IMPACTS OF SEDIMENTATION ON THE ABUNDANCE AND DIVERSITY OF CICHLID FISHES IN LAKE MALAWI

Atsushi Maruyama
Masahide Yuma
Bosco Rusuwa

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FISHES IN LAKE MALAWI

Atsushi Maruyama¹*, Masahide Yuma¹, and Bosco Rusuwa²
¹Science and Technology, Ryukoku University, Otsu, Shiga, Japan
²Department of Biology, University of Malawi, Zomba, Malawi

ABSTRACT

Deforestation and soil erosion across the catchment area of the African Great Lakes has been reported to pose severe environmental problems for aquatic communities. The effects of increasing sedimentation on the abundance and diversity of the extraordinarily diverse communities of endemic cichlid fishes in Lake Malawi were examined. We hypothesized that sedimentation on rock surfaces increases the feeding territoriality of aggressive and exclusive rock-dwelling cichlid species through its impact on the availability of their food, attached algae. This would force the less aggressive species to shift habitats. Comparative surveys in 7 study sites with different sediment quantities showed that the average number of species and individuals coexisting in 2 × 2-m quadrats decreased as the amount of sediment increased. The territory sizes of aggressive species were larger in the sediment-rich sites, suggesting deterioration of their habitat. In a field experiment, sediment clearance resulted in a reduction of territory sizes for aggressive species and a decrease in attacks on heterospecifics, especially at the rock edges as predicted. Less aggressive species shifted to positions with higher food supply that the aggressive species had dominated prior to clearance. The present study suggests that sedimentation affects cichlid abundance and diversity. Our results indicate that rock-dwelling cichlids shift habitats in response to sedimentation. These findings have implications for the prediction of community-level responses to the further expansion of sedimented areas.

* Corresponding author: E-mail: maruyama@rins.ryukoku.ac.jp, Faculty of Science and Technology, Ryukoku University, Otsu, 520-2194 Shiga, Japan. Tel: +81-77-544-7112.
**INTRODUCTION**

Neighboring ecosystems are known to be greatly influenced by each other through abiotic and biotic interactions, and functional losses of surrounding biotopes may exert more important effects on the maintenance of the system than internal factors (Kolasa & Zalewski, 1995; Polis, 1996). In particular, deforestation and soil erosion in terrestrial ecosystems have been reported to have an impact on aquatic ecosystems and pose particularly severe environmental problems in the aquatic communities of the African Great Lakes (Coulter *et al.*, 1986; Cohen *et al.*, 1993; Bootsma & Hecky, 1993; Ogutu-Ohwayo *et al.*, 1997). Denudation of forests across the catchment area of Lake Malawi, probably as a result of agricultural deforestation and excessive fuel-wood cutting (Pilskaln & Johnson, 1991; Eschweiler, 1993; Bootsma & Hecky, 1993; Calder *et al.*, 1995), is considered to have led to an increase in sedimentation in the lake since the 1960s, a theory supported by core sampling (Hecky *et al.*, 1999). Previous studies have focused on the effects of nutrient loading due to sediment increase and suggested the possibility of phytoplankton composition changes at the base of pelagic food webs (Hecky *et al.*, 2003; Guilford *et al.*, 2003). This chapter focuses on sedimentation on the rocky substrates of the littoral zones, and investigates its effects on the habitat quality and interspecific interactions among the littoral community, composed mainly of attached algae and diverse algae-feeding cichlids (Figure 1).

Similar to cichlids in other ancient lakes along the African Great Rift, Lake Malawi cichlids have been isolated for millions of years and have evolved into extraordinarily diverse communities of endemic fishes (Ribbink *et al.*, 1983a; Reinthal, 1993; Turner *et al.*, 2001). The rocky littoral zones of this lake comprises densities of up to 22 species and more than 500 individuals in an area of 50 m$^2$ (Ribbink *et al.*, 1983a; Figure 2). Importantly, most of these cichlids feed on attached algae. Whereas the diversity of these cichlids has been considered to be maintained by fine niche partitioning in their feeding strategies and habitats (Fryer, 1959; Ribbink *et al.*, 1983b; Marsh & Ribbink, 1985; Reinthal, 1990; Bootsma *et al.*, 1996), remarkable niche overlap and flexible feeding observed both in the field and aquaria suggests that interspecific competition is present and intense (Liem, 1980; McKay & Marsh, 1983; Genner *et al.*, 1999a). In fact, interspecific feeding territoriality has been reported to influence the feeding habits of cichlids (Ribbink *et al.*, 1983a; Genner *et al.*, 1999b). Such diversity and interaction intensity should be noted when predicting the consequences of environmental changes.

