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Ecomorphology as a tool in fisheries: identification and ecotyping of Lake Tana barbs (*Barbus intermedius* complex), Ethiopia

F.A. SIBBING, L.A.J. NAGELKERKE AND J.W.M. OSSE

Department of Experimental Animal Morphology and Cell Biology, Agricultural University, Marijkeweg 40, NL-6709 PG Wageningen, The Netherlands

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Abstract

Fisheries development of Lake Tana, Ethiopia, urgently requires the identification of its unknown units of fish stock. A diversity of large barbs (up to 80 cm SL), lumped into one species *Barbus intermedius* and contributing over 35% of the annual catch, consists of at least thirteen distinct morphotypes (Nagelkerke et al., 1994), possibly species. Their abilities and limitations in food selection and feeding can be predicted from structural specializations following functional morphological methods. Using ecomorphology, a spectrum of ecotypes ranging from detritivores to piscivores is predicted. Such hypotheses may be tested by analysing these fishes' intestinal contents. From knowledge of available food organisms and the trophic segregation thus found among barbs and sympatric species, a preliminary food web has been constructed. This food web, together with quantitative studies on population dynamics and energy flow, provides a biological framework for rational fisheries management aiming at sustainable production and protection of biodiversity.

Keywords: ecomorphology, cyprinids, feeding apparatus, barbs, *Barbus intermedius*, biodiversity, trophic segregation, resource partitioning, food web, stock identification, fisheries, Ethiopia, Lake Tana

Introduction

Knowledge of ecological processes in an aquatic system and insight into its biological potentials and constraints is a precondition for understanding the dynamics of fish production as harvested by Man. All biomass produced by a lake and exploited by fisheries (Figure 1) originates from solar energy trapped by algae and macrophytes (the producers). A large variety of small invertebrates and fish (the consumers) exploit these primary food resources. A wide diversity of fish stabilizes the production system, converting this biomass (producers and consumers) into fish production. Such major fish-food relationships are described in a food web and provide a framework for subsequent quantitative approaches, e.g. in population dynamics and energy flow.

The interactions between fish and their food organisms are dynamic in time (diurnal, seasonal, annual) and space (habitat). Fisheries will effect quantitative shifts in the food web by intensive and selective fishing activities (e.g. by selecting a particular season, fishing area or mesh size of nets), overexploiting some large species and size classes. The (harmful) consequences of such actions cannot be predicted and the remedial management measures cannot be formulated without qualitative and quantitative knowledge of the ecosystem. Such knowledge is not available for Lake Tana, Ethiopia's largest lake (315600 ha) and its developing fisheries. The purpose of this paper is to explain how an ecomorphological study may help to fill a part of this gap, by deducing the specific abilities and limitations of various fish species to exploit the available resources from their feeding structures. A concomitant quantitative study of energy flow and population dynamics is urgently required for the adequate management of fish stocks.

Lake Tana is located at 1829 m altitude, measures about 70 km in maximal length and width, is rather shallow (max. depth 14 m, mean 8,9 m) and is the source of the Blue Nile (Gasse, 1987). Both for assessment and monitoring the seperate fish stocks of Lake Tana (by catch-effort analysis per species) and for analysing the food web, we need to identify fish in their structural appearance (morphotypes) and in their ecological role (ecotypes) at all life stages. These are the primary questions to be answered in our current studies, especially for the fish named *Barbus intermedius*. This large-sized species contributes over 35% of the catch but was

