

Size-dependent distribution in littoral fish: optimization or competitive exclusion?

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HABITAT SELECTION AND SIZE-DEPENDENT DEPTH DISTRIBUTIONS IN FISH: AN OVERVIEW

In the littoral zone many ecological factors that are critical for the growth and survival of fishes vary strongly in space and time. In freshwater ecology, the littoral zone of a lake is defined as extending from the shore to a water depth where the action of wind and waves still has some influence (Goldman & Horne, 1983). In this zone, critical variables such as food availability, temperature and oxygen concentration are directly influenced by climate and weather. The major difference between the littoral zones of freshwater lakes and most marine environments is the absence of marked tides and, consequently an intertidal zone in the former.

In this paper I shall discuss the habitat selection of fishes in freshwater lakes. Special emphasis will be on spacing with regard to water depth. Depth profiles of critical variables influencing the life of fishes differ remarkably between lakes (e.g. Cole, 1983; Goldman & Horne, 1983), as they depend on a number of physical characteristics that are specific for

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each lake (e.g. total depth, clarity of water, or prevailing water currents). Hence, it is difficult to make general predictions about the spacing of fish in the littoral zones of freshwater lakes. In my approach towards this aim, I shall first outline principal effects of critical variables on the performance of fish. Then I shall briefly review existing evidence for two alternative mechanisms that may lead to size-structured habitat distributions of fish. With help of a case study of a tropical, herbivorous cichlid I shall illustrate how these two alternatives may be critically tested.

Depth-dependent factors

Four key factors have been identified to determine the distribution patterns of fish: food availability, predators, parasites and temperature (Huntingford, 1993). Especially in shallow, tropical water bodies oxygen may be limiting, therefore I would like to add this factor to the list. In the littoral zone of lakes, these factors vary systematically with depth. Primary production depends to a large extent on light intensity, which decreases exponentially with depth. The spectrum of predator species varies from non-gape size-limited wading or diving birds and mammals in shallow water to gape size-limited piscivorous fish in deeper water (Power, 1987). Water temperature is directly affected by the weather conditions (heat impact by sunshine, impact of wind which mixes water strata). The direct impact of weather decreases with distance from the surface. The oxygen concentration depends on photosynthesis and respiration, water movement and temperature (Goldman & Horne, 1983), which are depth-dependent variables. I shall exclude the influence of parasites for my discussion, as very little is known about the depth dependence of this factor.

The influence of depth-dependent factors on the life of fish

Food availability. Food availability limits energy supply and thereby it can directly influence the allocation of energy between maintenance and

other functions. The difference between energy income and energy used for maintenance was called 'surplus energy' and can be allocated to somatic growth and reproduction (Ware, 1980; Roff, 1983). If food is limited, proportionally less surplus energy is available.

Temperature. Temperature determines metabolism of fish to a large degree (e.g. Wootton, 1990). The standard metabolic rate (SMR) increases exponentially with temperature. The active metabolic rate (AMR), after increasing exponentially at an even faster rate with temperature compared to SMR, decreases with any further temperature increase (see evidence reviewed in Wootton, 1990). The difference between these two rates, termed the 'scope for activity' (e.g. measured as maximum possible swimming speed, Wootton, 1990), is hence temperature dependent as well.

Oxygen. From experimental studies on brook trout, *Salvelinus fontinalis* it can be concluded that SMR is relatively insensitive to changes in oxygen saturation, while AMR declines when oxygen concentrations fall below 100% (Fry, 1971). Consequently, the scope for activity declines at oxygen concentrations below saturation.

Influence of food, temperature and oxygen on growth. The specific growth rate of fish (i.e. the growth rate in % of original weight) increases asymptotically with food ration (reviewed in Wootton, 1990). At a given ration, the specific growth rate decelerates with increasing temperature. However, if fed on maximum rations, growth rates increase with temperature up to an optimum above which it decreases again (e.g. brown trout, *Salmo trutta*; Elliott, 1975). The increase of growth rate with temperature is due to an increased efficiency of food processing (faster gastric evacuation, higher assimilation efficiency; Wootton, 1990). Hence the optimal temperature strongly depends on the availability of food. Oxygen may limit the growth rate even if food is available in excess, if it falls below a certain critical threshold (Brett, 1979).

Conflicting demands may lead to regular switches between two habitats. For example, minnows, *Phoxinus phoxinus* preferred to use warmer,

shallow water embayments instead of the cooler water of the river bed, although a higher prey density was present in the river (Garner et al., 1998). In the shallow, they stayed inactive. They had to go regularly to the cool river water sections for feeding. Garner et al. (1998) concluded that this pattern results from the trade-off between good feeding opportunities and living at temperatures that favour somatic growth.

Predators. By changing the feeding habits of fish, the presence of predators can affect their energy consumption and thereby growth rate. In response to predators, fish may prefer less profitable but safe patches or they may restrict their feeding time (reviewed in Huntingford, 1993; Sih, 1993), they may switch to less profitable prey types (Godin, 1990) or they may reduce the attack distance for catching prey (Dill & Fraser, 1984; Metcalfe et al., 1987). As a consequence of these behavioural adaptations to predator density less energy is consumed and growth rates slow down. Hence, an important trade-off in fish habitat choice exists between patch profitability and safety from predators.

Size-dependent habitat selection: multiple optima or competitive interference

Differently sized fish often use different food items or are hunted by different predators, and they also may have different physical optima. Different size classes of a species should distribute themselves in response to these depth dependent factors. As expected, differently sized fish are often distributed unequally over depths. In the very most cases, a 'bigger-deeper distribution' (Power, 1987) has been found, i.e. small species or small sizes of a species use rather shallow habitats while large individuals occupy deeper habitats (review in Helfman, 1978; Power, 1984). An opposite trend was found in *Tropheus moorii*, however, a herbivorous cichlid from Lake Tanganyika (Kohda & Yanagisawa, 1992; this study). There are two principal lines of arguments to explain size-structured distributions along depth gradients.

- (I) The maximum pay-off yielded by different habitats may vary between body size classes of a species, due to size specific food sources, differential sensitivity to predation or to variation in reproductive state (e.g. reproductive individuals may move into habitats to reproduce which are less suitable for juveniles).
- (II) Even if a single habitat yields the highest pay-off for different size classes, the size distributions may differ between habitats, because due to competition, smaller individuals may be excluded from their optimal habitat.