Increase in the sediment covering rocky substrates may affect the primary production of attached algae by shading out sunlight. Even without changes in the production rate, sedimentation could affect the time required for feeding on attached algae or the quality of the algae as food. Rusuwa *et al.* (2006) showed that several cichlid genera and species groups prefer sediment-free rocky substrates as feeding spots (Figure 1). Habitat deterioration due to sedimentation may lead to an enlarged feeding territory, as predicted by simple graphical models when assuming linear or decelerating increase of defense costs with territory area (Hixon, 1980; Schoener, 1983; Hansen & Closs, 2005). The increased size of feeding territory would affect feeding habitat segregation among cichlids through interspecific and territorial interference, since levels of aggression vary among species (Ribbink *et al.*, 1983a; Maruyama *et al.* 2010). Furthermore, subordinate species may suffer great impacts through interspecific competition in addition to habitat deterioration due to sedimentation.
Impacts of Sedimentation on the Abundance and Diversity of Cichlid Fishes

Figure 1. The effects of soil erosion across the catchment area of the African Great Lakes on cichlid fish communities, studied in previous reports (*1: Bootsma & Hecky, 1993; *2: Seehausen et al., 1997; *3: Hecky et al., 2003; *4: Rusuwa et al., 2006) and this chapter (**)

The objective of this chapter is to test the hypothesis that sedimentation impacts the community structure of cichlids. Special attention has been paid to the role of increased interspecific feeding territoriality and its effects in the community. Comparative field surveys were first conducted to examine the relationship between the quantity of sediment and the abundance and diversity of cichlids. At the same time, the territorial behavior of the most aggressive species was observed to determine the relationship between sedimentation and territory size. A field experiment was then performed to test the effect of sedimentation on feeding territoriality and positions.


MATERIALS AND METHODS

Study Sites and Environmental Factors

Lake Malawi is located at the southernmost tip of the Great Rift Valley in Africa. The lake has a surface area of approximately 30,800 km$^2$ and a maximum depth of approximately 700 m. Seven rectangular study sites of 60–100 m$^2$ were established in the rocky littoral zones near Nkhata Bay (sites A–D) and Thumbi West Island (sites E–G, Figure 3). These regions are characterized by high species richness associated with the translocation of some cichlid taxa from other regions of the lake (Ribbink et al., 1983a; Genner et al., 2006). In all sites, 2-m interval grids were prepared with measuring tapes to make 2 × 2-m quadrats ($n = 15–25$). In the last 2 months of the dry season (October–November) of 1999 and 2000, when the sediment load from rivers was relatively light (Hecky et al., 2003), comparative surveys were conducted using SCUBA in all sites (A–G) and a field experiment was performed in 1 site (E).

Study sites were selected to cover the intralacustrine variation in the sediment quantities (Figure 2). In all sites, environmental factors that may potentially affect the cichlid community structure were measured immediately after cichlid counting described in the section below (Genner et al., 2004; Table 1). The depth and size of the study sites were determined to keep a distance of approximately 10 m from the neighboring sandy bottom. According to previous reports (Ribbink et al., 1983a; Genner et al., 2004), depths of study sites were maintained within a range of 2–5 m so that the cichlid abundance and diversity is not affected. Sediment accumulation was quantified by collecting all sediments within 20 × 20-cm squares (3–7 random samples for each site) on the upper sides of rocks approximately 60 cm in diameter using a hand pump. Sediment samples were dried at 60°C for 48 h and weighed to the nearest 0.1 mg. The amount of attached algae was evaluated by sampling algae within 2 × 2-cm squares on the upper sides of 3–6 rocks approximately 25 cm in diameter at each site. Algae were brushed off the rocks in the laboratory, collected on glass fiber filters (GF/F, Whatman International Ltd, Maidstone, Kent, UK), and quantified using a photo spectrometer (Lorenzen, 1967). The mean size of the bottom substrate was determined by measuring the diameters of 8 substrates to the nearest 1 cm in all 2 × 2-m quadrats (15–25 replications) for each site.

Study Fishes and Their Interspecific Feeding Territoriality

The rock-dwelling cichlids of Lake Malawi comprise more than 200 putative species (Ribbink et al., 1983a). Of these, 34 species occur at Nkhata Bay and 44 occur at Thumbi West Island. The species composition for both areas is given by Ribbink et al. (1983a). Species identification in the underwater observations of this study was based on the illustrations of Konings (1991).

Most rock-dwelling cichlids feed on attached algae and have finely partitioned feeding strategies and habitats (Ribbink et al., 1983b; Marsh & Ribbink, 1985; Bootsma et al., 1996). Most species that feed on algae defend their feeding territories against most conspecifics and algae-feeding heterospecifics (Genner et al., 1999b). Based on qualitative observations,
Ribbink et al. (1983a) reported that the strength of feeding territoriality differs among species. Based on the observations of interspecific aggression in 10 different species, our recent study confirmed that the frequency of heterospecific attacks varies among species and is negatively correlated with the frequency of heterospecific territorial evacuation (Maruyama et al., 2010).

