the survival of morphologically and ecologically generalized species. However, the diversification from one or two ancestral species (Fryer and Iles, 1972), although it can not be excluded, is highly unlikely considering that rivers provide a diversity of habitats, ecological and trophic niches and a variety of physical, chemical and biotic features (Lowe-McConnell, 1969). Several species, therefore, might have achieved species specific distinctness with respect to habitat preference in the riverine environment through isolation and diversification of allopatric populations. In newly developing lakes, these species provided the first inoculum in the sandy, rocky, vegetated and open water habitats. Because of the sedentary nature related to mouthbrooding these colonizers became rapidly isolated from their sister species in the rivers, giving rise to the first step towards diversification.

This set up corresponds to the situation observed in the present day poorly diversified species flocks, such as Lake Kivu, characterized by comminution of the ecosystem into the major habitats and division of the constituent species within the major trophic groups. Because of the lake wide distribution pattern of the ecologically generalized species (eurytopes), extralacustrine speciation events might be expected to be a major driving force to diversification in young developing lakes. Considering that lakes in their early evolution all go through a shallow waters stage, separation in isolated pools is likely to be an important phase preparing the basic setting from which all further diversification is dependant on. It is only when a certain level of specialisation with respect to habitat restriction in physically isolated pools is reached, that intralacustrine allopatric speciation can participate in the diversification of the species flocks.

In isolated pools, characters affecting the SMRS of a population diverge in adapting to the constellation of the new environment. This environment, being small, is likely to be ecologically restricted and to be slightly different from any other such pool. Consequently, the preference for a specific breeding territory, an important component of the SMRS, is likely to evolve differently in each small water body. After syngamy, the diverged species, although still generalized with respect to their normal habitat will have become increasingly

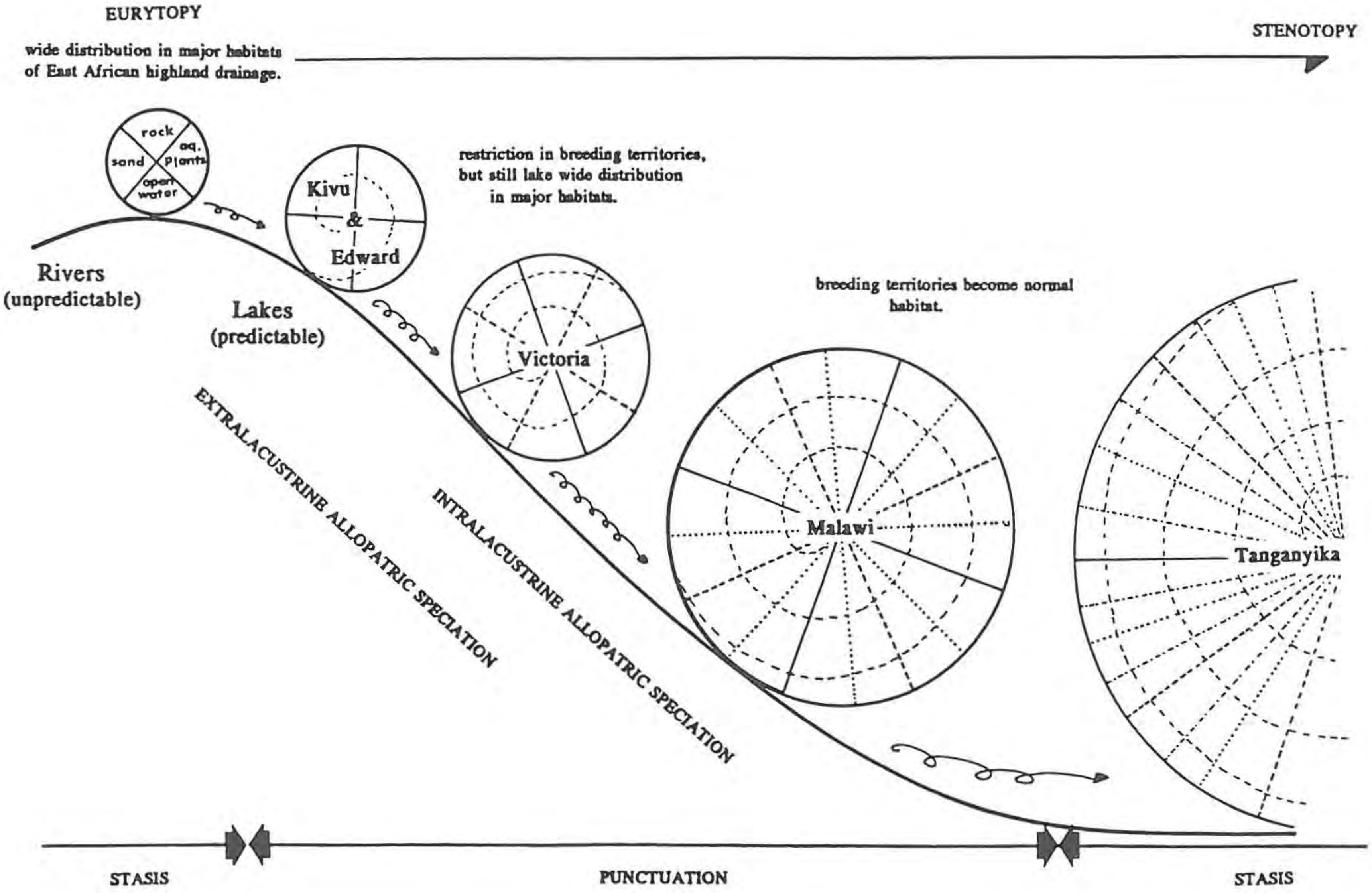


Figure 61: Diversification in the African Great Lakes from generalized riverine species to highly diversified lacustrine species flocks.

specific with respect to their preferred breeding habitat. This was clearly displayed in the species studied (Appendix E). As species evolve further with time, the specific sites for breeding appear to become ultimately the preferred habitat, as illustrated in the Mbuna, and allowed from then on habitudinal segregation and consequently intralacustrine allopatric speciation.