Hypothesis (I): Multiple optima in habitat selection. Several empirical studies have demonstrated that multiple optima may lead to size structured distributions. For example, small individuals may suffer a stronger predation pressure than large individuals, and therefore use habitats offering better shelter even if they provide less food than habitats used by larger individuals (e.g. L'Abbé-Lund et al., 1993). An experimental study suggested that in armored catfish, *Ancistrus spinosus* the selective force of two different groups of predators generates a bigger-deeper distribution in this species (Power, 1987). Small individuals which are hunted by piscivorous fish use the shallow areas of river pools. Large specimen outgrow the swimming predators, but may be eaten by non-gape size-limited wading and diving birds (herons, kingfisher). These predators are constrained to hunt in shallow depths, and large catfish avoid these predators by moving to deeper water.

Juveniles of predatory fish often use other food sources than adults (e.g. zooplankton vs. fishes). This may lead to size specific habitat segregation if the prey species occur in different habitats (Werner & Gilliam, 1984).

A spatial habitat segregation between reproductive adults and juveniles may occur if specific habitats are required for spawning. While many species performing true migrations to their spawning sites, either anadromous or catadromous, never return to their juvenile habitats (see for examples Dodson, 1998), others, like cyprinids, move back and forth between non-reproductive and spawning habitats (Mills, 1991).

Hypothesis (II): Competition. Theoretical treatments of habitat specific distributions have modelled usually single optimum-situations, because these are the easiest to handle (reviews in Milinski & Parker, 1991; Kacelnik et al., 1992). They are based on the ideal-free distribution model developed by Fretwell and Lucas (1969). Generally, these models assume the existence of several habitats (or patches) with different 'basic suitability'. The most important assumption of ideal free distribution models is that individuals are free to move between habitats. Many of these models assume that competitors are equal, which makes them unsuitable for explaining size-structured distributions in fish, as smaller individuals generally are competitively inferior to large ones.

Models with *unequal* competitors assume that the pay-offs differ between phenotypes in relation to their competitive ability. Depending on the assumptions, these models generate different predictions for the distribution of individuals. *(II.a) Ideal-free like distributions:* If the payoff of a phenotype remains constant, regardless of which patch it uses, several stable distributions may result, in which the sums of 'competitive weights' of individuals in each habitat match its respective input rate (Sutherland & Parker, 1985; Parker & Sutherland, 1986; Milinski, 1988). But only in one of these stable distributions the average pay-off of patches is equal. This distribution, where the frequencies of phenotypes in each patch match the frequencies of phenotypes in the population, is the most likely one to occur by chance at low population sizes (Houston & McNamara, 1988). This distribution has been demonstrated to occur in experimental studies using sticklebacks (see Milinski, 1988 and references therein). *(II.b) Truncated size distribution:* If the relative pay-offs of phenotypes among patches are *not* equal, because differences in competitive ability (e.g. size differences) are more important in some patches than in others, a truncated size distribution is predicted. The smallest individuals occupy habitats where the effects of size are least important and the largest individuals occupy habitats with the strongest effects of size (Parker & Sutherland, 1986). In

case of dominance interactions less competitive individuals are forced to occupy patches of poorer quality (see Gotceitas & Godin, 1992; Hughes, 1992; Hughes & Dill, 1992 for experimental studies). Dominance interactions may also lead to a size-dependent temporal partition of major feeding times over the day rather than to a spatial segregation (Kadri et al., 1997). Extreme cases of size truncated distributions may occur in territorial systems where resources are aggressively monopolized. Although territories may be compressible to a degree with increasing densities of territory owners, patches are exploited by fewer individuals than expected under an ideal free distribution ('despotic distribution' after Fretwell, 1972). If there are more individuals in the population than there is space for territories 'surplus individuals' (*sensu* Brown, 1969) may become floaters like in *Parablennius sanguinolentus* (M. Taborsky & D. Limberger, MS). Similarly, *Neolamprologus brichardi* join feeding aggregations when all available shelters are occupied (Taborsky & Limberger, 1981).

SIZE-DEPENDENT DEPTH DISTRIBUTION OF *TROPHEUS MOORII* IN THE LITTORAL ZONE OF LAKE TANGANYIKA: A CASE STUDY

Lake Tanganyika is one of the Great Lakes in the African rift valley. Along the shore of this lake, only few parts are inhabited by rooted plants. Most of the lake shore consists either of sandy stretches or rocks, pebbles and gravel covered by a thin layer of turf algae. This 'Aufwuchs' sustains a diversified guild of cichlid algae grazers, browsers and peckers (Yamaoka, 1997). Most of these species are endemic to Lake Tanganyika, such as *Tropheus moorii*, a maternal mouthbrooder which is perhaps the most common species in the littoral zone of this lake. Compared to other algae eating species, *T. moorii* inhabit an extraordinarily wide range of depths. In two populations, they were found down to 18m and 30m depth, respectively,

with the highest densities between zero and 2m (Kohda & Yanagisawa, 1992). Also, size classes of this species were not distributed evenly over different depths in this study. I investigated which of the two alternative mechanisms – multiple optima or competitive interference – determine the depth dependent size structure of *T. moorii*.

Study area. The study area comprised a depth range from zero to 5m and a stretch of 250m length along the shore line of Kasakalawe Bay, Zambia, at the southern tip of Lake Tanganyika, which is 650km long and at most 80km wide. Below 5m the density of *T. moorii* was negligible.

Production. Epilithic multicellular algae, the only food source of *T. moorii*, grew on the pebbles which covered the bottom of the study area completely. Production of these turf algae was determined at three depths, 0.5m, 1m and 2m. I collected four pebbles (approximate dimensions: 30x20x10cm) at each depth and scraped off the algae layer entirely with razor blades. After they had been scraped, the pebbles were returned to their original position. They were placed under a coarse net, allowing light to penetrate, but keeping algae eaters well away at a distance from their surface. After 48 days the regrown algae were scraped off again, by taking several samples from each pebble. The production ($\text{kJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) was calculated by multiplying the biomass (dry weight of algae per m^2) with the median caloric content of algae harvested at unmanipulated rocks close to the experimental pebbles. Production of algae decreased exponentially with depth (Figure 1; $H_{(2, N=38)}=18.1, p<0.001, N_{(\text{groups})}=16, 14, 8$; Kruskal-Wallis test), which can be explained by the exponential drop of light levels with water depth.