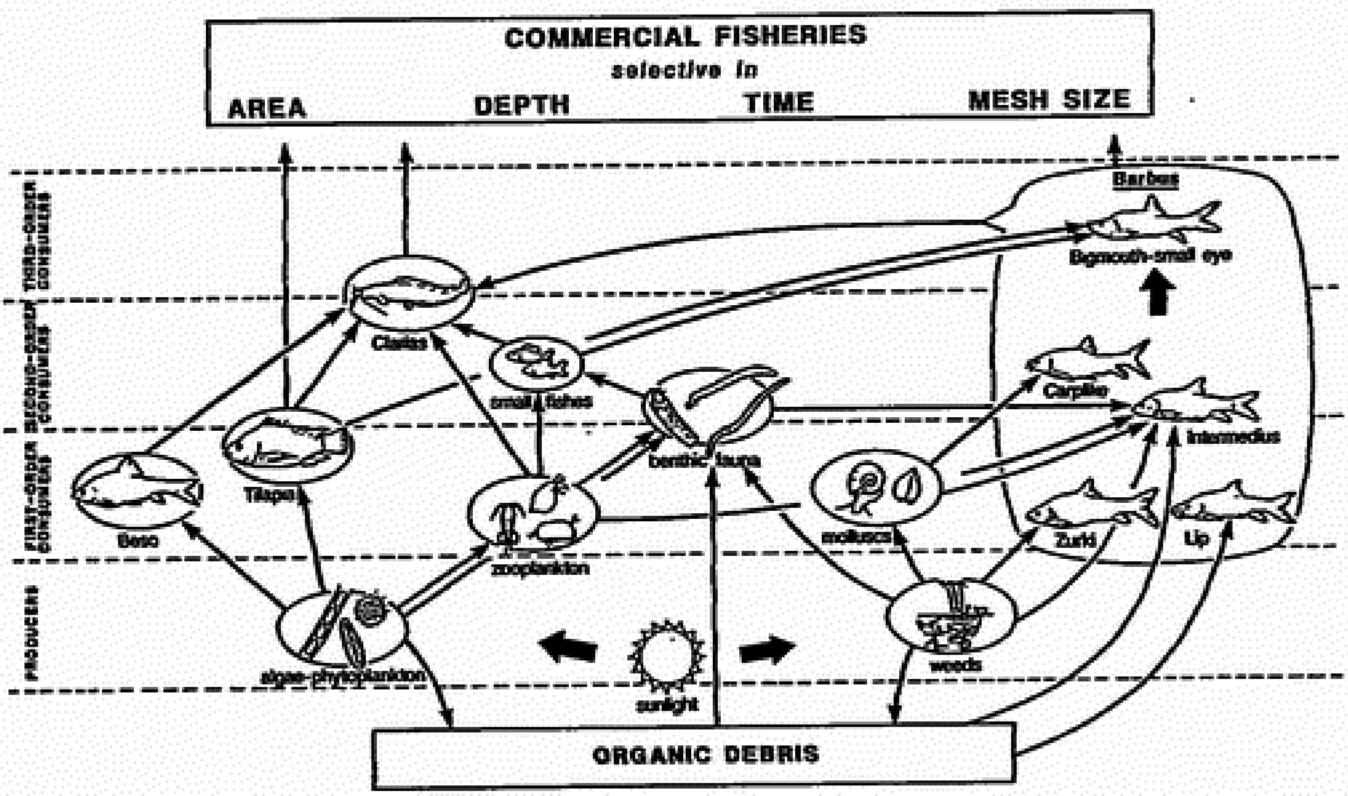

Figure 1. Preliminary food web of Lake Tana showing the different roles of some barb morphotypes. These and other morphotypes are described in Nagelkerke et al. (1994).

readily recognized during our pilot study in 1990 as a group of at least thirteen strikingly different morphotypes (Nagelkerke et al., 1994): all these may need to be managed as distinct fish stocks. The five most abundant morphotypes have been incorporated in fisheries research since then. Catfish (*Clarias gariepinus*) and tilapia (*Oreochromis niloticus*) give no identification problems and are the other important units of fish stock in the lake. Beso (*Varicorhinus beso*) is a well-described cyprinid but contributes less to the commercial catches, whereas *Barbus trispilopleura* is an abundant small species (<8 cm SL) and probably an important prey for the piscivores.

Morphotypes and units of fish stock

Is Banister (1973) right when he states that all barbs belong to one single, polymorphic species, or are our morphotypes separate, genetically isolated, fish stocks and possibly even species (cf. Mina et al., 1993; Osse et al., 1993)? If they form one very plastic species, overexploitation of some morphotypes will readily be balanced by transitions from others into the now underexploited ecological niches. If the types are separate species, separate units of reproduction, such transitions will not occur and the management model for sustainable fisheries becomes much more complex.

The answer to the above question will eventually be given by:

1. Morphometric measurements particularly of head shape, its structures (such as jaws, lips, eyes) and their movements (e.g. opening and protrusion of jaws) to identify the morphotypes as unambiguously distinct. To date thirteen morphotypes have been identified using multivariate statistical techniques. Details are given in Nagelkerke et al. (1994). These morphotypes have only 'informal names'.
2. Investigations into whether breeding is separated in time and/or area.
3. Comparing the genetic differences among morphotypes through e.g. DNA fingerprinting.

What is the role of each barb morphotype in the production system?