To sum up, speciation in the African Great Lakes could be compared to a snowball rolling down a hill (figure 61). First, new species accumulate slowly through physical isolation into separated water bodies (= extralacustrine allopatric speciation), where populations develop new morphological and ecological characters, such as breeding colours, trophic adaptations and habitat criteria for breeding territories. With increase in species number, specialization and related stenotopic behaviour, new species arise more and more rapidly by ecological and habitudinal barriers within the lake basin (= intralacustrine allopatric speciation).

As the present day lakes contain generalized and specialized species, both intralacustrine and extralacustrine speciation events are likely to take place in all African Great Lakes. The predominance of the one or the other depends on the abundance of stenotopic and eurytopic species being present within the system, which in turn is dependant on time of diversification.

b. EVOLUTIONARY STATUS OF LAKE KIVU.

When compared with the other East African Rift Lakes, the state of affairs in Lake Kivu is highly comparable to that of the small haplochromine assemblages in Lakes Albert, Edward and Turkana (Greenwood, 1984)(Appendix B). All exhibit diversification into the major trophic groups and major habitats, but with low diversification within each group. In those lakes, the lack of diversity within the trophic groups is explained by young age and/or lack of isolation (Greenwood, 1974).

In Lake Kivu, lack of isolation can be entirely excluded on basis of the geological evidence, as pointed out earlier on. On the other hand, although Lake Kivu is known to be geologically older than the latter ones and even Lake Victoria, young age of its fauna is possible and would be explained by partial or total destruction of a previously existing fauna during the late Pleistocene and Recent volcanic events (Appendix B).

Considering the possibility of a complete extinction phase during the volcanic events, the present day fauna must have evolved within the Lake Kivu basin since the restabilisation of the lake about 1 200 years ago. The question to be raised here is: could generalized species of surrounding rivers have possibly given rise to the present-day fauna in such a short time without any major physical or habitudinal barriers? As pointed out earlier on, although the Lake Kivu haplochromines tend to be generalized, they have nevertheless reached a certain level of morphological and ecological specialization (figure 60).

Intralacustrine allopatric speciation can not be envisaged because of the uniform distribution of all haplochromine species throughout the lake. Extralacustrine allopatric speciation through the isolation and reunion of small pools in shallow water basins, as is believed to have happened in Lake Victoria (Greenwood, 1965), is unlikely to have operated within the confines of the present-day basin considering its much greater depth.

Another, more likely explanation, therefore, is that the present day fauna are remnants of a pre-existing fauna. Escape in surrounding rivers could have enabled survival of some generalized members of the pre-existing species flock, but the presence of deep dwelling species such as *H. grauerie, vittatus* and others (table 3) would suggest survival of a relict fauna in an isolated bay. This bay would have been closed during the volcanic events (at least 10 000 years B.P.) and subsequently reopened when lake conditions returned to normal (at about 1 200 years B.P.).

This historical event of the isolation of a bay and its fauna can be compared to the present-day situation of Lake Victoria and its isolated bay, now Lake Nabugabo. This bay became isolated from the major water body about 4 000 years ago. Its fauna, when compared with that of a similar bay of comparable size in Lake Victoria shows a reduction in number of species from 30 to 8, a reduction in trophic groups, a reduction in intra-group specialisation and a change in the proportion of the various trophic groups. These changes result in a situation highly similar to that found in Lake Kivu, apart from the fact that the isolated communities differ in the composition of the trophic groups and number of species. This is of course entirely related to the size and prevailing environmental conditions, which are known to be different from bay to bay (Van der Ben, 1959; Greenwood, 1965).

Therefore, in analogy with the situation in Lake Nabugabo, the present-day Lake Kivu haplochromines are likely to be genetically derived from the ancestral strain of the main basin and consequently are different from the original fauna in the proto-lake. This relict fauna is predominantly generalized either because the pre-existing fauna was not highly diversified or because only the more generalized forms of each lineage were able to survive the hydrological, chemical and physical changes at the time when the bay became sealed off. It is important to note that bays are likely to undergo wider environmental fluctuations when compared with lakes, larger water masses having a greater buffering effect.

c. CONCLUSION.

The hallmark of the Lake Kivu haplochromines, in similarity with the other young diversifying species flocks, is the radiation of endemic species into the major trophic groups and the invasion of the major habitats, regardless of their low numbers. Overall low diversification within each trophic group, lake wide distribution patterns, and altricial life history styles indicate a generalised nature both in the species studied and in the Lake Kivu haplochromines in general.