Temperature and oxygen. Water temperature and oxygen saturation were measured at three sites at 0.5m depth intervals (Figure 2). While temperature and oxygen dropped sharply within the upper 3.5m, below that depth they were almost constant. Although both factors varied considerably over the day (temperature range 27.3-28.9°C; range of oxygen saturation 71-138%, measured every full hour between 07:00 and

18:00 over one day in 0.5m), oxygen did not fall below 100% for most of the active period of *T. moorii*. It was hence not considered as a limiting factor in the study area.

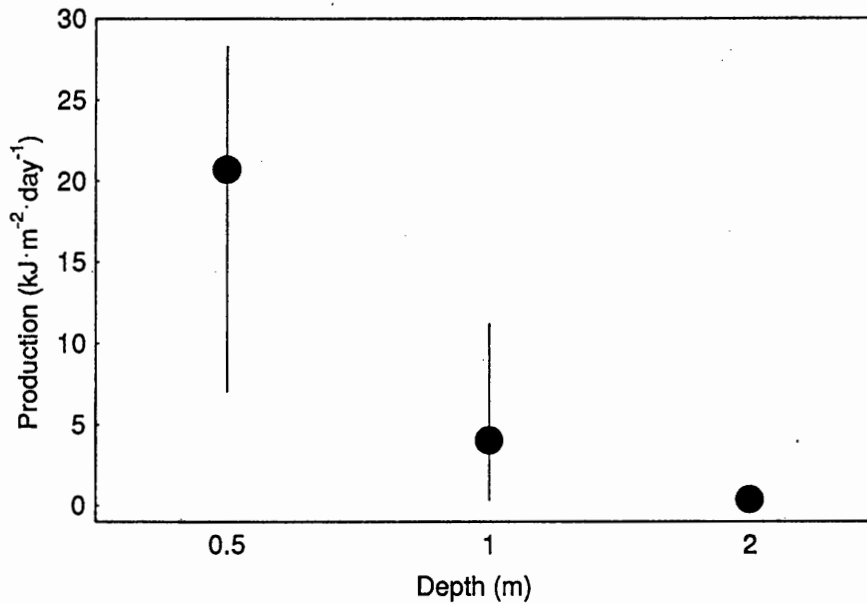


Figure 1. Medians and quartiles of the production of algae in three different depths

Predation. In the study area, there were two groups of potential predators of *T. moorii* present: piscivorous fish and terrestrial predators. Predation on *T. moorii* has never been observed directly. Among the first group of potential predators, stalking hunters like large *Lepidolamprologus elongatus*, *L. profundicola* and *Neolamprologus fasciatus*, and smaller individuals of spiny eels (Mastacembelidae) and catfish were the potential predators for small *T. moorii* (total length (TL) of about 2 to 5cm). The diurnal eel *Caecomastacembelus moorii* may also hunt medium sized and large *T. moorii*. *T. moorii* of all sizes were found hidden deep under pebbles at night, and hence were probably rather safe from predators during the dark

phase. Only preliminary data on predator densities are available as yet. The result of one predator count demonstrated a clear increase of potential predators below 3m. Out of 50 individuals of piscivorous fish counted between zero and 6m depth, 45 fish (90%) were found at or below 3m, 4 (8%) were at 1.5m and 1 (2%) at 0.5m. Forty-four individuals (88%) of the predators were smaller than 10cm (estimated TL). I assume they would pose a threat only to the smaller stages of juvenile *T. moorii* (2 to 5cm TL).

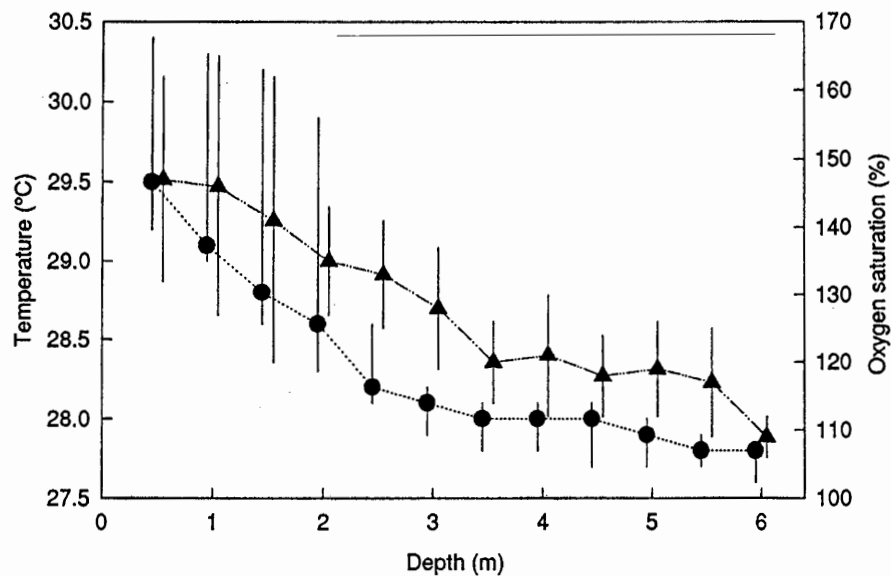


Figure 2. Medians and ranges of temperature ● and oxygen saturation ▲ measured in different depths at 15:00h on three days

Among the terrestrial predators, malachite kingfishers (*Alcedo cristata*), pied kingfishers (*Ceryle rudis*), giant kingfishers (*Ceryle maxima*) and palmnut vultures (*Gypohierax angolensis*) were regularly seen. These birds hunt fish within the uppermost meter of water depth. As they are not gape size-limited, they may be able to hunt also medium sized and large *T. moorii*.

Body condition. In order to get an estimate of body fat reserves I applied a non-invasive method suggested by Adams et al. (1995). With this method, a set of body measurements is compared to the fat contents of a limited number of sacrificed specimens. In this study, the fat content of 15 *T. moorii* specimens ranging from 5.0 to 9.5cm fork length was determined by Soxhlet extraction. Three body length measures, eight different width and height measures, weight and a condition factor calculated from length and weight were taken before fish were sacrificed. However, as all body measures correlated highly with length of the fish, I calculated a stepwise multiple regression only with length, weight and condition factor as independent variables. Body weight was the only factor kept in the regression model ($p < 0.001$, $N = 15$). However, fish occurring deeper than 2m could not be weighed, because of decompression problems when brought to the surface, while body measures could be taken easily under water using callipers. Body width in the cloacal region (W_c), raised to the power of 2.15 to correct for allometry gave the highest correlation with weight ($r = 0.93$, $p < 0.001$, $N = 52$) and was also highly correlated with fat content itself ($r = 0.92$, $p < 0.001$, $N = 15$).

