Impact of Sediment Pollution on the Littoral Zone of Lake Tanganyika: A Case Study of Two Cichlid Fish, *Petrochromis polyodon* and *Tropheus brichardi.*

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Introduction

Lake Tanganyika is the oldest and deepest of the East African Rift Valley lakes and has one of the most unique ecosystems in the world. Remarkable biodiversity occurs across taxa, including sponges, arthropods, mollusks, and fish; it is estimated that Lake Tanganyika contains 1300 species, >600 of which are endemic (Coulter, 1981). Most of the Tanganyikan shoreline is relatively pristine, but recent development and agriculture have led to sediment pollution in littoral zones near human populations. Anthropogenic sedimentation poses a significant threat to benthic ecosystems, reducing species diversity and eliminating habitats for rock-dwelling organisms (Cohen et al., 1993; Alin et al., 1999). The piscine response to sedimentation is examined in this case study of two algal-grazing cichlids, *Petrochromis polyodon* and *Tropheus brichardi*.

This study was made at Kigoma, Tanzania, on the northeastern shore of Lake Tanganyika, from June to August 2003. With a population of 80,000, the Kigoma region is one of the most populated areas on Lake Tanganyika. As settlement has spread, most of forest and savannah woodlands have been cleared for agriculture and further development. In Tanzania, the burning of fuel wood represents 90% of total energy consumption. This high fuel demand carries an equally high deforestation rate, resulting in increased soil erosion and subsequent discharge into the lake (Cohen et al., 1996). The steep slope of the Tanganyikan rift basin exacerbates this problem; Cohen et al. (1996) estimate that the north end of Lake Tanganyika suffers erosion rates of about 27 tons/ha/yr; such rates may rise to 100 tons/ha/yr in highly sloped areas.

Sedimentation has many effects on the littoral environment. Sediments cover benthic algae, harming algal communities (Grobbelaar, 1985), and decreasing the foraging efficiency of herbivorous fish (Cohen et al., 1993). Sedimentation also affects fish populations by reducing the nutritional value of detritus (Graham, 1990) and decreasing habitat complexity, filling crevices and other sheltered areas among rocks (Cohen, 1994). This latter effect is of particular concern in Lake Tanganyika, where 98 of the known 200 fish species live on rocky shores (Takamura, 1984).

Most of these rock-dwelling fish are cichlids, advanced teleosts well known for their explosive adaptive radiations in the East African Great Lakes (Fryer and Iles, 1972). In studies of the cichlids of Lake Malawi, Fryer (1959) concluded that competition is the major interspecific relationship among rock-dwelling cichlids. It is assumed, then, that decreases in available habitats and food quality will intensify this relationship and may result in compelling behavioral adaptations. For this reason, this study will focus on herbivores, as settling sediment is likely to strongly affect algal communities (Cohen et al., 1993). Two herbivorous cichlid genera common in the Kigoma region are *Petrochromis* and *Tropheus*. These genera present an interesting case of opposing feeding strategies: *Petrochromis* sp. use mobile, brush-like, premaxillary pads of tricuspid teeth to consume epilithic and epiphytic unicellular algae, whereas *Tropheus* sp. have premaxillary combs of fused bicuspid teeth to graze on filamentous algae, shown in Figure 0 (Brichard, 1989; Takamura, 1984; Kohda, 1997). Although the fish may ingest other algae, the relative amount in stomach contents is small (Takamura, 1997). The species *P. polyodon* and *T. brichardi* have been selected for use in this study, both for reasons of high relative abundance and ease of identification.

The behavior and interspecific interactions of *Petrochromis* sp. and *Tropheus* sp. have been studied extensively (e.g. the work of M. Hori, H. Kawanabe, M. Kohda, M. Nishida, K. Takamura, K. Yamaoka, and others). Due to their difference in food preference, agonistic interactions between *Tropheus* sp. and *Petrochromis* sp. are rare, even though the genera often share adjacent feeding territories and forage at the same time (Kohda, 1997; Takamura, 1997). As *P. polyodon* combs unicellular algae, it removes sand and silt from the rock surface; such conditions may help *T. moorii* to scrape the filamentous algae (Takamura, 1984). At sedimented sites, *T. moorii* has been observed grazing at the same points where *P. polyodon* has grazed, enhancing the effectiveness of its feeding; *T. moorii* does not perform this behavior at unsedimented sites (Kohda, pers. obs., 1997).