Figure 2. Photographs of the cichlid fish community in the sediment-free (a, photographed in site E) and sediment-rich areas (b, site A)
The most aggressive species in each site, *Pseudotropheus (Tropheops)* “black” (0.43 attacks·min$^{-1}$) in sites A–D and *P. (T)* “red cheek” (0.72 attacks·min$^{-1}$) in sites E–G, were selected for the comparison of territory sizes in fish observations. Furthermore, the latter was used in the field experiment to observe responses in territorial behavior to sediment clearance. Changes in feeding positions were examined for 6 species with varying levels of aggression: the *P. (T)* species mentioned above, *P. (Maylandia) zebra* (0.27 attacks·min$^{-1}$), *P. (M.) callainos* (0.22 attacks·min$^{-1}$), *Labeotropheus fuelleborni* (0.16 attacks·min$^{-1}$), and *P. (M.) heteropictus* (0.0 attacks·min$^{-1}$). Some of these species are putative but are known to be reproductively isolated (Stauffer et al., 1997; van Oppen et al., 1998). They are all known to feed on attached algae and sometimes zooplankton (Ribbink et al., 1983a; Konings, 1991). They exhibit mating behavior throughout the year with peaks of reproductive activity from August to October (Marsh et al., 1986; Konings, 1991).

**Fish Observations in Study Sites with Different Sediment Quantities**

Individual and species number of coexisting cichlids were counted by a diver (Y.M.) at 7 sites with different sediment quantities (A–G; Figure 3; Table 1). Observation within a 2-min period was replicated in all 2 × 2-m quadrats (15–25 replications in each site), a size that
corresponded to 3–12 feeding territories of aggressive cichlids, and hence, was considered adequate for detecting the consequences of changes in territorial behaviors. Individual fish feeding from the rock surface or staying within approximately 20 cm of the rock surface were treated as those at the bottom, and the remainder as those in the water column.

Feeding territory sizes of *P. (T.)* “black” and *P. (T.)* “red cheek” were measured in sites A–D and E–G, respectively, by a diver (A.M.). These 2 species were selected because they were considered to directly respond to the habitat deterioration independent of interference from other species. Simple graphical models predict the enlargement of the feeding territory in response to habitat deterioration, when assuming a linear or decelerating increase of defense cost with territory area (Hixon, 1980; Schoener, 1983). Males were selected since they guard obvious feeding territories around the spawning nests (Genner et al., 1999b). The feeding positions of the territory owner and those of heterospecifics when the owner first displayed interspecific aggression toward them were observed 1–2 m above the substrate and recorded on a map (after Kohda, 1995). Territories were defined by the outermost positions. Since interval grids of 2 m were prepared with measuring tapes and all substrates were mapped in advance, positions of owners and heterospecifics at the inception of the attacks could be accurately recorded with errors within 10 cm (= fish total length). Intraspecific male–male interference was sometimes observed, but not recorded since it may have occurred within the boundaries of the mating territory, which tends to be larger than the feeding territory (Kohda, 1995; Genner et al., 1999b). Each observation lasted for 15 min. A preliminary 60-min observation period indicated that 15 min was sufficient to estimate territory size. Observations were replicated for 3–6 territorial males in each site. After observations, the observed individuals were captured using gillnets, if possible, and their sizes (standard lengths) were measured with slide calipers to the nearest 0.1 mm to examine the effect of fish size on territory size.

Table 1. Depth (min–max), size (horizontal × vertical length), sediment dry weight, amount of algal chlorophyll *a*, and substrate diameter (mean ± SD) compared among study sites. Figures in parentheses indicate sample sizes. Inter-site variations were tested using ANOVA. Sediment dry weight was log10-transformed to equalize variances. Statistical significances are indicated by *** (*P* < 0.001)