I estimated the percentage of body mass of adult females inhabiting three different depths, 0.5m (data from 1996), 2m (1997), plus 3m (1998) combined, and 5m (1998). The year of collection is important to note, as at the onset of the study season in 1998 the water level had risen by one metre compared to the level one year before, due to heavy rains caused by an El Niño event. Population counts suggested that most of the adult *T. moorii* had remained in their former areas, hence fish caught at 2m in 1997 lived at 3m one year later. Fat content decreased with depth over the total size range of the samples (Figure 3; $F_{(2,43)} = 8.23$, $p < 0.001$; ANCOVA) and W_c covaried significantly with fork length ($r = 0.76$, $F_{(1,42)} = 56.49$, $p < 0.001$).

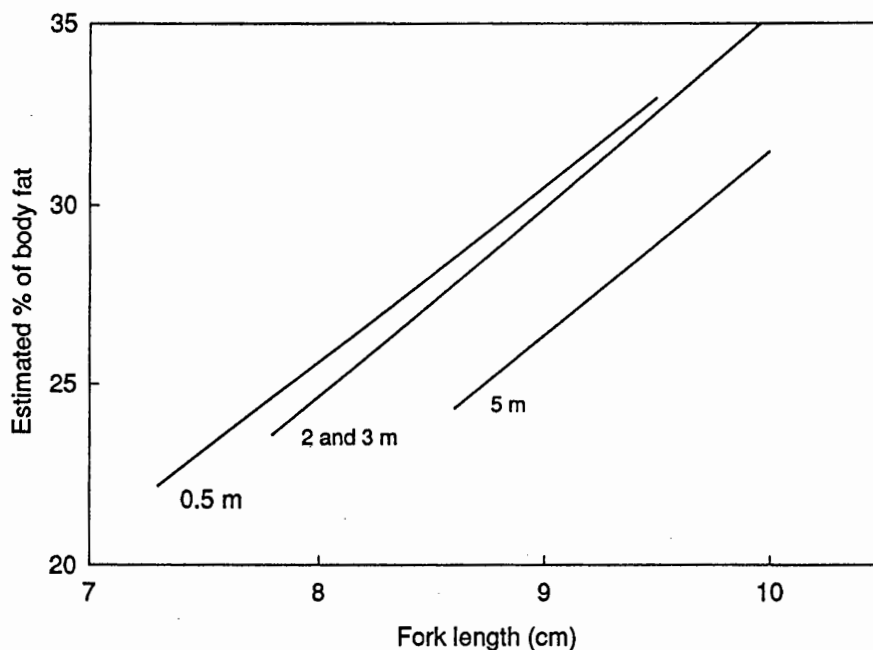


Figure 3. Fat content estimated as % of body weight for *T. moorii* caught at three different depths ($N=21$ at 0.5m, $N=17$ at 2m, $N=7$ at 5m)

Growth. Growth rates could not be measured directly in the field. Instead, I applied a method suggested by Doyle et al. (1987) where the distance between a defined number of outer circuli on scales is used as a measure of growth rate. This method allows the comparison of relative growth rates between groups of fish of a given size. The distances between the first and the fifth circulus from two scales per fish were measured at five locations at the anterior side of each scale. Mean values for each scale were calculated and the mean of the two scales were used as growth rate estimate of an individual (=CIRC in Figure 4). The scales were taken from the middle axis (i.e. well below the lateral line in *T. moorii*) of the left body side of each fish.

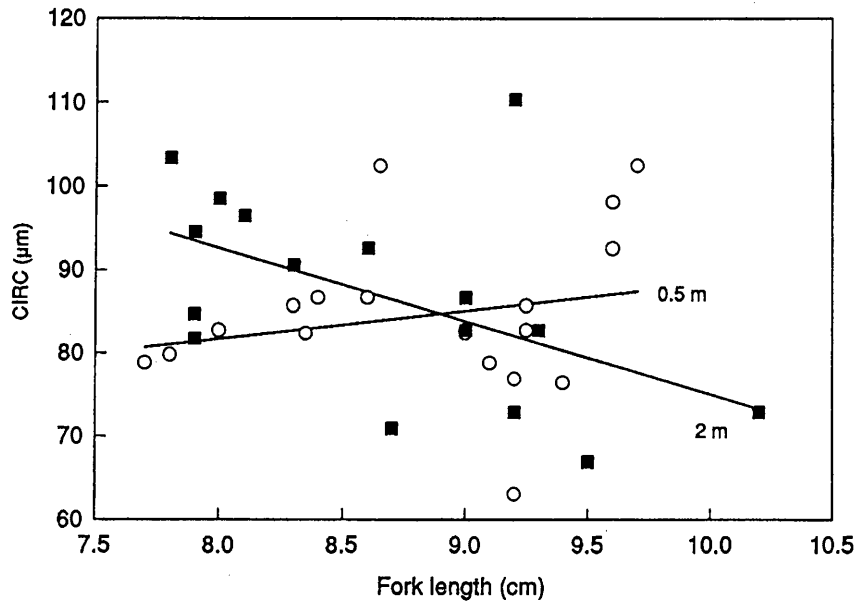


Figure 4. Estimated growth rates of adult females at 0.5m (○; $r=0.2$, $p>0.1$) and at 2m (■; $r=-0.51$, $p<0.05$)

Overall differences in the growth rate estimate did not differ between depths ($t=-0.61$, $df=33$, $p>0.1$; two tailed t-test). However, smaller females grew faster at 2 m and more slowly at 0.5 m relative to larger females (Figure 4). A two-way ANOVA revealed a significant interactive effect of size and depth ($F_{(2,29)}=7.8$, $p<0.002$; the size range of sampled individuals was divided into three classes: 7.5 to 8.4, 8.5 to 9.4, 9.5 to 10.4cm).