However, this fauna is believed to be too evolved to have differentiated within the confines of the present day basin after the two major Recent volcanic phases and related extinction periods which disturbed the entire lake basin until about 1 200 years ago. Because of the complete isolation of the basin since the first eruption affecting the hydrology of the lake, invasions from Lakes Victoria, Edward or Tanganyika can be excluded. Riverine species are likely to have contributed to some generalized members of the flock, but deep dwelling and more derived forms, such as *H. grauerie* and *H. astatodon* respectively, are likely to have invaded the lake from a bay after a period of isolation during the Recent volcanic activity. During the period of isolation between at least 10 000 and 1 200 years B.P., this small flock is likely to have diverged from the ancestral forms by adaptations to the constellation of the new and more restricted environment.

3. Vulnerability of Lake Kivu.

During the first limnological observations it was demonstrated that Lake Kivu was rich in plankton, but lacked a pelagic fish that could consume it. *Limnothrissa miodon* became introduced as a means to channel zooplankton protein to human consumption, rather than becoming lost to the hypolimnion. Today, the introduction of this clupeid of Lake Tanganyika into Lake Kivu is claimed to be successful by most. Since 1980, the catch per unit of effort (CPUE) has not changed, whereas the fishing effort has been multiplied by 20 (Marchall, 1990). The abundance of *L. miodon* has been estimated 4.601 tonnes (Lamboeuf et al., 1990). With the ever increasing population size in the surroundings of Lake Kivu, *Limnothrissa* has become a natural food source of great value.

A major problem with this fishery, however, is that it is characterized by considerable irregular variations in abundance. Because the fishery disposes of only a one 2-year limnological survey (Verbeke, 1957a), these variations in abundance can not be fully explained. Increase in nutrients in the pelagic zone at the end of the dry season (Frank et al., 1983) and the inflow of nutrient rich water during the rainy seasons into the littoral zone (Marchall, 1990) are believed to be the major causes influencing stock abundance. The increase in nutrient content and its influence on the zooplankton population has a direct effect on the survival of the larvae of *L. miodon*. Although both juveniles and adults are known to feed optionally on chironomid larvae and terrestrial insects, variation in stock abundance is believed to be mainly related to plankton abundance (Marchall, 1990).

Planktivores fishes on zooplankton and phytoplankton communities are known to have an important effect on the latter, by reducing their size and composition (Lazzaro, 1987). Before the introduction of *Limnothrissa*, the open water was invaded by a zooplankton consisting of large, pigmented pond species composed of Copepoda and Cladocera (Dumont, 1986). *Limnothrissa* is believed to have modified this original zooplankton community with an increase in diversity, drop in standing crop and decrease in size of the zooplankton (Dumont, 1986). Change in transparency of the water since the introduction of *Limnothrissa* is further evidence of the changing plankton community in Lake Kivu.

Despite this change, *Limnothrissa* appears to continue to prosper, at least up until now. Critical long term evaluation, however, may prove this sardine success to be dubious. The social cost in case of a possible collapse would be enormous.

In turn, *Limnothrissa* may have an effect on the endemic haplochromine population. During periods of food scarcity, *Limnothrissa* is known to feed on its own juveniles in the coastal waters. The chance that juvenile haplochromines are also preyed upon by the adult *Limnothrissa*, as suggested by Dumont (1986), is believed to be low because they are preadapted to the predation pressure exerted by the adult haplochromines. Most of the haplochromines during their juvenile phase hide in rock crevices until they have reached a size where they are no longer preyed upon. However, the clupeid community and haplochromine juvenile population could be in competition with each other with respect to plankton availability. As was suggested (pp 61), juvenile abundance appears to be related to plankton abundance. Therefore, decrease in abundance and size, and change in the plankton community could be a threat to the endemic haplochromine fauna.

The introduction of *Limnothrissa* is not the only cause of lake environmental change. Average surface temperatures seem to be increasing slightly, average oxygen levels and h levels have lowered and the N-NO_3 level has increased (Spliethoff et al., 1980). These changes point towards a slow eutrophication of the lake. Population growth, deforestation and erosion are the likely causes of these changing water conditions. Two important breweries, one at Bukavu and one at Gisenyi, which sewerage flows immediately into the lake, are most likely an additional cause in deteriorating the water. One way to remedy against this kind of pollution would be by discharging the sewerage immediately into the permanent stratified zone where it can only benefit the methane gas production (Reyntjens, 1982).

Although Lake Kivu is most likely still close to pristine condition, first indications of water pollution are present. As suggested by Coulter et al. (1986), the large water bodies of the East African Rift Lakes represent large water resources in the middle of an arid continent. As human populations grow, their value in supplying the many water needs of these populations will be invaluable. Pollution of the lake, because of its long retention time, would be permanent on a human time scale.