Since increased deposit presents a more significant obstacle to the immobile combs of *Tropheus* sp. than to the brush-like pads of *P. polyodon*, sedimentation is thus predicted to affect *T. brichardi* more strongly than *P. polyodon* due to differences in oral tooth structure.

Here I investigate population density, grazing frequency, stomach contents, and territorial behavior of *Tropheus brichardi* and *Petrochromis polyodon* in sedimented and non-sedimented (reference) habitats. It is expected that sediment pollution will not have a significant effect on *Petrochromis*, as feeding will not relatively unhindered. Preliminary results indicate that populations of *Petrochromis* sp. may actually be larger in sedimented areas (Mulongaibalu, 2000), perhaps because of higher environmental pressure on other species that occupy the same habitat. Sedimentation is predicted to have an observable effect on *T. brichardi*; differences are likely to be observed in feeding strategy and behavior. A pilot study suggests that *Tropheus* sp. are more aggressive in sediment-polluted habitats (Sapp, 2002).

Methods

Site Description

This study concerns six rocky littoral-zone sites near Kigoma, depicted on Figure 1. Three of these sites are reference areas that are relatively unaffected by sedimentation (qualitative assessment): Jakobsen's Beach, "Cobralangabo", and Bangwe Point, and three are sediment-polluted areas: Hilltop Beach, Katabe, and Kalalangabo. These six sites are separated both by distance and stretches of deep water and sand. Neither *Tropheus* sp. nor *Petrochromis* sp. are likely to cross such barriers (Brichard, 1989).

Jakobsen's Beach (JKB) is located seven kilometers south of Kigoma. The site is renowned for clear water in the littoral zone (M. Olsgard, pers. comm., 2003). The substrate at JKB consists of quartzite boulders and cobbles. The second reference area is the north-facing side of Bangwe Point (BWP). The site is far from human settlement; its substrate is composed of cemented boulders along the shoreline, separated by short stretches of cobbles and sand. The third reference site, Cobralangabo (CBR), is six kilometers north of Kigoma. Its watershed is steep and relatively forested; the major substrate at CBR is cemented quartzite boulders.

Hilltop Beach, Katabe, and Kalalangabo are sediment-polluted due to forest clearing for development and agriculture. Hilltop Beach (HTP) and Katabe (KTB) are impacted by sediment from sandstone bluffs where construction of the Kigoma Hilltop Hotel resulted in heavy erosion that persists at the present, years after the conclusion of development. HTP is located to the north of the bluffs, while KTB is on the southern side, in Katabe Bay. The benthos at both sites consists of quartzite boulders, cobbles, and stromatolites that begin around 3m depth. The third sedimented site (KAL) is seven kilometers to the north of Kigoma, near the village of Kalalangabo. Although Kalalangabo is a fishing village, villagers rely on cassava as their major source of starch; cassava fields on the lakeside slopes result in significant sedimentation in the surrounding littoral zone (Sapp, 2002). The substrate at KAL is quartzite boulders and cobbles.

Site Characterization

Sediment Sampling

Attached and non-attached material was collected with the capping method (Rivers, 2001). A small, surface-oriented rock at 2 m depth was selected. A flat upward area was covered with a cap (area = 8.05 cm^2) and the rock brought to shore. The area around the cap was scrubbed and rinsed, then the cap was removed and non-attached material washed into a collection tray. This slurry was poured into a sample vial and distilled water added to constitute a final sample volume of 70 mL. The attached material under the cap was removed with a wire brush and the brush rinsed with distilled water into a collection tray. The rock surface was also rinsed into the same tray. This mixture was poured into a sample vial and distilled water added to a final volume of 70 mL.

Epilithic and Filamentous Algae Biomass

Algae biomass is strongly correlated with the chlorophyll a concentration in a sample (Bullock, 1996). Chlorophyll a concentrations were obtained with the method detailed by Rivers (2001). The sample, collected as described previously, was resuspended; 30 mL was removed and passed through a 1 micron glass-fiber filter. The filter was then incubated in 10 mL 90% ethanol at 4 ºC for 24 hrs. Absorbance of the extract was read at 665 and 750 nm. The extract was acidified with 20 µL 1.5M HCl and absorbance readings at 665 and 750 nm were then repeated. Chlorophyll a concentration was calculated using the equation (Nucsh, 1980):

$$\text{Chlorophyll a concentration } (\mu g/cm^2) = 29.6(A_b - A_a)\,(EVL/?a)$$

where A_b = abs_{665} - abs_{750} before acidification, A_a = abs_{665} - abs_{750} after acidification, E = volume of ethanol used for extraction, V = volume of algal slurry, L = cuvette path length, ? = volume of subsample, and a = surface area sampled.