Expectations for the distribution of T. moorii over depths. To test whether multiple ecological optima exist for *T. moorii* (Hypothesis I) two questions need to be answered: Do habitats yield different pay-offs to different size-classes? If yes, do these differences determine the depth distribution of *T. moorii*?

Algae eating fish should prefer the shallow parts of the littoral zone as there, higher algae production in combination with higher temperatures

offer a better scope for growth and energy accumulation. Additionally, a preference for shallow, warm water by reproductive females would reduce the length of the energy demanding phase of mouthbrooding due to a quicker development of eggs. Oxygen is not a limiting factor in the shallow zones of Lake Tanganyika as it is the case in some shallow tropical lakes. Also, small *T. moorii* appear to be relatively safe from large predatory fish in the upper 2.5m.

However, as terrestrial predators are restricted to the uppermost depth metre, medium sized and large *T. moorii* should be relatively more frequent below 1m.

To test whether competition influences the depth distribution of fish sizes (Hypothesis II), one has to ask whether the distribution of small, competitively inferior individuals is determined by the behaviour of large individuals. Adults of *T. moorii* defend territories to monopolize food resources (Kohda, 1997). At sufficiently high population densities, large, competitively superior individuals should be able to monopolize preferred areas completely. Small individuals should then be non-territorial floaters, or they should occupy areas in low-quality habitats, which may not be saturated.

Distribution of T. moorii. In each of the three study seasons, population density and size structure between 0.5 and 5m were estimated by counting individuals along ten 100m-transects parallel to the shore line. Every 10m along a transect, the area of a half circle with a radius of 2m was scanned once, all *T. moori* were counted and their total length was estimated to the nearest cm. Densities declined with depth in all three years (Figure 5). On average, more than 60% of all individuals were found in the upper 2m. As expected, the shallow depths were strongly preferred by *T. moorii*.

Similarly, the shallow water was preferentially used also by other algae eating species. In 1996/97, all algae eaters were counted at 0.5 and 2m depth. Areas of 2x1m were scanned 10 times each for the presence of algae eaters and the median number of individuals was calculated from these

scans. At nine areas at 0.5m, on average 7.5 algae eaters were present per square metre (=mean; range: 4-12.2), which was about twice the number found at three areas at 2m (mean=4 ind. \cdot m⁻², range: 2.2-5) ($U=2.0$, $p<0.05$, Mann-Whitney U -test; all counts between 10:00-14:00 h). Densities were even lower at 3m (1 ind. \cdot m⁻²; range: 0.5-1, $N=3$) and at 5 m (1 ind. \cdot m⁻²; range: 1-1.5, $N=3$) in 1998.

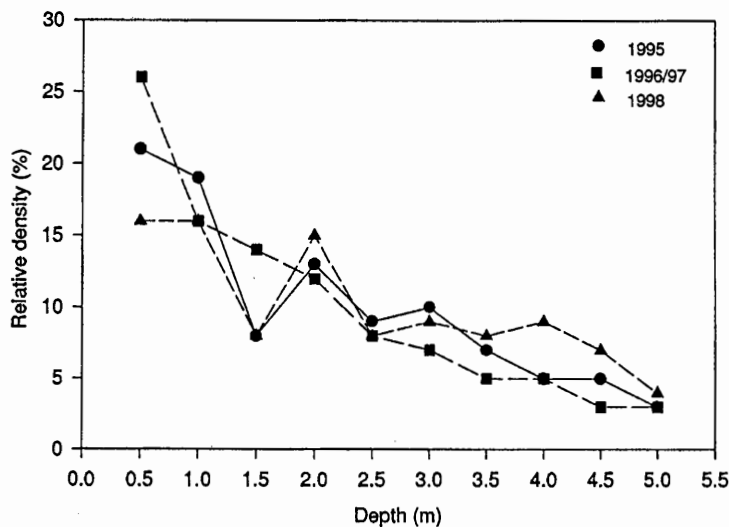


Figure 5. Percentages of individuals counted three times (once per study season) at different depths

In *T. moorii*, the size distributions differed significantly between depths in all three study seasons (Figure 6; 1995: $H_{(9, N=562)}=53.05$, $p<0.001$; 1996/97: $H_{(9, N=291)}=45.50$, $p<0.001$; 1998: $H_{(9, N=497)}=74.72$, $p<0.001$; Kruskal-Wallis test). I regarded individuals larger than 7cm as adults, as the smallest breeding female found had an estimated total length of 7.5cm. Larger adults (10 to 11cm total length) occurred deeper than smaller ones (8 to 9cm) (chi-square test=19.9, $df=9$, $p<0.02$). This conforms to the expectation from Hypothesis I, that larger *T. moorii* should escape the predation risk caused by birds by settling in deeper water.

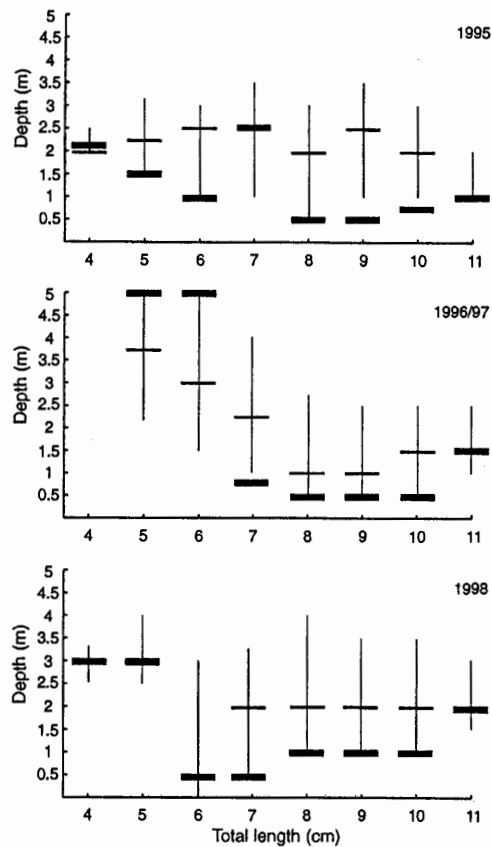


Figure 6. Modes (thick bars), and medians (thin horizontal lines) and interquartile ranges (vertical lines) of depths at which different size classes of *T. moorii* occurred in the three study seasons

Compared to adults, juveniles (<7cm) were more strongly represented in moderately deep water around 3m (Figure 6). These depths are less preferred by *T. moorii* in general and I did not find any plausible ecological advantage for settling below 2.5m. Additionally, in a patch with small pebbles (a local harbour) besides the area where transect counts were made many juveniles were found between zero and 2m. This area represented a distinct habitat type from the remaining study area in that it contained only

few possibilities to hide. It is hence supposed to be of lower quality than a habitat with large pebbles in comparable depths. In the small-pebble habitat juveniles fed in loose groups, while in the large-pebble habitat they fed solitary between rocks. The stronger representation of small individuals below 2.5m in the large-pebble habitat suggests competitive displacement by larger fish and supports Hypothesis II.