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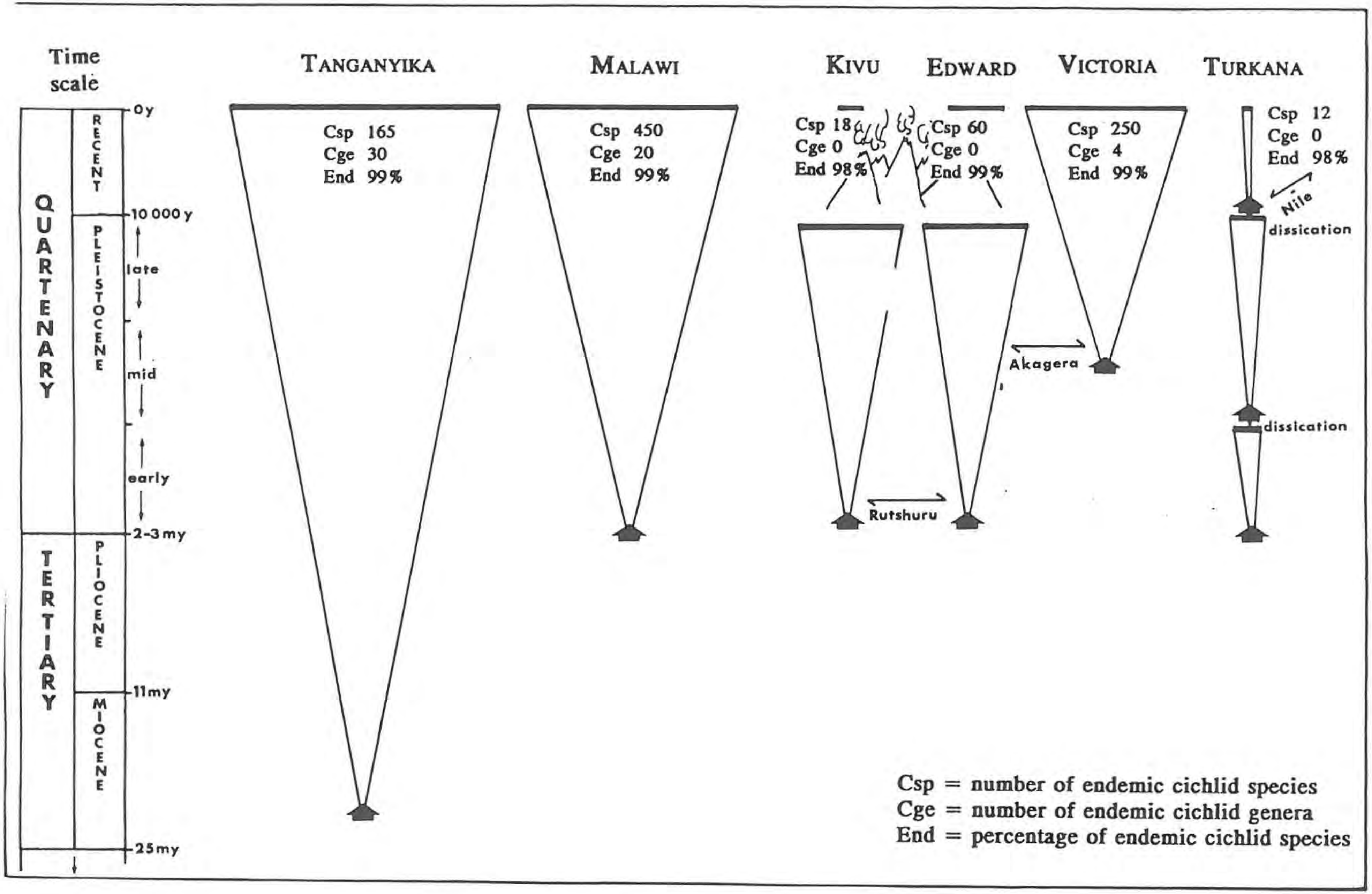
APPENDIX

A. FISH DIVERSITY IN LAKE KIVU

(from Thys van den Audenaerde et al., 1982 & Snoeks, in prep.)