Sediment Load and Total Organic Matter

Sediment load and total organic matter are frequently obtained with combustion methods; this study used the protocol described by Rivers (2001). A 40 mL subsample of the algal slurry was passed through a 1 micron, pre-burned and pre-weighed, glass-fiber filter. The filter was desiccated for 24 hrs at 60 ^{o}C. It was weighed and then burned at 550 ^{o}C for three hours. Final mass was recorded. Inorganic sediment load was calculated from the formula: $mass_{burned}$ – $mass_{filter}$. Total organic matter was taken as equivalent to the ash-free dry mass: ($mass_{dry}$ – $mass_{burned}$).

Organic Content of Algae (Filamentous and Unicellular) and Sediments

Non-attached and attached algae and sediment were analyzed for organic content with ash-free dry mass (P. McIntyre, pers. comm.). Non-attached and attached samples of volume 50 mL were collected as described previously (see "Sediment Sampling"). The samples were centrifuged, the supernatant discarded, and the pellet homogenized. One milliliter of the pellet was placed in a 100% Ludox colloidal silica solution (? = 1.4 g/mL) and centrifuged for five minutes; after spinning, the algae were collected from above the matrix while the sediments were collected from a pellet beneath the matrix. These are passed through 1 micron, pre-burned, pre-weighed glass-fiber filters and subsequently analyzed for ash-free dry mass. A portion of the algae (1 mL) was placed in an 80% Ludox silica solution and centrifuged for five minutes; this separated the algae into filamentous material (above the silica) and unicellular algae/diatoms (below the silica). These were filtered and examined for ash-free dry mass.

Fish Populations, Stomach Contents, and Behavior

Population Density

Population counts of *Petrochromis polyodon* and *Tropheus brichardi* at 2 m depth were obtained with 25 m x 2 m belt transects (Coyer et al., 1999). *P. polyodon* and *T. brichardi* were individually censused over the belt transect by snorkelers over a two-week period from 14 July to 28 July (n = 32/site). Population density was calculated as ? = N/A, where N is the number of a given species obtained in a single count and A is the transect area.

Grazing Frequency and Territorial Interactions

Fish behavior was noted by snorkelers, following the method described by Sapp (2002). A focal fish of either *P. polyodon* or *T. brichardi* was selected on the basis of proximity, ignorant of any behavior already observed. The depth, size, and sex of the focal fish were recorded. The fish was observed for ten minutes: in the first five-minute segment, grazing frequency was recorded (grazing is defined as biting at rock surfaces) and in the second five-minute segment, the fish's territorial interactions were noted. These included aggressions and victimizations towards/by conspecifics, the other subject species: *P. polyodon/T. brichardi*, and other species. Fish were observed at 1 m to 5 m depth and at 900 h to 1330 h; observations began on 5 July and concluded on 28 July.

Stomach Contents

Eight *P. polyodon* and eight *T. brichardi* were collected at each site from 21 July to 6 August. Specimens were pithed immediately upon collection and the gut injected with ethanol. Fish were dissected; length, mass, and gut length (stomach to rectum) were noted. Stomach contents were analyzed by desiccation/combustion for total dry mass, ash-free dry mass, and inorganic sediments.

Fish were also sampled for stable isotope studies. A small strip of dorsalis muscle was removed, without skin or bone, and desiccated at 60 ºC for 72 hours. A similar strip of muscle was removed and placed in ethanol for further study. Lastly, four fish of each species from each site were preserved in 10% formalin.

Results

Site Characterization

This study involved six sites in the Kigoma region (Figure 1): three reference – Jakobsen's Beach (JKB), Cobralangabo (CBR), and Bangwe Point (BWP) – and three impacted by sediment – Hilltop Beach (HTP), Katabe (KTB), and Kalalangabo (KAL). To quantify sediment pollution, non-attached and attached material was sampled from rocks at each site and analyzed for algae biomass, organic sediments, and inorganic sediments (Table 1). Statistical analysis with a nested ANOVA showed only levels of inorganic sediments to be significantly different between reference and sedimented sites, in both non-attached (among categories: $F_{2,1}$=16.13, $p < 0.05$; among sites within categories: $F_{3,4}$=0.042 , $p = 0.50$) and attached material (among categories: $F_{2,1}$=22.32, $p < 0.02$; among sites within categories: $F_{3,4}$=0.025 , $p = 0.50$).