Under the assumption of a decreasing competition for food with depth, I searched for behavioural and ecological correlates of competition.

Feeding areas. I measured the maximum length and width of the area used by adults of comparable body size (9-11cm) during five minutes of focal observation, calculated the resulting ellipse and defined this as the 'feeding area' of an individual. As food resources are defended, the estimated feeding areas should be highly correlated with territory size. The size of feeding areas increased significantly with depth (Figure 7; $H_{(3, N=48)}=7.7, p=0.05, N_{(groups)}=12, 13, 11, 12$; Kruskal-Wallis test).

Aggression. Chases of neighbours were by far the predominantly observed aggressive interactions. The amount of all aggressive interactions determined in 10 min time budgets decreased nearly by a factor of 10 from 0.5 to 2 m depth (mean=56.5sec; interquartile range, iqr: 31-106.8 and 6sec, iqr: 4-25.5sec; $U=9.5, p<0.02, N=8, 8$; Mann-Whitney U-test; these figures include body vibrating, which is shown in the context of aggression as well as during courtship).

Standing crop. The standing crop of algae was determined by collecting algae samples from unmanipulated pebbles. Energy content was measured by bomb calorimetry. While the energy content of algae ($\text{kJ}\cdot\text{g}^{-1}$) collected at different depths did not differ significantly ($H_{(2, N=34)}=3.81, p>0.1, N_{(groups)}=14, 9, 11$; Kruskal-Wallis test), the energy content per area ($\text{kJ}\cdot\text{m}^{-2}$) differed significantly between depths (Figure 8; $H_{(2, N=44)}=15.7, p<0.001$; Kruskal-Wallis test).

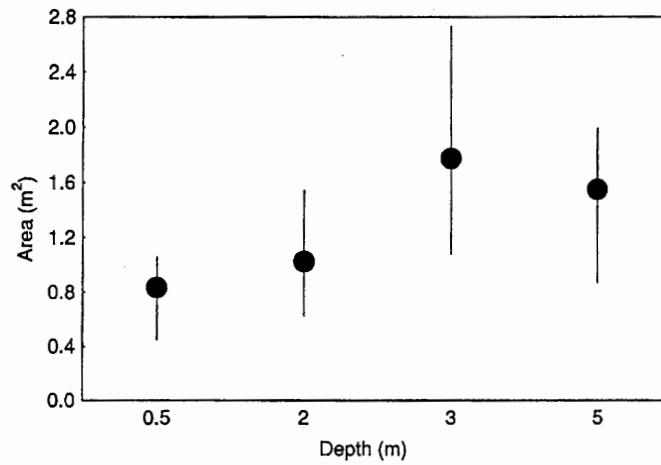


Figure 7. Estimated sizes of feeding areas in different depths (medians and quartiles)

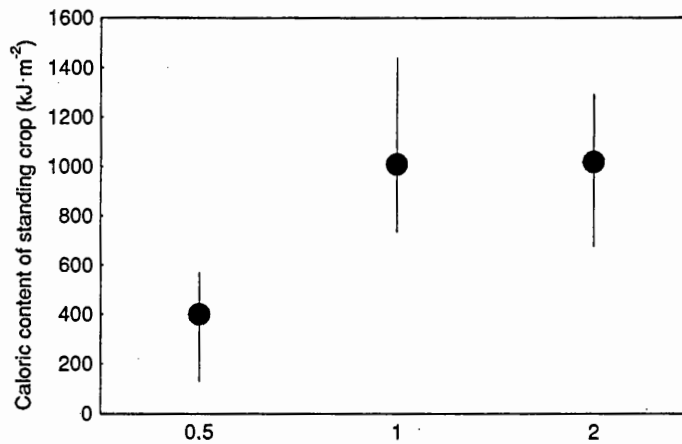


Figure 8. Caloric content of standing crop collected in three different depths at 15:00h (medians and quartiles)

CONCLUSIONS FROM THE CASE STUDY OF *T. MOORII*

In my study on *T. moorii*, I tested predictions derived from two alternative, but not mutually exclusive hypotheses, to explain the causes of

size-structured depth distributions in fish. The hypotheses were derived from theoretical and empirical studies of habitat and patch choice. 'Water depths' were treated equivalently to habitats or patches in my study. Size-structured depth distributions within species should be expected, if the maximum pay-off yielded by different depths varies between fish of different body sizes, and fish choose the depths that are optimal for their size (Hypothesis I), or if a certain depth yields the highest pay-off for several different size classes, but smaller, competitively inferior individuals are excluded from the optimal depth range by dominant or territorial conspecifics (Hypothesis II). Fishes of all sizes of *T. moorii* seem to prefer shallow water (zero to 2m depth) probably due to the high algae productivity, warmer temperatures and low mortality risk caused by predatory fish. Within the preferred depths, larger adults tend to use slightly deeper water. This pattern was predicted by Hypothesis I, as larger specimens are especially prone to attacks by terrestrial predators hunting in the uppermost depth metre. Hence large adults have a slightly different depth optimum than smaller conspecifics. Juveniles, which are competitively inferior due to their small size, are partly displaced from preferred habitats as predicted by Hypothesis II. Juveniles settle in depths with either a lower food production and higher predator density, or in a habitat with fewer shelters (i.e. small-pebble habitat). However, some juveniles manage to live in the preferred habitats, which does not fully accord with Hypothesis (II.b), which predicted a completely size truncated distribution. It may be that at even higher population densities, smaller individuals are completely excluded from their optimal depth range. The conclusions about critical factors for the habitat choice of *T. moorii* are only preliminary, as no experimental test of the effects of single factors on habitat choice has been made.