One way of positioning the morphotypes in the food web is to analyse their intestinal contents over several years, accounting for diurnal, seasonal and spatial (horizontal and vertical) variation. Such an extensive approach starts from the actual situation in the lake and has little predictive value once environmental conditions change. The present study is based on ecomorphological principles.

Ecomorphology investigates the ecological significance of organismal form at all levels of observation (cell, tissue, organ, organism). Such significance is based on functional analyses of form elements explaining structures as being optimized to one or more functions following functional morphological methods (Figure 2). The biological role of a particular function is investigated in behavioural ecology evaluating functions in environmental profiles, thereby explaining the survival value of structure-function complexes. Once the relation between form, function and environment

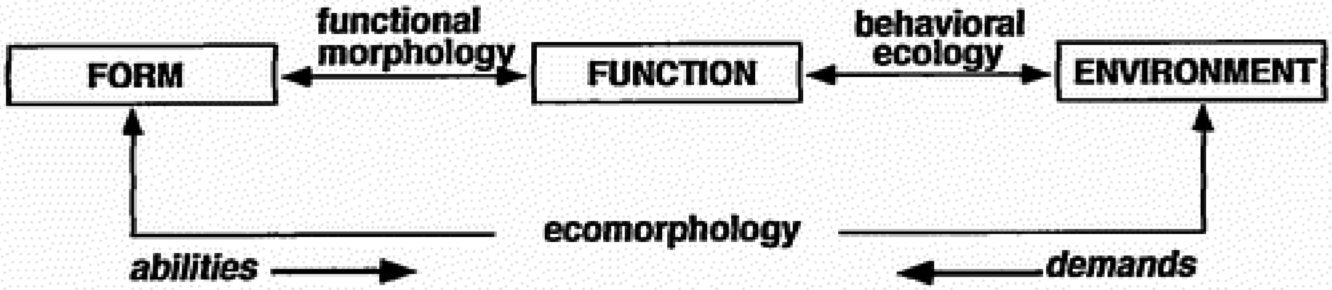

Figure 2. Ecomorphology and its position among related disciplines.

has thus been hypothesized and tested, (1) specific functional and structural demands to the organism can be formulated from its particular ecological niche, or vice versa (2) environmental constraints and abilities can be predicted for a specific structure.

A well-documented example following such hypotheses and tests is the comparison of architecture (by microscopic reconstruction), functioning (by X-ray movies of internal events), performance (by aquarium experiments) and ecological significance (by field studies) of the branchial sieve in three sympatric species of cyprinid fish (van den Berg, 1993). Such a holistic study is rare (Motta & Kotrschal, 1992). Van den Berg's study explains the dominance of bream (*Abramis brama*) after eutrophication as a result of its unique small branchial sieve muscles allowing for reduction of its mesh size during filter feeding in contrast to other species with a similar construction.

The diversity of food resources is larger for aquatic than for terrestrial vertebrates. The wide variety in size, shape, location, mobility, physical and chemical properties of food sources makes us expect specializations in architecture, functioning and food-handling behaviour of fish species to optimize utilization of some food types while necessarily limiting the use of others. Thus the effective food niche of each barb morphotype can be defined from detailed knowledge of cyprinid specializations in feeding (Sibbing, 1991), including: (1) sense organs for detection, localization and selection of prey; (2) specializations in swimming, suction and biting for prey pursuit and intake; (3) branchial sieving for retention of small (planktonic) prey; (4) the palatal organ for sorting food from non-food in bottom feeders; (5) pharyngeal jaws (modified fifth gill arches, Figure 3) for mechanical breakdown (cyprinid fish lack teeth on oral jaws, a stomach and cellulases); and (6) the intestine for chemical breakdown.

The required character set for a piscivorous, a benthic molluscivorous and a phytoplanktivorous cyprinid fish are compared in Table 1, which shows the specializations in the separate feeding components for the specific food type.

The length of the lower jaw and intestine are compared for the morphotypes called Zurki, Acute and Intermedius in Figure 4. According to these characters, these three belong respectively to a herbivorous, a piscivorous and an omnivorous ecotype. Among the Lake Tana barbs, molluscivores, zooplankton feeders, insectivores and detritivores have also been distinguished. Further differentiation within trophic groups in how they feed will be attempted using more specialized characters (cf. Witte & Van Oijen, 1990, for cichlids).