Total organic content of algae (filamentous and unicellular) and sediments were examined at one reference site, BWP, and one sedimented site, HTP. Organic content was used to compute amount of filamentous/unicellular algae in non-attached and attached material (Figure 2) and relative amounts of filamentous algae, unicellular algae, inorganic sediments, and other organic matter in non-attached and attached material (Figures 3a-d). For the reference site, the amount of unicellular algae in non-attached and attached material is uniform, while attached material has a greater amount of filamentous algae. The sedimented site has relatively lower levels of filamentous and unicellular algae in non-attached and attached material. Figures 3a-d show the relative mass of algae (filamentous and unicellular) and sediments (inorganic and other organic matter) per unit area of benthic substrate at a reference and a sedimented site. Hilltop (HTP), the sedimented site, has a higher relative amount of inorganic sediment and a lower relative amount of algae in both non-attached and attached materials.

Population Density

Populations of *Tropheus brichardi* and *Petrochromis polyodon* were surveyed with 25x2m line transects at each site, with a total of 32 counts per species per site. These results are presented in Figure 4. No significant differences in population density were observed in either species (nested ANOVA. *T. brichardi*, among categories: $F_{2,1}$=0.937, $p = 0.50$; among sites within categories: $F_{3,4}$=0.864, $p = 0.50$. *P. polyodon*, among categories: $F_{2,1}$=0.542, $p = 0.50$; among sites within categories: $F_{3,4}$=2.69, $p < 0.10$).

Fish Behavior

Sixteen *T. brichardi* and *P. polyodon* were observed at each site. Grazing frequency and agonistic behavior were recorded and are presented in Table 2. In sedimented areas, *T. brichardi* defend their territory more actively towards conspecifics but not towards other species. This evidence is seen in both aggressions and victimizations with reference to the focal fish. *T. brichardi* rarely interacts with *P. polyodon* and is neither more agonistic nor more tolerant of *P. polyodon* in sedimented areas. Although *P. polyodon* is on average more aggressive, this difference is not significant. However, *P. polyodon* are found to graze less frequently in sedimented areas.

Digestive Tract Length and Stomach Contents

Eight fish of each species were collected from each site. The digestive tract was measured from the duodenum to the rectum; this measurement was standardized with division by total length (Fryer and Iles, 1972). The mean standardized lengths for each species are reported in Table 3; there are no observable differences.

Stomach contents were extracted and analyzed for inorganic and organic content by loss-on-combustion. A nested ANOVA (Table 4) reveals that both *T. brichardi* and *P. polyodon* at sedimented sites have significantly higher inorganic stomach content, while *P. polyodon* at sedimented sites also have lower organic content. Total stomach contents, organic content, and inorganic content were plotted against each site's value for percent total organic content for all benthic material (Figures 5a, 5b). Linear regression analysis shows that benthic organic content is positively correlated with stomach organic content for *P. polyodon* and inversely correlated with total stomach content for *T. brichardi* and inorganic stomach content for both species (*T. brichardi*, organic content: $y=.078x+1.66$, $r^2=0.50$, $p < 0.15$; inorganic content: $y=-.260x+17.6$, $r^2=0.95$, $p = 0.001$; total contents: $y=-.182x+19.3$, $r^2=0.89$, $p < 0.01$. *P. polyodon*, organic content: $y=.249x+5.92$, $r^2=0.91$, $p < 0.005$; inorganic content: $y=-.454x+35.2$, $r^2=0.72$, $p < 0.05$; total contents: $y=-.205x+41.1$, $r^2=0.46$, $p < 0.15$).

The relative amounts of algae and sediments in non-attached and attached material (Figures 3a-d) were used to predict the percent inorganic content expected to be found in *T. brichardi* (attached) and *P.*

polyodon (non-attached) stomachs; these are compared with the observed values in Table 5. There is no significance to the relationship (?^{2} test: ?^{2}=2198.7, df=95, p = 0.5).