<table>
<thead>
<tr>
<th>Sites</th>
<th>Depth (m)</th>
<th>Size (m)</th>
<th>Sediment dry weight (g·m⁻²)</th>
<th>Algae chlorophyll <em>a</em> (mg·m⁻²)</th>
<th>Substrate diameter (cm)</th>
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<tbody>
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<td>A</td>
<td>3.0–5.1</td>
<td>10 × 8</td>
<td>500.8 ± 405.0 (4)</td>
<td>48.2 ± 30.6 (5)</td>
<td>55 ± 16 (20)</td>
</tr>
<tr>
<td>B</td>
<td>3.4–5.8</td>
<td>10 × 10</td>
<td>336.4 ± 149.4 (3)</td>
<td>60.7 ± 21.6 (3)</td>
<td>87 ± 16 (25)</td>
</tr>
<tr>
<td>C</td>
<td>4.0–5.0</td>
<td>10 × 10</td>
<td>156.7 ± 44.5 (3)</td>
<td>55.8 ± 19.3 (6)</td>
<td>93 ± 29 (25)</td>
</tr>
<tr>
<td>D</td>
<td>3.3–4.6</td>
<td>8 × 8</td>
<td>98.5 ± 37.1 (4)</td>
<td>27.2 ± 9.1 (5)</td>
<td>68 ± 23 (16)</td>
</tr>
<tr>
<td>E</td>
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<td>35.1 ± 20.6 (6)</td>
<td>45 ± 8 (25)</td>
</tr>
<tr>
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<td>2.0–3.0</td>
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<td>7.3 ± 2.6 (3)</td>
<td>49.1 ± 12.8 (3)</td>
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<td>7.6 ± 6.6 (4)</td>
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<td></td>
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</table>

\[ \text{ANOVA} \quad F_{6,21} = 17.4*** \quad F_{6,24} = 1.5 \quad F_{6,114} = 27.2*** \]
Field Experiment Examining the Effect of Sediment

A sediment clearance experiment was performed to examine the effect of sediment on the territory size of the most aggressive species and feeding positions of 6 cichlid species with different levels of aggression (from most- to non-aggressive species). The experiment was replicated for cichlid individuals in site E, where the sediment was moderately loaded and appeared to be affecting the cichlid abundance and diversity (Table 1; Figure 4). The experiment was performed over a period of 3 days, during which the weather was calm and the recovery of sediment was low (11.6 ± 3.3 g·m⁻²), to minimize the possible effects of unknown factors. This time period was considered sufficient for cichlids to behave naturally according to the preliminary observations.

Prior to clearing sediment (09:00–14:00 hours of day 1), the territory size of the most aggressive species, *P. (T.)* “red cheek” male (*n* = 8), was determined by a diver (A.M.), as described in the fish observation section above. The attack rate was calculated as the frequency of attacks against heterospecifics divided by the observation time (15 min). The ratio of attacks at the rock edges (defined as 30–60° slope of each rock) was calculated as the frequency of attacks against heterospecifics at the edge of rocks divided by the total frequency of attacks against heterospecifics. Since territorial behavior must be observed from above, the rock edge was simplified as the 10% margin of each rock (in diameter) in this observation.

Figure 4. The number (mean ± SD) of individuals (a) and species (b) at the lake bottom and in the water column, observed in 2 × 2-m quadrats as a function of the sediment dry weight. Observations were replicated in all quadrats (16–25, Table 1) of each study site.
On the basis of 3- to 10-min observations \( (n = 3–11) \) by a diver (M.Y.), the feeding positions of 6 species were determined before the sediment clearance. The 6 species were selected based on different aggression levels; all 6 were abundant at the site. Feeding sites were categorized into 4 positions; in the water column, on the upper sides (slope of 0–30°), edges (30–60°), and undersides (60–180°) of rocks, so that feeding time could be allocated to the 4 positions (Genner et al., 1999a).

After these observations (15:00–16:00 hours of day 1), all the sediment in the study site was cleared by hand, such that no sediment remained. At 40 h after clearance (09:00–14:00 hours of day 3), observations of the same territory owners (easily recognized by their body coloration and courtship position) were performed in the same manner. Furthermore, the feeding positions of 6 species were observed.

**Statistical Analyses**

Inter-site variations in environmental variables (sediment dry weight, amount of algal chlorophyll \( a \), and substrate diameter), number of individuals and species at the lake bottom and in the water column, as well as the territory sizes of the 2 “Tropheops” cichlids were examined using ANOVA. Sediment dry weight was log\(_{10}\)-transformed before conducting ANOVA to equalize variances. For variables on individual number and species richness with significant inter-site variation, multivariable linear regression models were calculated by stepwise variable-selection procedures with forward selection and minimum \( P \) values of 0.10 was set for variables to enter into the models. The stepwise procedure included 4 site variables: mean sediment dry weight, mean algal chlorophyll \( a \) amount, mean substrate diameter, and median depth. Partial correlation analyses were also performed to evaluate the effect of each site variable on individual number and species richness of cichlids. The mean sediment dry weight was square root-transformed before regression and correlation analyses to normalize distribution.

Changes in territorial behaviors (territory size, attack rate, and ratio of attacks at the rock edge) of \( P. \ (T.) \ “red cheek” \) in response to sediment clearance were examined using Wilcoxon signed-ranks tests. Because sample sizes were small \( (n < 25) \), statistical significance was judged by \( T \) values using a statistical table (Zar, 1999). Changes in feeding positions were examined using a two-way MANOVA (Wilk’s \( \lambda \)), with treatments of before and after sediment clearance for 6 species and dependent variables of percentage feeding time spent at the 4 positions. After this, two-way ANOVA was used separately for each of the 4 positions.