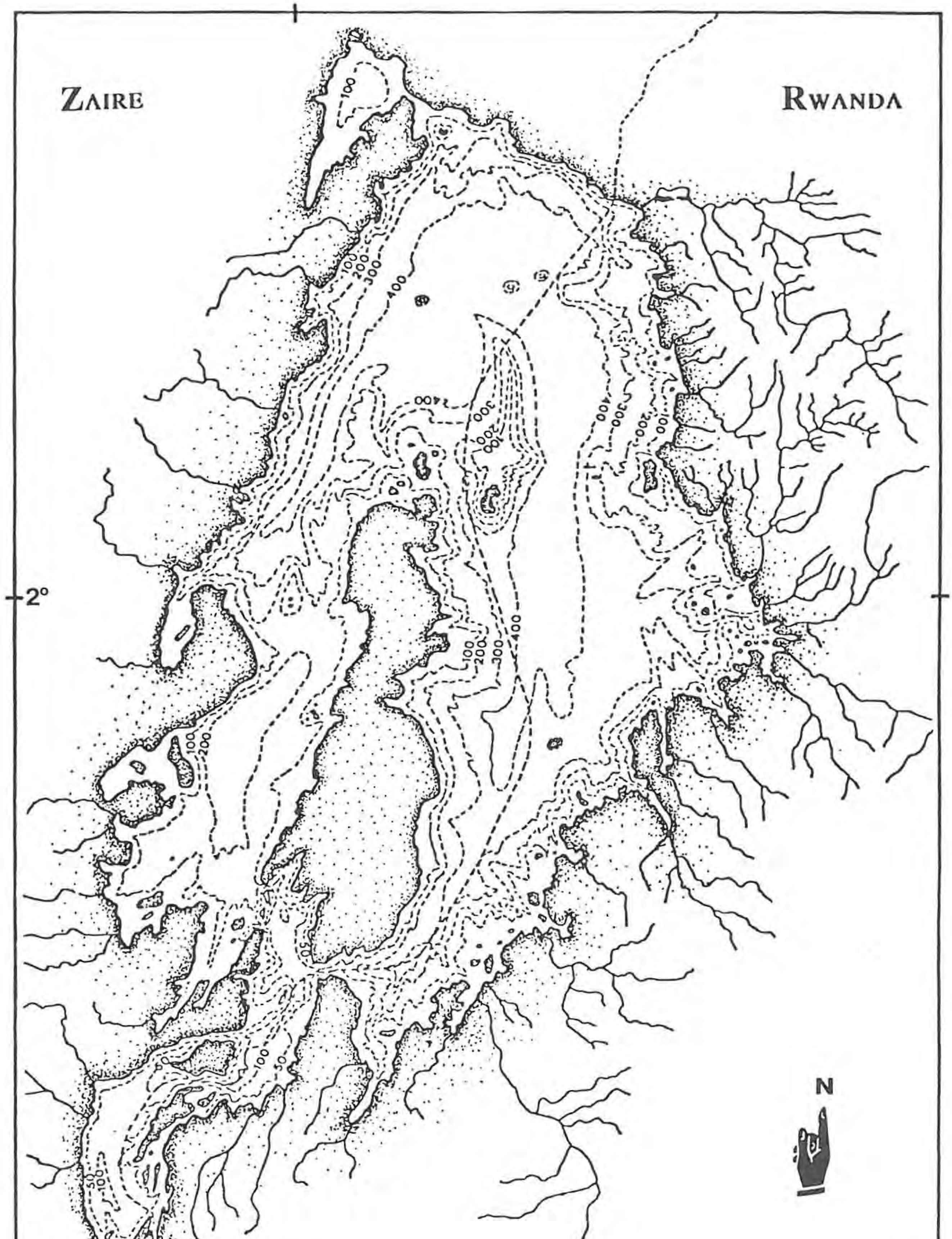
Family	Species	Origin
Clupeidae	*Limnothrissa miodon* (Boulenger, 1906)	Tanganyika
Cyprinidae	*Barbus altianalis altianalis* (Boulenger, 1900)	Rivers
	B. apleurogamma (Boulenger, 1911)	Rivers
	B. kerstenii kerstenii (Peters, 1868)	Autochtonous
	B. pellegrini (Poll, 1939)	Rivers
	Barilius moorii (Boulenger, 1900)	Tanganyika
Clariidae	*Clarias gariepinus* (Burchell, 1882)	Autochtonous
	C. liocephalus (Boulenger, ?)	Autochtonous
Cichlidae	*Tilapia macrochir* (Boulenger,1912)	Ponds
	T. nilotica eduardiana (Boulenger, 1912)	Autochtonous
	T. rendalli (Boulenger, 1896)	Ponds
	Haplochromis adolphifrederichi (Boulenger, 1914)	Endemic
	H. astatodon (Regan, 1921)	Endemic
	H. crebridens (Snoeks et al., 1990)	Endemic
	H. gracilior (Boulenger, 1914)	Endemic
	H. graueri (Boulenger, 1914)	Endemic
	H. i (Snoeks, in prep.)	Endemic
	H. kamiranzovu (Snoeks et al., 1984)	Endemic
	H. m (Snoeks, in prep.)	Endemic
	H. nigroïdes (Pellegrin, 1939)	Endemic
	H. occultidens (Snoeks, 1988)	Endemic
	H. olivaceus (Snoeks et al.,1990)	Endemic
	H. paucidens (Regan, 1921)	Endemic
	H. r (Snoeks, in prep.)	Endemic
	H. scheffersi (Snoeks et al., 1990)	Endemic
	H. vittatus (Boulenger, 1901)	Endemic



B. GEOLOGICAL TIME SCALE AND ADAPTIVE RADIATION OF CICHLIDS IN AFRICAN GREAT LAKES (from Beadle, 1981 & Greenwood, 1991).

C. BATHOMETRIC MAP OF LAKE KIVU

(from Thys van den Audenaerde et al., 1982).