Discussion

This study concerns the herbivorous cichlids *Tropheus brichardi* and *Petrochromis polyodon* at unsedimented (reference) and sedimented sites in the Kigoma, Tanzania, region of Lake Tanganyika. *Tropheus* sp. and *Petrochromis* sp. are well-studied taxa, but their response to anthropogenic sedimentation, which threatens much of their littoral-zone habitat in the northern areas of L. Tanganyika, is poorly understood. Here I focus on several possible macro- and micro-scale responses: population density, territoriality, feeding behavior, and digestive physiology.

T. brichardi possess fused combs as oral teeth, which are used to graze filamentous algae, or aufwuchs. In contrast, *P. polyodon* has mobile pads of brush-like teeth that aid in consuming diatoms and other unicellular algae. These specializations result in different consequences for *T. brichardi* and *P. polyodon* in sedimented areas: while *P. polyodon* is able to selectively browse non-attached material, possibly avoiding sand and silt, *T. brichardi* is confined to scraping attached material from the entire rock surface (Takamura, 1984). Sediment pollution is thus likely to have more serious consequences for *T. brichardi*.

This study involves six sites near Kigoma, three reference: Jakobsen's Beach (JKB), Cobralangabo (CBR), and Bangwe Point (BWP), and three sediment-polluted: Hilltop Beach (HTP), Kalalangabo (KAL), and Katabe (KTB). To characterize sedimentation, non-attached and attached benthic materials from 2 m depth at each site were examined for algae biomass, organic matter, and inorganic matter (Table 1). A nested ANOVA of these results reveals that HTP, KAL, and KTB are sedimented to a significant extent, that both non-attached and attached material at these sites has a higher proportion of inorganic matter than those at reference sites. Thus, "reference" and "sedimented" are valid qualifiers.

First, the effect of sedimentation on food quantity and quality was determined. Non-attached and attached material were separated into filamentous algae, diatomaceous algae, and sediments with silica density columns; the organic and inorganic proportions of these constituents were determined with loss-on-combustion. From this data, I calculated the relative amounts of filamentous algae, unicellular algae, sediments, and other organic matter (feces, detritus, etc.) in each unit of non-attached and attached material, thereby obtaining some understanding of what *T. brichardi* and *P. polyodon* are ingesting when they graze on attached and non-attached material, respectively, at reference and sedimented sites (Figures 3a-d).

Not only do sedimented sites have less filamentous and less unicellular algae, but they also have more inorganic sediments per unit area of rock, meaning that food quantity and quality are decreased for both *T. brichardi* and *P. polyodon*. It is expected that this might have noticeable effects on organismic and population levels.

Population densities of *T. brichardi* and *P. polyodon* were estimated with 25x2 m line transects, 32 counts per species per site. Nested ANOVAs of these counts show no significant difference in the abundance of either species. This contradicts the results of a preliminary study (M-, 2000), but that study focused on *Tropheus* and *Petrochromis* at the genus level and used a minimal number of counts. Population density is likely to be controlled by several other factors not accounted for in this report, including but not limited to, predator population, competing congenerics and other species, substrate composition, and availability of nesting territories. This is a consideration for further study.

Fish behavior was quantified by snorkelers, who noted grazing frequency and number and type of agonistic interactions for 16 fish per species per site. Agonistic interactions were separated into aggressions towards conspecifics, aggressions towards other species, victimizations by conspecifics, and victimizations by other species. Any interaction between *T. brichardi* and *P. polyodon* was specially noted.

T. brichardi is found to defend their territory more actively at sedimented sites. As food quantity and quality decrease, territory becomes increasingly valuable, especially for algal-gardening species that rely on specific, relatively unchanging sources and locations of food. Surprisingly, *P. polyodon* is not significantly more agonistic in sedimented areas, perhaps because their mobile oral dentition allows them to better cope with excessive sedimentation.

Another surprising result with *Petrochromis polyodon* is that those at sedimented sites graze significantly less frequently. This is counterintuitive; if food quantity and quality are decreased, an organism would need to eat more often to maintain the same rate of growth and fitness level. However, it is important to note than not only do sedimented sites contain more inorganic material, but that they have higher levels of total benthic material, up to twice as much as similar reference sites (Table 1). With every scrub of a rock surface, *P. polyodon* at sedimented sites ingest up to 170% more mass. This is likely to have a satiating effect. This could be tested with a tag-recapture growth study; *P. polyodon* at sedimented sites would be expected to grow more slowly and perhaps even fail to reach maximum adult size. Limited field time restricted the possibilities of expanding this study in such a way.