Wilcoxon signed-ranks tests were performed with the aid of Excel software (version 11.2, Microsoft Corporation, Redmond, WA, USA) and other statistical tests were performed using Stata (version 9.2, StataCorp LP, College Station, TX, USA). All statistical tests were two-tailed and used an alpha value of 0.05 for statistical significance.
RESULTS

Field Surveys in Study Sites with Different Amounts of Sediment

Among the environmental factors, sediment dry weight and substrate diameter in the 7 study sites were significantly different (Table 1). Amounts of algal chlorophyll a in the 7 sites were not statistically different, irrespective of differences in sediment dry weight (Spearman’s correlation coefficient, \( n = 7, r_s = 0.32, P = 0.48 \)). Thus, the sediment dry weight and substrate diameter showed significant inter-site variations, which may potentially produce inter-site variations in individual number and species richness.

Among individual number and species richness of cichlids, significant inter-site variations were found in the individual number at the lake bottom, species number at the lake bottom, and species number in the water column, but not individual number in the water column (Table 2; Figure 4). Inter-site variation in individual number at the lake bottom was explained by mean sediment dry weight and mean substrate diameter (both negative; Table 2; Figure 4a). The partial correlation coefficient was only significant (negative) for mean sediment dry weight. Inter-site variation in species number at the lake bottom was explained by and negatively correlated with sediment dry weight (Table 2; Figure 4b). No significant model to explain inter-site variation in species number in the water column was obtained, and all measured variables correlated with the mean species number in the water column (Table 2).

Table 2. Results of ANOVA, stepwise multivariable regression analyses, and partial correlation analyses to examine and explain inter-site variations in the number of individuals and species at the lake bottom and in the water column. “—” indicates variables not selected in the models in stepwise procedures (\( P > 0.10 \)). Statistical significances are indicated by * (\( P < 0.05 \)), ** (\( P < 0.01 \)), and *** (\( P < 0.001 \))

<table>
<thead>
<tr>
<th>Dependent variables</th>
<th>ANOVA ( F ) (d. f.)</th>
<th>Independent variables</th>
<th>Multivariable regression ( F ) (d. f.)</th>
<th>( R^2 )</th>
<th>Coefficient</th>
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<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Substrate diameter</td>
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<td></td>
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<td></td>
<td></td>
<td>Depth</td>
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<tr>
<td>Individual number in the water column</td>
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<td></td>
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<td></td>
<td>(6, 134)</td>
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<td></td>
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</tr>
<tr>
<td>Species number at the lake bottom</td>
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<td>0.35**</td>
<td>19.6**</td>
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<td>(6, 134)</td>
<td>Algae amount</td>
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<td>(1, 5)</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Substrate diameter</td>
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<td></td>
<td></td>
<td>Depth</td>
<td>—</td>
<td></td>
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<td>(6, 134)</td>
<td>Algae amount</td>
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<td>(0, 6)</td>
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<tr>
<td></td>
<td></td>
<td>Substrate diameter</td>
<td>—</td>
<td></td>
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<td></td>
<td></td>
<td>Depth</td>
<td>—</td>
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</table>
Impacts of Sedimentation on the Abundance and Diversity of Cichlid Fishes

Figure 5. The sizes (mean ± SD) of interspecific feeding territories guarded by *Pseudotropheus* (*Tropheops*) “red cheek” males in Nkhata Bay (sites A–D) and *P. (T.) “black”* males in Lake Malawi National Park (sites E–G) as a function of the sediment dry weight. Figures near plots indicate numbers of observed individuals.

Feeding territory sizes of *P. (T.) “black”* in the 4 sites (A–D) significantly differed from each other (*F*<sub>3,15</sub> = 4.79, *P* = 0.016; Figure 5). Furthermore, those of *P. (T.) “red cheek”* in the 3 sites (E–G) were significantly different from each other (ANOVA; *F*<sub>2,12</sub> = 16.39, *P* < 0.001). The mean territory sizes of both species tended to increase with increasing mean sediment load. The effect of fish size on territory size was not statistically significant according to Spearman’s correlation coefficient analysis (*P. (T.) “black”*: *n* = 14 (5 fish lost), *r*<sub>s</sub> = −0.38, *P* = 0.19; *P. (T.) “red cheek”*: *n* = 12 (3 fish lost), *r*<sub>s</sub> = 0.10, *P* = 0.75).

**Field Experiment Examining the Effect of Sediment**

The territorial behavior of *P. (T.) “red cheek”* significantly changed in all 3 observed variables in response to the experimental sediment clearance (Table 3). After sediment clearance, feeding territory size decreased by almost half. The attack rate and ratio of attacks at rock edges showed a 2/3 reduction after sediment clearance.