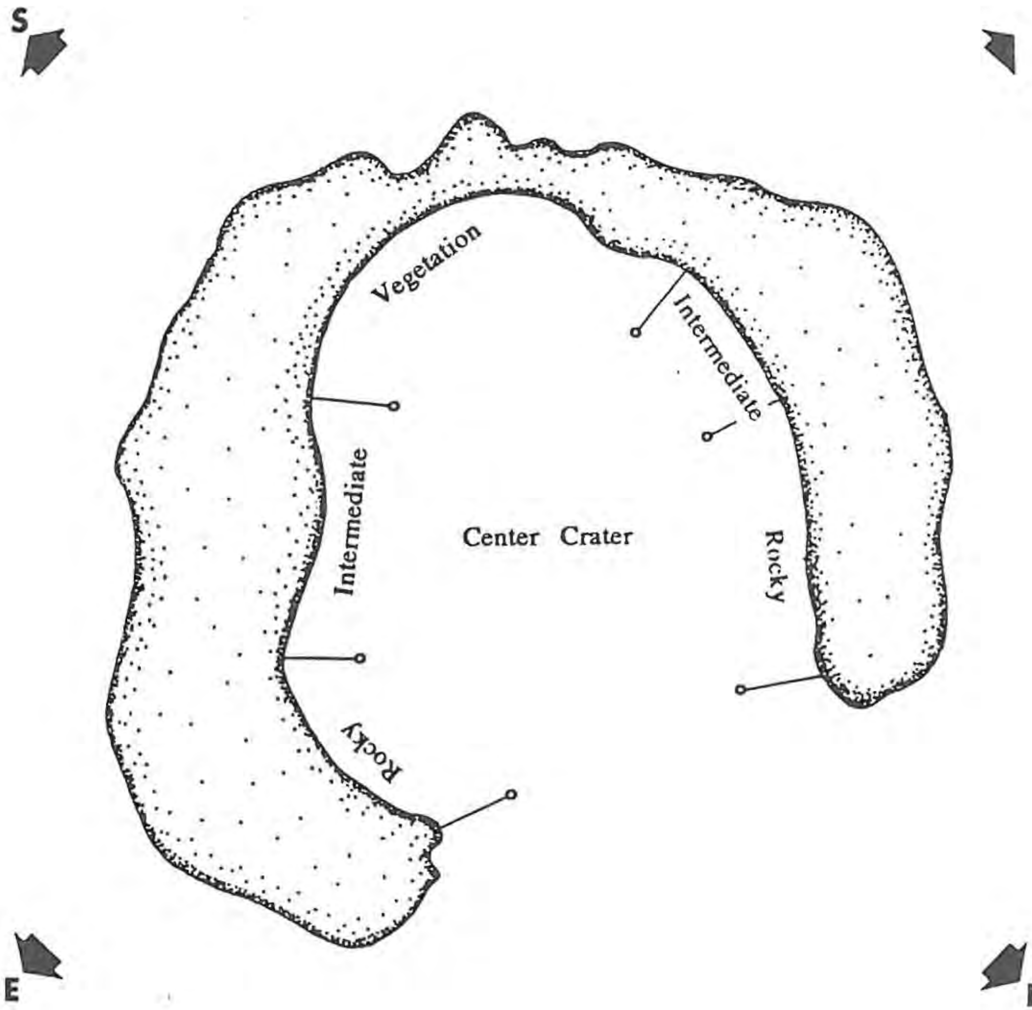
LEGEND

NET:

A: 0.8, 1.0, 1.2, 1.5, 2.0 and 2.4 cm top and bottom nets.
AB: 0.8, 1.0, 1.2, 1.5, 2.0 and 2.4 cm bottom nets.
AT: 0.8, 1.0, 1.2, 1.5, 2.0 and 2.4 cm top nets.
N: 1.2 and 1.5 cm top and bottom nets.
NB: 1.2 and 1.5 cm bottom nets.
NT: 1.2 and 1.5 cm top nets.
SCB: Scuba diving.

SITE:

R W: Rocky zone, West arm.
R E: Rocky zone, East arm.
V W: Vegetation zone, West arm.
V E: Vegetation zone, East arm.
V S: Vegetation zone, South.
VR W: Intermediate zone, West arm.
VR E: Intermediate zone, East arm
C C: Center crater.
VC C: From Vegetation zone to Center crater.