Table 1. Major structural trends to be expected in some trophically specialized cyprinid fish. Symbols indicate numbers and size

	Piscivore	Benthic molluscivore	Phytoplanktivore
Body shape	shallow	deep	intermediate
External sense organs	+++	+	+
Barbels	–	+++	–
Mouth position	terminal	subterminal	terminal
Mouth opening	large	small	intermediate
Protrusion upper jaw	little	strong	absent
Internal sense organs	+	+++	++
Gill rakers	+	++	+++
Pharyngeal jaws	slender	stout	intermediate
Pharyngeal teeth	puncturing lacerating	crushing	grinding
Intenstine	short	intermediate	long

Whereas in Europe only one true piscivorous cyprinid is known (*Aspius aspius*), Lake Tana has at least eight large fish-eaters (Nagelkerke et al., 1994), ranging from facultative to obligate piscivores even though they, like all cyprinids, lack teeth on their oral jaws as well as a stomach. This radiation is mainly due to the complete absence of other specialized piscivores in Lake Tana, leaving this niche open to the barbs and Clarias.

Eventually our results will enable us to construct a feeding hierarchy of different fish showing the relative effectiveness of each species in utilizing different food categories. Such hypotheses can be tested by comparison of the intestinal contents of each morphotype and the available food spectrum (frequency of occurrence for each food category).

The food web of Lake Tana

Based on current knowledge, the initial food web with merely three fish species (*Barbus intermedius sensu latu, Oreochromis niloticus* and *Clarias gariepinus*) has been extended (Figure 1) to incorporate some of the ecologically specialized barb morphotypes, stressing the multispecies character of Lake Tana fisheries. The position of each fish species in the food web is determined by: (1) its specializations for feeding; (2) the availability of different food categories; (3) competition from other species; (4) the risk of being eaten while foraging. The reproductive success of each species as measured e.g. from the survival of its larvae largely determines its population size in competition for food resources. Changes in the availability and competition for food types will induce shifts in the food web, thus affecting the biomass, and in the composition of fish species contributing to the biomass. Some scenarios are:

1. Commercial fisheries will especially reduce the number of large piscivores such as White hunch, Bigmouth-big eye, Bigmouth-small eye and Bighead (cf. Nagelkerke et al. 1994). This will reduce the predation pressure on the full spec-