**Table 3. Changes in territorial behaviors (feeding territory size, attack rate, and ratio of attacks at rock edges) of *Pseudotropheus* (*Tropheops*) “red cheek”, the most aggressive territorial species, in response to experimental sediment clearance over a 10 x 10 m study site (E). Statistical significances are indicated by * (P < 0.05) and ** (P < 0.01)**

<table>
<thead>
<tr>
<th>Variables</th>
<th>Mean ± SD</th>
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<tr>
<td></td>
<td>Before</td>
<td>After</td>
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<tr>
<td>Feeding territory size (m²)</td>
<td>0.78 ± 0.34</td>
<td>0.42 ± 0.18</td>
</tr>
<tr>
<td>Attack rate (number·min⁻¹)</td>
<td>3.03 ± 1.11</td>
<td>2.19 ± 1.02</td>
</tr>
<tr>
<td>Ratio of attacks at rock edges</td>
<td>0.70 ± 0.16</td>
<td>0.50 ± 0.06</td>
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</table>
Figure 6. Changes in the percentage of feeding time spent at 4 positions (upper sides, edges, and undersides of rocks, as well as the water column) in response to experimental sediment clearance over a 10 × 10 m study site (E) by 6 species: (a) *Pseudotropheus* (*Tropheops*) “red cheek”; (b) *P. (T.)* “black”; (c) *P. (Maylandia) zebra*; (d) *P. (M.) callainos*; (e) *Labeotropheus fuelleborni*; and (f) *P. (M.) heteropictus*, arranged according to level of aggression exhibited in interspecific feeding territoriality (Maruyama et al. 2010). Figures in parentheses indicate numbers of individuals observed before and after the sediment clearance.

The two-way MANOVA model, with treatments of before and after sediment clearance for 6 species, significantly accounted for variation in the percentage of feeding time at each of the 4 positions (Table 4; Figure 6). Feeding time was significantly affected by the sediment clearance and differed among species. Furthermore, the effect of the sediment clearance on the feeding time was significantly different among species.
Table 4. Results of two-way MANOVA and separate two-way ANOVA to examine the changes in the percentage feeding time at the 4 positions in response to experimental sediment clearance over a 10 × 10 m study site (E) by 6 species arranged according to level of aggression exhibited in interspecific feeding territoriality

<table>
<thead>
<tr>
<th>Dependent variables</th>
<th>Factors</th>
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<th>P</th>
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<td>Sediment clearance (S)</td>
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<td>3.27</td>
<td>0.019</td>
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<tr>
<td>at 4 positions</td>
<td>Cichlid species (C)</td>
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<td>2.35</td>
<td>0.002</td>
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<td>S × C</td>
<td>20, 154</td>
<td>2.17</td>
<td>0.004</td>
<td></td>
</tr>
<tr>
<td>Separate ANOVA</td>
<td>Sediment clearance (S)</td>
<td>1, 49</td>
<td>4.35</td>
<td>0.042</td>
</tr>
<tr>
<td>at upper sides of rocks</td>
<td>Cichlid species (C)</td>
<td>5, 49</td>
<td>1.80</td>
<td>0.131</td>
</tr>
<tr>
<td>S × C</td>
<td>5, 49</td>
<td>0.68</td>
<td>0.638</td>
<td></td>
</tr>
<tr>
<td>The percentage of feeding time at edges of rocks</td>
<td>Cichlid species (C)</td>
<td>5, 49</td>
<td>0.59</td>
<td>0.705</td>
</tr>
<tr>
<td>S × C</td>
<td>5, 49</td>
<td>2.39</td>
<td>0.051</td>
<td></td>
</tr>
<tr>
<td>The percentage of feeding time at undersides of rocks</td>
<td>Cichlid species (C)</td>
<td>5, 49</td>
<td>1.51</td>
<td>0.205</td>
</tr>
<tr>
<td>S × C</td>
<td>5, 49</td>
<td>1.24</td>
<td>0.305</td>
<td></td>
</tr>
<tr>
<td>The percentage of feeding time in the water column</td>
<td>Cichlid species (C)</td>
<td>5, 49</td>
<td>6.42</td>
<td>0.000</td>
</tr>
<tr>
<td>S × C</td>
<td>5, 49</td>
<td>4.83</td>
<td>0.001</td>
<td></td>
</tr>
</tbody>
</table>

The percentage of feeding time at the upper sides of rocks significantly increased after sediment clearance, but was not accounted for by the species or interaction effect (Table 4). Variations in the percentage of feeding time at the edges and undersides of rocks were not significantly explained by the two-way ANOVA models. The percentage of feeding time in the water column significantly decreased after the sediment clearance and differed among species. Furthermore, the interaction effect (sediment clearance × cichlid species) was significant.