D. AGENDA OF SAMPLING EVENTS.

Month	Day	Fishing Time Start	Fishing Time End	asta.	oliv.	creb.	pauc.	Net	Site
Year 1988									
January	19.01	9.30	11	0	0	0	0	AB	R W
	21.01	9.30	11.30	0	6	0	11	AB	R W
	23.01	8	10	0	4	0	1	AB	R W
	23.01	16	18	0	8	2	2	AB	R W
	26.01	6	8	0	5	1	0	AB	R W
	26.01	16	18	0	12	0	0	AB	R W
	Total			0	35	3	14		
February	15.02	20	22	0	4	0	0	A	R W
	17.02	6	8	0	7	0	1	A	R W
	17.02	16	18	0	4	0	3	A	V W
	19.02	6	8	0	2	1	0	AB	R W
	19.02	17	18	0	6	0	0	AB	R W
	26.02	18	19	0	19	46	1	N	R W
	8.03	19	20	0	4	19	2	N	R W
	Total			0	46	66	7		
March	13.03	16	18	0	6	7	3	NB	R E
	14.03	16	18	0	8	0	3	NB	R E
	15.03	18.30	20.30	3	22	12	4	N	VR E
	Total			3	36	19	10		
April	15.04	16	18	1	5	3	6	NB	VR W
	17.04	15	18	0	1	0	1	NB	V S
	18.04	16	19	27	14	11	3	NB	V S
	26.04	5	8	19	12	5	1	N	VR E
	28.04	17	19	0	25	31	1	N	R E
	28.04	PM	PM	0	0	0	8	SCB	–
	Total			47	57	50	20		
May	17.05	17	19	2	34	15	1	N	VR E
	25.05	16.35	17.45	0	1	5	17	NB	VR E
	25.05	18	20	4	0	34	1	NT	VR E
	25.05	18.30	20	16	14	9	0	NB	VR E
	28.05	16.30	17.30	0	0	0	0	NT	VR W
	28.05	16	18	0	0	0	3	NB	VR W
	29.05	17.30	20	21	0	0	4	NB	V E
	29.05	PM	PM	0	0	0	14	SCB	–
	Total			43	49	63	40		
June	22.06	15.30	17.45	0	43	2	16	NB	R W
	22.06	18	20	0	1	27	0	NT	V W
	22.06	18.30	20.30	19	12	7	0	NB	V S
	24.06	16	18	0	0	0	3	NB	R E
	24.06	18.30	20.30	7	0	2	0	NB	V W
	24.06	19	20.30	4	0	8	0	NT	VC C
	25.06	20	21	0	0	0	14	SCB	–
	Total			30	56	46	33		
July	9.07	16	20	25	35	33	14	A	V E
	9.07	20	24	0	7	2	2	A	V E
	10.07	24	4	2	1	3	0	A	V E
	10.07	4	8	14	10	5	4	A	V E
	10.07	8	12	2	8	2	2	A	V E
	10.07	12	16	0	2	1	1	A	V E
	10.07	16	20	35	19	21	3	A	V E
	18.07	18	20	9	36	12	1	A	VR W
	19.07	PM	PM	0	0	0	2	SCB	–
	20.07	PM	PM	0	0	0	12	SCB	–
	20.07	20	21	1	0	0	0	NB	VR W
	Total			88	118	79	41		
August	30.08	18	19	10	8	45	2	N	V S
	31.08	19	20	41	14	6	0	N	V S
	4.09	17	18	2	0	2	0	NB	V S
	5.09	PM	PM	0	0	0	23	SCB	–
	Total			53	22	53	25		
September	29.09	5.30	7	11	26	7	1	N	V W
	30.09	4	5.30	44	29	37	0	N	RV W
	5.10	16.30	20	6	36	21	6	NB	RV W
	5.10	PM	PM	0	0	0	Lost	SCB	–
	Total			61	91	65	7		
October	28.10	5.15	6.15	38	13	38	0	N	V S
	29.10	4.15	5.15	16	10	11	1	N	V S
	29.10	6.15	7.15	2	5	7	1	N	V S
	30.10	17	19	1	61	14	4	N	R W
	30.10	PM	PM	0	0	0	21	SCB	–
	Total			57	89	70	27		
November	27.11	4	8	10	18	13	7	A	V E
	27.11	8	12	0	0	0	3	A	V E
	27.11	12	16	0	0	3	1	A	V E
	27.11	16	20	15	6	38	1	A	V E
	27.11	20	24	4	0	24	0	A	V E
	28.11	24	4	6	3	12	0	A	V E
	28.11	4	8	3	6	6	1	A	V E
	4.12	18.30	20.30	1	0	6	0	N	V S
	4.12	PM	PM	0	0	0	8	SCB	–
	Total			39	33	102	21		
December	22.12	4.45	5.45	0	15	14	0	N	R E
	27.12	3.45	4.45	1	8	15	4	N	R
	27.12	5.45	6.45	0	6	6	7	N	R
	28.12	5.45	6.45	22	17	18	2	N	V W
	26.12	PM	PM	0	0	0	9	SCB	–
	2.01	17.30	20	8	38	26	2	NB	V W
	2.01	PM	PM	0	0	0	13	SCB	–
	Total			31	84	79	37		
Year 1989									
January	1.02	17.30	20	36	35	43	2	N	V W
	2.02	17.30	20	6	13	23	6	N	VR W
	2.02	PM	PM	0	0	0	23	SCB	–
	Total			42	48	66	31		
February	28.02	4.15	5.15	3	6	17	0	N	V S
	28.02	6.15	7.15	4	11	6	1	N	V S
	27.02	17.15	18.15	0	1	5	1	N	V E
	27.02	19.15	20.15	1	9	13	1	N	V E
	1.03	17.15	18.15	0	11	5	0	NB	R
	1.03	19.15	20.15	0	10	1	0	NB	R
	2.03	18.15	19.15	7	11	40	2	N	V W
	2.03	4.15	5.15	3	4	18	1	N	R
	2.03	6.15	7.15	0	9	2	6	NB	R
	3.03	17.15	18.15	25	12	31	0	N	V W
	4.03	5.15	6.15	2	31	14	3	N	R
	5.03	18.15	19.15	2	28	7	3	N	R
	6.03	PM	PM	0	0	0	18	SCB	–
	Total			47	143	159	36		
March	27.03	17.45	19.15	41	28	37	4	N	V S
	30.03	18	19.15	16	49	7	2	N	V S
	2.04	PM	PM	0	0	0	18	SCB	–
	4.04	8	12	0	16	0	2	A	C C
	4.04	12	16	0	5	0	1	A	C C
	4.04	16	20	0	9	6	1	A	C C
	4.04	20	24	0	0	9	0	A	C C
	5.04	24	4	0	0	0	0	A	C C
	5.04	4	8	0	0	0	0	A	C C
	Total			57	107	59	28		
OVERALL TOTAL				598	1014	979	377		

E. BREEDING TERRITORY DISTRIBUTION OF THE SPECIES STUDIED.

1. Description.

Dominant breeding males of *H. crebridens* occurred in two to six meters depth, most commonly in areas where large rocks were densely packed. Boundaries between breeding territories did not overlap with at least three meter in between each territory. Dominant breeding males swam most of the time at least 0.10 m above the substrate and occasionally left their territory for several minutes.