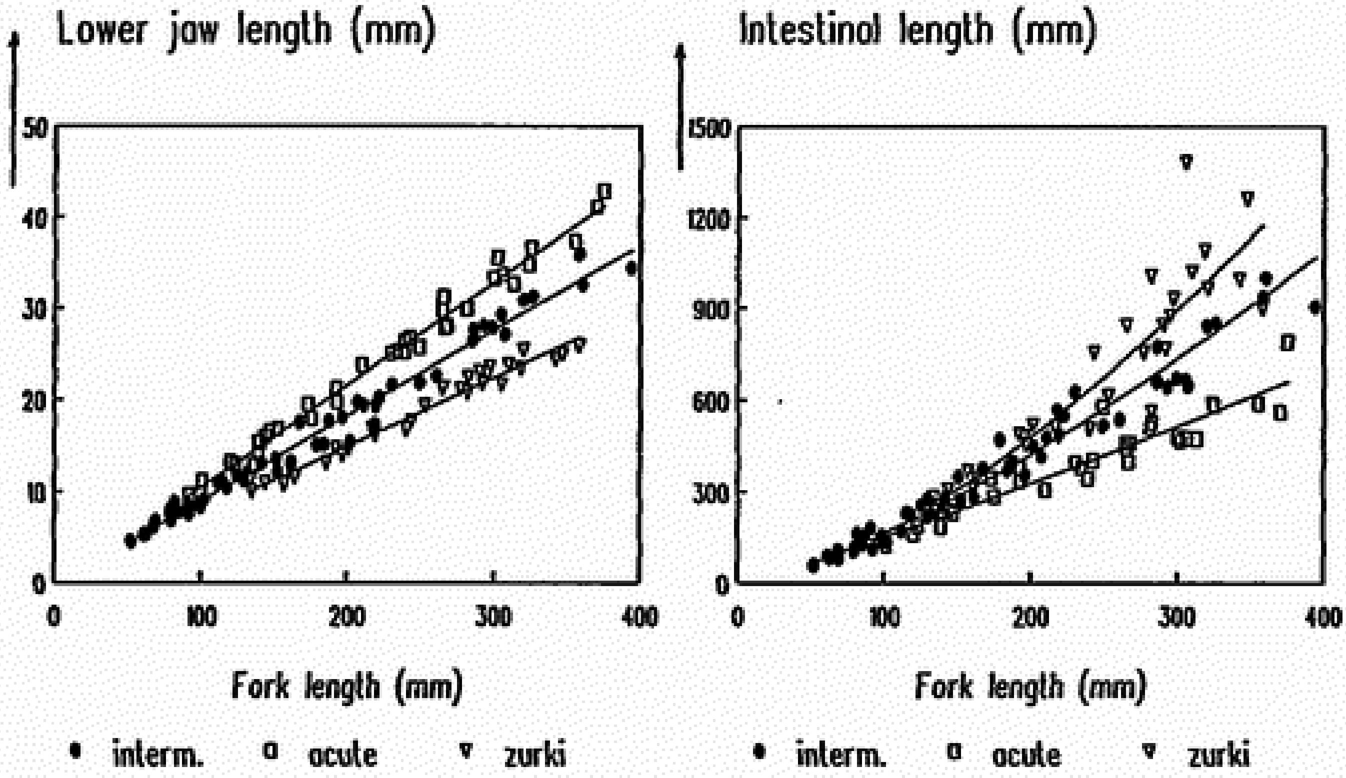

Figure 4. Structural characters determining feeding plotted against fork length for three morphotypes of *Barbus intermedius*: (left) length of lower jaw; (right) length of intestine. Note the larger lower jaw and short intestine indicating the Acute morphotype to be a piscivore, and the short lower jaw and long intestine of Zurki for feeding on macrophytes. Curves are fitted by least-squares regression. Morphotypes are defined in Nagelkerke et al. (1994).

trum of young and small adult fish, increasing their number as long as their food resources (e.g. zooplankton) are abundant. Their increased consumption of zooplankton, however, may lead to algal bloom, increase of phytoplanktivorous tilapia and/or disappearance of macrophytes (owing to reduced penetration of light) and so to a decrease of fish species associated with the macrophyte biotope. Overexploitation of large piscivores will cause shifts towards smaller, less commercial species (depending on their strength in competition with the juvenile large barbs) and challenge fishermen to use smaller mesh sizes, reinforcing these effects.

2. Overexploitation of omnivorous barbs like Intermedius probably will have less effect on shifts in species composition because it affects a large spectrum of food organisms more equally. In addition, Intermedius is particularly opportunistic in foraging.
3. Overexploitation of macrophyte feeders (such as Zurki) may result in increase of weeds and associated snails which are vectors of tropical diseases (e.g. bilharzia). In addition, few other fish are able to utilize this large primary food resource, whereas energy gain and biomass production from the lake is especially efficient at these low trophic levels.
4. Absence of other true piscivorous fish allows the barbs, although even lacking oral teeth, to occupy this niche. The economically important commercial fish are among them. Introduction of specialized piscivores, like that of the Nile perch

(*Lates niloticus*) to Lake Victoria, would certainly cause major shifts in fish production and fish composition, reducing the biodiversity of the lake (cf. Witte et al., 1992).

In all the above scenarios, the balance of the lake ecosystem is shifted, with risks for its productivity and biodiversity. Our project aims at providing basic biological knowledge as a start to rational exploitation of this natural resource.

Evolution of Lake Tana barbs

Lake Tana is a geographically isolated system. Its barbs probably compose a unique species flock. No other undamaged freshwater system is known where the evolutionary history of a group of such closely related cyprinid species can be studied to answer basic questions like which selective forces caused their adaptive radiation, and which mechanisms were involved in their segregation. In other words, how did environmental conditions interact with the endemic stock to produce the present variety of cyprinid species. Ontogenetic studies will show how and when morphotypes and ecotypes diverge during larval growth and which factors trigger these changes. Knowledge of the evolutionary relations of these barbs will also help to clarify the true relations between all fish lumped into the genus *Barbus* all over the world (Howes, 1991). Lake Tana is a unique natural laboratory for evolutionary studies of this largest freshwater family (the Cyprinidae). This is another important argument for the study of these fishes.

Conclusion

Ecomorphological studies strongly suggest that Lake Tana includes 15 rather than three fish stocks. Ecomorphology is a most helpful tool in the identification, assessment and ecotyping of fish stocks. Knowledge of Laka Tana's food web enables predictions about the consequences of human impact on the composition of this natural production system and contributes to the necessary biological framework for fisheries biology and management scenarios (regulations of mesh size, closed areas or seasons, number of boats and nets) and as such towards balanced harvesting and sustainable production. This paper advocates the integration of fisheries practice, fisheries research and fish biology at an early stage.

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