In the following three sections I shall discuss some open questions regarding the results of my study of *T. moorii*.

- (I) From 0.5 to 2m, productivity of algae decreased strongly, while the standing crop increased. This may appear to be contradictory, but it

may be explained by the influence of herbivores. The biomass of algae eaters that can be sustained in an area depends on productivity, and not on standing crop. Although absolute numbers and biomass of algae eaters were higher in 0.5m, relative to production, more fish were present in 2m depth (Table 1). Consequently, the limitation of food increased with depth, which explains why the fat content of fish decreased correspondingly. As large adults tended to prefer a suboptimal depth with regard to food (2m), predation risk by terrestrial predators may have primacy over availability of algae for these fish. Small adults may be at risk from terrestrial predators as well, especially by the smaller kingfisher species. One may speculate that the relatively low numbers of small adults in 2m depth indicates a competitive displacement from this depth by large adults.

Table 1

Ratios between biomass ($g \cdot m^{-2}$) of T. moorii counted in three years, and the production of algae ($g \cdot m^{-2} \cdot day^{-1}$; measured in 1996/97)

	1995	1996/97	1998
0.5m	1.5	1.0	0.6
1m	7.9	3.2	4.9
2m	56.3	26.51	51.8

(II) If food is limited at 2m, why is the standing crop of algae higher in this depth than at 0.5m depth? Any existing standing crop can be assumed to be in a stable equilibrium between production and consumption rate (Lessels, 1995). At 2m fewer individuals were present and sizes of feeding areas increased with depth (due to the risen lake level in 1998, the sizes of feeding areas measured at 3m depth in 1998 corresponded to standing crops at 2m when measured

in 1996/97). The larger feeding areas, and possibly lower intrusion rates as suggested from a lower aggression rate suggest that a single individual has more complete control over its territory at 2m than at 0.5m depth. This may explain the higher standing crops at 2m depth.

(III) Why did small adult females grow better at 2m, while large adult females grew relatively faster at 0.5m depth? There may be two separate reasons for these results. Although food is abundant at 0.5m, growth of small adult females may be inhibited at this depth by high levels of stress elicited by the large number of aggressive interactions with larger, dominant individuals. Large adults may grow worse at 2m due to their higher energy demands compared to the demands of small adults, which perhaps they cannot compensate fully at the food limited depth of 2m (see Table 1).

In conclusion, the combined effects of two critical ecological factors seem to determine the habitat preferences of *T. moorii*: food and predation risk. In the general overview at the beginning of this paper, both factors have been identified to be depth dependent and to influence metabolism and growth of fish. A rapid decline of food productivity with depth, and the presence of two different groups of predators, non-gape size-limited species in the shallow and gape size-limited species in deeper water, may cause the size-structured distribution in *T. moorii* (this study) and also in other herbivorous fish (Power, 1987). The influence of these factors on herbivores is probably characteristic for littoral zones in general. In contrast to marine littoral zones, strong water movements are usually not a limiting factor in freshwater lakes.

Studies of fish distributions in different habitats either investigated how different ecological optima determine the distribution of different groups of fish (e.g. Werner & Gilliam, 1984; Power, 1987; L'Abbé-Lund et al., 1992), or they tested theoretical predictions of fish distributions derived from the distribution of a single resource (reviewed in Milinski & Parker, 1991). I would suggest that future studies of habitat use should take both

approaches into account, in order to elucidate the possible interplay between individual optimization and competition effects, as demonstrated in the case study of *T. moorii*.

SUMMARY

In the littoral zone of freshwater lakes several important ecological factors vary strongly with water depth, such as primary production, temperature, oxygen concentrations and the abundance of terrestrial and aquatic predators. Accordingly, the size distributions of many fish species vary systematically with depth. A review of habitat selection studies of littoral fish revealed two basic mechanisms that may lead to size structured distributions. (I) Differently sized conspecifics may have different optima with regard to habitat quality. (II) Smaller individuals may be displaced from their optimal habitat by competition, if the same habitat is optimal for a range of different sizes. In a case study of the herbivorous Lake Tanganyika cichlid *Tropheus moorii*, I tested predictions of the size-dependent depth distribution of this species, that have been derived from the two hypotheses. The highest densities of specimen occurred in the depth range that was most productive and least prone to aquatic predators (zero to 2 m depth). However, large adults tended to occur deeper than smaller ones within this preferred depths range, possibly because the predation risk may be especially high for large fish in the uppermost metre of the water column due to the action of terrestrial, non-gape size-limited predators. Therefore, this size class may partly evade the most productive feeding substrate. Although all sizes of *T. moorii* occurred in the preferred depth range, juveniles were found relatively more often in lower quality habitats, either with a lower algae productivity and higher predator density or with less shelter sites. Juveniles seemed to be displaced from high quality habitats due to their competitive inferiority (i.e. mainly due to small size).

This case study outlines the potential interplay between individual optimization and competition effects, which is likely to determine habitat use in many littoral fish species.

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REFERENCES

- Adams, C.E., Huntingford, F.A., & Jobling, M. (1995). A non-destructive morphometric technique for estimation of body and mesenteric lipid in Arctic charr: a case study of its application. *J. Fish. Biol.*, 47, 82-90.
- Brett, J.R. (1979). Environmental factors and growth. In W.S. Hoar, D.J. Randall, & J.R. Brett (Eds.), *Fish Physiology* (vol. VIII, pp. 599-675). London: Academic Press.
- Brown, J.L. (1969). Territorial behaviour and population regulation in birds. *Wilson Bull.*, 81, 293-329.
- Cole, G.A. (1983). *Textbook of Limnology* (3. ed.). St Louis: Mosby.
- Dill, L.M., & Fraser, A.H.G. (1984). Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behav. Ecol. Sociobiol.*, 16, 65-71.
- Dodson, J.J. (1998). Fish migration: an evolutionary perspective. In J.-G.J. Godin (Ed.), *Behavioural Ecology of Teleost Fishes* (pp. 10-36). Oxford: Oxford University Press.