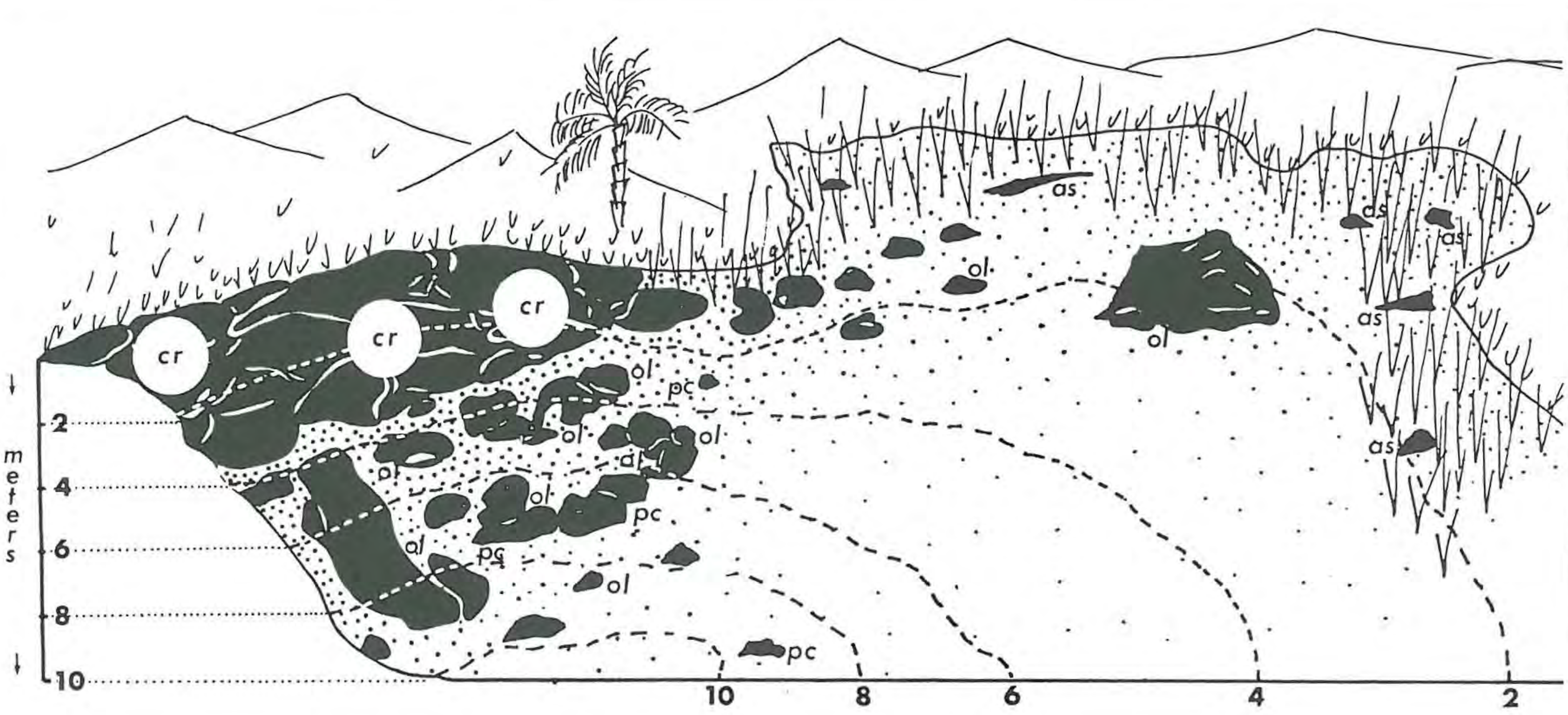
The breeding territories of *H. olivaceus* were found in more exposed rocky environments with fewer hiding places around and within the breeding territory compared to *H. crebridens*. The males swam preferably close to the substrate and left their territory only briefly when chasing away intruders. Along the coastline of Goma, where mainly rocky substrate is available, groups of mating stations in close proximity were commonly observed. At Thsegera Island breeding territories were also observed scattered about on the sandy substrate but always in the vicinity of a pebble or rocky outcrop which was used both as hiding place and mating station.

H. paucidens selected its breeding sites usually below five meters depth in a rocky to sandy debris environment. Along the coastline of Goma, the territories of dominant males were often observed in close proximity to a group of territorial breeding *H. olivaceus'* males. Occasionally, dominant males were observed in the vegetation zone at Tshegera Island, but it is uncertain whether breeding territories were established in this environment.

Dominant breeding males of *H. astatodon* were only observed at Tshegera Island within the densely packed vegetation zone between one and three meters depth. Their mating stations were always situated near to a pebble, dead tree trunk or stem of *Scirpus* vegetation (figure 58).

E. Breeding territory distribution of the species studied.

2. Illustration.



BREEDING TERRITORY CHARACTERISTICS	*H. crebridens* (cr)	*H. olivaceus* (ol)	*H. paucidens* (pc)	*H. astatodon* (as)
Substratum	Large rocks	Small rocks	Rocky to sandy	Sandy with vegetation
Depth preference	1.5-3m	3-8m	3-10m	1.5-3m
Distance above substratum	~ 0.10m	close	close	close
Distance between territories	wide	close proximity	wide to scattered	scattered