**DISCUSSION**

Cichlid Abundance and Diversity under the Effect of Sedimentation

While previous studies have paid a great deal of attention to the impacts of denudation of forests across the catchment area of the African Great Lakes on aquatic ecosystems (Coulter *et al*., 1986; Cohen *et al*., 1993; Bootsma & Hecky, 1993; Ogutu-Ohwayo *et al*., 1997), the present study is among the first to consider and help to predict the consequences of further sedimentation. Therefore, our field surveys were designed simply to detect the impact of sedimentation by establishing study sites with different quantities of sedimentation, and hence, were not sufficient to understand its relative importance among other environmental factors in the field.
Field surveys detected marked negative relationships between the sediment quantity and the abundance and diversity of cichlids coexisting in 2 × 2-m quadrats at the lake bottom, whereas the effects of increased sediment were not evident among cichlids in the water column (Table 2; Figure 4). Changes in the cichlid community were only found at the lake bottom where increased sedimentation may have directly affected attached algae. These results corresponded to previous findings that cichlids prefer a sediment-free bottom as a feeding habitat (Rusuwa et al., 2006). Our survey results, however, showed no significant effects of sedimentation on standing crops of their food: the amount of attached algae was not different among study sites, and it was not related to the abundance and diversity of cichlids. Hence, sedimentation is considered to decrease the carrying capacity of the habitat by reducing the feeding efficiency of cichlids, the algal production rate, and/or the food quality of the algal mat (composed of algae, sediment, and microbes). Experimental investigations of algal production, with careful attention to the effects of cichlid grazing, would show how sedimentation decreases the carrying capacity of the habitat.

In addition to the effects of sedimentation, the substrate size was a secondary contributor to cichlid abundance at the lake bottom (Table 2). This result partly supported previous reports that substrate composition significantly (but only slightly) affects the community structure of rock-dwelling cichlids in this lake (Genner et al., 2004). Some factors that were not measured in this study may also be responsible for the inter-site variations in individual number and species richness. Such factors include shoreline slopes, water clarity, predation pressure on cichlids, dispersal of cichlids, and food supply rate (i.e., primary production rate of attached algae) as mentioned by Genner et al. (2004). Nevertheless, the sediment amount accounted for most of the inter-site variation in individual number and species richness of cichlids at the lake bottom (Table 2). These results suggest that sedimentation has a great potential to directly or indirectly impact the cichlid community.

**Interspecific Feeding Territoriality under the Effect of Sedimentation**

The feeding territory sizes of the 2 observed species were larger in the sediment-rich sites than in the sediment-poor ones (Figure 5). Feeding-territory size has been theoretically and empirically shown to change in response to environmental conditions including habitat quality and intrusion pressures (Schoener, 1983; Keeley & McPhail, 1998; Hansen & Closs, 2005). In this study, the observed territory owners belonged to the most aggressive species, which are also the least frequent evacuees of the respective sites (Maruyama et al., 2010). Such superiority in interspecific interaction leads to the speculation that the correlation between the sediment quantity and the territory size is more likely to result from changes in habitat quality, rather than from competition with heterospecific owners of neighboring feeding territories. Habitat quality was considered to be reduced in sediment-rich sites where a larger area would be required for cichlids that prefer sediment-free rock surfaces as feeding places (Rusuwa et al., 2006).

The effect of sediment quantity on territory size was supported by the experimental sediment clearance (Table 3). In addition to territory size, the experiment showed that the attack rate decreased after sediment clearance. These results suggested the mitigation of interspecific competition due to decreased sedimentation. Importantly, the ratio of attacks on
heterospecifics at rock edges decreased after sediment clearance. These changes may imply that aggressive species would allow others to feed more readily in spaces that they dominated before clearance, especially at the edge of rocks.

**Feeding Positions under the Effect of Sedimentation**

During observations of feeding positions, interspecific variation was obvious before the sediment clearance (Figure 6). Such variation can be interpreted in 2 ways: these cichlids are evolutionarily adapted to their respective feeding positions (specialization) and/or their feeding positions are organized by social rank in the community (competition). Apparently, the aggression level of each species seems to be associated with feeding positions. More aggressive species tended to feed at positions with higher food supply rates, such as upper sides and edges of rocks, where the algal production rate is high with strong sunlight (as confirmed by the carbon isotopic signatures of the attached algae; Bootsma et al., 1996).