- Doyle, R.W., Talbot, A.J., & Nicholas, R.R. (1987). Statistical interrelation of length, growth, and scale circulus spacing: appraisal of a growth rate estimator for fish. *Can. J. Fisheries Aquat. Sci.*, 44, 1520-1528.
- Elliott, J.M. (1975). The growth rate of brown trout, *Salmo trutta* L., fed on maximum rations. *J. Anim. Ecol.*, 44, 805-821.
- Fretwell, S.D. (1972). *Populations in a Seasonal Environment*. Princeton: Princeton University Press.
- Fretwell, S.D., & Lucas, H.J. (1969). On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.*, 19, 16-36.
- Fry, F.E.J. (1971). The effect of environmental factors on the physiology of fish. In W.S. Hoar & D.J. Randall (Eds.), *Fish Physiology* (vol. VI, pp. 1-98). London: Academic Press.
- Garner, P., Clough, S., Griffiths, S.W., Deans, D., & Ibbotson, A. (1998). Use of shallow marginal habitat by *Phoxinus phoxinus*: a trade-off between temperature and food? *J. Fish Biol.*, 52, 600-609.
- Godin, J.-G.J. (1990). Diet selection under the risk of predation. In R.N. Hughes (Ed.), *Behavioural Mechanisms of Food Selection* (pp. 797-819). Berlin: Springer-Verlag.
- Goldman, C.R., & Horne, A.J. (1983). *Limnology*. N.Y.: McGraw-Hill.
- Gotceitas, V., & Godin, J.-G.J. (1992). Effects of location of food delivery and social status on foraging-site selection by juvenile Atlantic salmon. *Env. Biol. Fish.*, 35, 291-300.
- Helfman, G.S. (1978). Patterns of community structure in fishes: summary and overview. *Env. Biol. Fish.*, 3, 129-148.
- Houston, A.I., & McNamara, J.M. (1988). The ideal free distribution when competitive abilities differ: an approach based on statistical mechanics. *Anim. Behav.*, 36, 166-174.
- Hughes, N.F. (1992). Ranking of feeding positions by drift-feeding Arctic grayling (*Thymallus arcticus*) in dominance hierarchies. *Can. J. Fisheries Aquat. Sci.*, 49, 1994-1998.
- Hughes, N.F., & Dill, L.M. (1992). Position choice drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, Interior Alaska. *Can. J. Fisheries Aquat. Sci.*, 47, 2039-2048.

- Huntingford, F.A. (1993). Can cost-benefit analysis explain fish distribution patterns? *J. Fish Biol.*, 43 (Suppl. A), 289-308.
- Kacelnik, A., Krebs, J.R., & Berstein, C. (1992). The ideal free distribution and predator-prey populations. *Trend. Ecol. Evolut.*, 7, 50-55.
- Kadri, S., Metcalfe, N.B., Huntingford, F.A., & Thorpe, J.E. (1997). Daily feeding rhythms in Atlantic salmon. II: Size-related variation in feeding patterns of post-smolts under constant environmental conditions. *J. Fish Biol.*, 50, 273-279.
- Kohda, M. (1997). Interspecific society among herbivorous cichlid fishes. In H. Kawanabe, M. Hori, & M. Nagoshi (Eds.), *Fish Communities in Lake Tanganyika* (pp. 105-120). Kyoto: Kyoto University Press.
- Kohda, M., & Yanagisawa, Y. (1992). Vertical distributions of two herbivorous cichlid fishes of the genus *Tropheus* in Lake Tanganyika, Africa. *Ecol. Freshw. Fish*, 1, 99-103.
- L'Abbé-Lund, J.H., Langeland, A., Jonsson, B., & Ugedal, O. (1993). Spatial segregation by age and size in Arctic charr: a trade off between feeding possibility and risk of predation. *J. Anim. Ecol.*, 62, 160-168.
- Lessels, C.M. (1995). Putting resource dynamics into continuous input ideal free distribution models. *Anim. Behav.*, 49, 487-494.
- Metcalfe, N.B., Huntingford, F.A., & Thorpe, J.E. (1987). The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Anim. Behav.*, 35, 901-911.
- Milinski, M. (1988). Games fish play: making decisions as a social forager. *Trend. Ecol. Evolut.*, 3, 325-330.
- Milinski, M., & Parker, G.A. (1991). Competition for resources. In J.R. Krebs & N.B. Davies (Eds.), *Behavioural Ecology* (3rd ed., pp. 137-168). Oxford: Blackwell.
- Mills, C.A. (1991). Reproduction and life history. In I.J. Winfield & J.S. Nelson (Eds.), *Cyprinid Fishes* (pp. 483-508). London: Chapman & Hall.
- Parker, G.A., & Sutherland, W.J. (1986). Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Anim. Behav.*, 34, 1222-1242.

- Power, M.E. (1984). Depth-distributions of armored catfish: predator-induced resource avoidance? *Ecology*, *65*, 523-528.
- Power, M.E. (1987). Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. In W.C. Kerfoot & A. Sih (Eds.), *Predation* (pp. 333-351). Hanover: University Press of New England.
- Roff, D.A. (1983). An allocation model of growth and reproduction in fish. *Can. J. Fisheries Aquat. Sci.*, *40*, 1395-1404.
- Sih, A. (1993). Effects of ecological interactions on forager diets: competition, predation risk, parasitism and prey behaviour. In R.N. Hughes (Ed.), *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour* (pp. 182-211). Oxford: Blackwell.
- Sutherland, W.J., & Parker, G.A. (1985). Distribution of unequal competitors. In R.M. Sibley & R.H. Smith (Eds.), *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (pp. 255-274). Oxford: Blackwell.
- Taborsky, M., & Limberger, D. (1981). Helpers in fish. *Behav. Ecol. Sociobiol.*, *8*, 143-145.
- Taborsky, M. & Limberger, D. (MS). Territory holders and floaters: spacing patterns in *Parablennius sanguinolentus* Pallas as a result of the economic defendability of food resources.
- Ware, D.M. (1980). Bioenergetics of stock and recruitment. *Can. J. Fisheries Aquat. Sci.*, *37*, 1012-1024.
- Werner, E.E., & Gilliam, J.F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.*, *15*, 393-425.
- Wootton, R.J. (1990). *Ecology of Teleost Fishes*. London: Chapman & Hall.
- Yamaoka, K. (1997). Trophic ecomorphology of Tanganyikan cichlids. In H. Kawanabe, M. Hori, & M. Nagoshi (Eds.), *Fish Communities in Lake Tanganyika* (pp. 25-56). Kyoto: Kyoto University Press.