In general, after sediment clearance, cichlids, except for *P. (M.) zebra*, changed their feeding places from positions with lower primary production rates (water column and undersides of rocks) to those with higher rates (upper sides and edges of rocks). Less aggressive species tended to respond to the sediment clearance more drastically than others, which was statistically detected as interspecific variation in the effect of the sediment clearance (interaction term, Table 4). Nevertheless, the relationships between aggressiveness and feeding position were maintained even after the sediment clearance. Importantly, increases in feeding time by less aggressive species were seen at the edges of rocks, where territorial attacks decreased after sediment clearance (Table 2). These results indirectly supported interspecific competition rather than evolutionary specialization as a mechanism for the apparent segregation in feeding positions. This inference is consistent with previous reports on flexible feeding by some cichlids in the field and aquaria (e.g., Liem, 1980; McKaye & Marsh, 1983).

Significant changes in feeding time at both end positions (i.e., upper sides of rocks and water column; Table 4) are consistent with the decrease in the cichlid abundance and diversity at the lake bottom with increasing sediment observed during comparative surveys (Figure 4). This correspondence indicates that sedimentation is associated with individual number at the lake bottom, and suggests that the enlarged territories of the most aggressive and exclusive species affect the feeding behavior of less aggressive species, reflecting feeding habits that are organized by social rank within the community (Marsh & Ribbink, 1985). In a recent experiment in which feeding bites from algal mats were counted before and after the removal of territory owners, the territorial behaviors of *P. (T.*) “black” caused a 94.5% reduction in feeding by intruders (Maruyama et al., 2010). Consideration of such exclusive feeding territoriality in addition to asymmetric interspecific territoriality leads to the speculation that the effect of sedimentation can cascade over the community via interspecific feeding territoriality (competition). In future, experimental removal of aggressive territory owners is required to give a conclusive result.
Management Considerations

In predicting the effects of environmental alterations, the spatial and temporal heterogeneity under natural conditions need to be considered. Even without the effects of human activities around the lake, the amount of sediment varies within and among rocky areas and fluctuates according to the seasonal changes of precipitation and wind (Pilskaln & Johnson, 1991; Hecky et al., 2003). The experiment showed that territory size and feeding habits of cichlids are considered to change dynamically in response to such short-term changes in the sediment loads (Table 2, 4; Figure 6). However, recent denudation of forests around the lake raises the average input of sediment throughout the year (Hecky et al., 1999). An increase in the average sediment input could affect cichlids in different manners from such spatial and temporal variation under natural conditions because subordinate species would have less space or time in which to recover from stressful circumstances. The number of rocky areas that harbor dense and diverse cichlid communities would decrease with increasing average sediment input from the catchment area of the lake.

The experimental results allow for the prediction that less aggressive cichlids will shift their habitats from the lake bottom to the water column in response to the sediment increase. However, the survey results showed constant numbers of individuals and species in the water column across study sites with different amounts of sediment. This may be because the scale of the time period required for such adaptation may be different from that of sediment increase since the 1960s (Hecky et al., 1999). A species transition into a new niche in the water column may have been prevented by other competitors specialized for the water column such as *Cynotilapia afra* (Ribbink et al., 1983a), even though most cichlid species have been reported to be able to switch among foods opportunistically (Liem, 1980; McKay & Marsh, 1983). It should be further examined whether less aggressive species are forced to shift habitats and compete with water-column specialists and/or have reduced growth or survival rate when rocky substrates are covered by large amounts of sediment.

A contrary speculation is that since sediment contains organic as well as inorganic matter (Hecky et al., 2003), the sediment increase may make both attached and planktonic algae more productive (Schindler, 1977; Guilford et al., 2003), thus providing more food for cichlids feeding on attached algae. Such a mechanism may exist, but could not be examined in this study in which algal production rates were not measured. Comparative surveys, however, showed constant standing crops of attached algae across study sites with different sediment quantities (Table 1). At least in the rocky littoral zone, the sediment seemed to function mainly as an obstruction to feeding on attached algae by cichlids rather than as a nutrient source for the attached algae.

**CONCLUSION**

Deforestation and soil erosion are among the most severe environmental problems faced by the aquatic communities of the African Great Lakes (Coulter et al., 1986; Cohen et al., 1993; Bootsma & Hecky, 1993; Calder et al., 1995; Ogutu-Ohwayo et al., 1997). Previous studies have shown that the local diversity of cichlids in Lake Victoria are threatened by turbidity associated with eutrophication (Seehausen et al., 1997) and plankton composition
may be altered with further nutrient loads (Hecky et al., 2003; Guilford et al., 2003). The present study, as an early attempt to understand whether and how the cichlid diversity and abundance are threatened, suggests that sedimentation has a great potential to directly or indirectly have an impact on cichlid communities (Figure 1). There is a possibility that such impacts may spread over the community through asymmetric interspecific territoriality (Maruyama et al. 2010), forcing subordinate species to shift habitats. An understanding of the interactions between species in the aquatic community and between terrestrial and aquatic ecosystems is necessary for the holistic and sustainable management of aquatic ecosystems, especially if organisms coexist and interact with each other.

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