Lastly, eight fish per species per site were collected for dissection. Digestive tract length was recorded and stomach contents combusted for analysis of organic/inorganic content. Both species were found to have consumed more inorganic material at sedimented sites. Benthic material composition, computed from organic content of algae (filamentous and unicellular) and sediments and shown in Figures 3a-d, was used to predict percent inorganic matter in total stomach contents (Table 5). Although a $?^2$ test revealed no significant relationship, *P. polyodon* stomach content has a lower percentage of inorganic sediment than the non-attached material content would predict, implying that *P. polyodon* are at least partially successful at avoiding the consumption of sediments. There is no significant difference in digestive tract length between populations at reference and sedimented sites for either species.

Total stomach content, organic content, and inorganic content were plotted against percent organic matter of all benthic material (Figure 5). For *T. brichardi*, total stomach content and inorganic content are inversely correlated with percent organics. The latter relationship is expected from sedimented sites, while the former provides evidence for a satiating-effect hypothesis. For *P. polyodon*, inorganic content is also inversely correlated with percent organics; organic content is positively correlated with percent organics. Relative organic content of the non-attached material (on which *P. polyodon* feeds) is higher at reference sites, so a positive relationship between stomach organic and percent benthic organic material is anticipated.

Anthropogenic sedimentation poses many varied and complex threats to the benthic environment (Cohen et al., 1993). For herbivorous fish in the littoral zone, this includes reduction in food quantity and quality and habitat loss. Recent soil erosion and ensuing sediment pollution in the Kigoma region of Lake Tanganyika has affected local populations of *Tropheus brichardi* and *Petrochromis polyodon*. *T. brichardi* in sedimented areas are more territorial, spending comparatively more energy defending their territory than those at reference sites. *P. polyodon* in sedimented areas graze less frequently, perhaps because of a satiating effect. Although population densities do not differ to a significant extent, the impact of sediment pollution is seen in these wide-scale behavioral adaptations. As human populations in the East African Rift Valley continue to grow, anthropogenic sedimentation becomes an increasingly significant danger to the health of the African Great Lakes, threatening delicate, unique ecosystems. Further study must be undertaken to fully grasp the effect of sediment pollution and thus understand what may lay ahead for the cichlids of Lake Tanganyika and the other organisms of ancient lakes worldwide.

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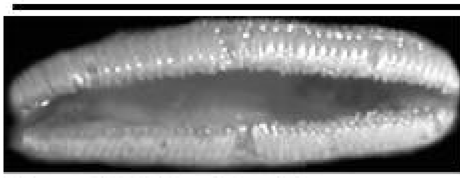
Figures and Tables

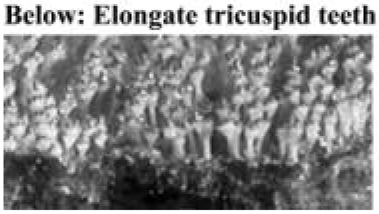
Figure 0. Oral dentition of *Tropheus brichardi* and *Petrochromis polyodon*



Above: *T. brichardi* oral jaws

Right: *P. polyodon* oral jaws

Below: Elongate tricuspid teeth of *P. polyodon*



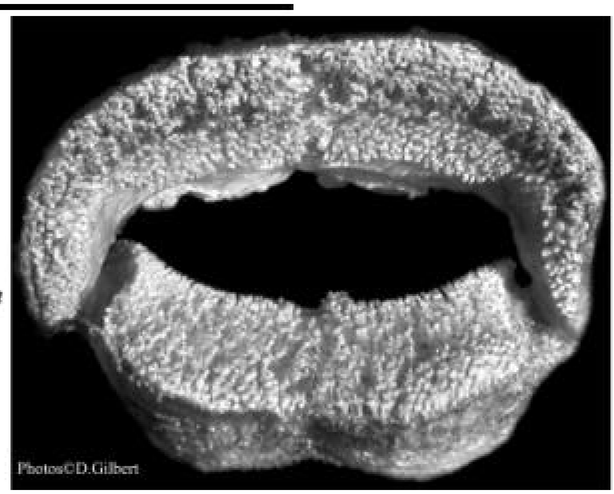


Figure 1. Map of study area: Kigoma and surrounding sedimented site region, Lake Tanganyika.

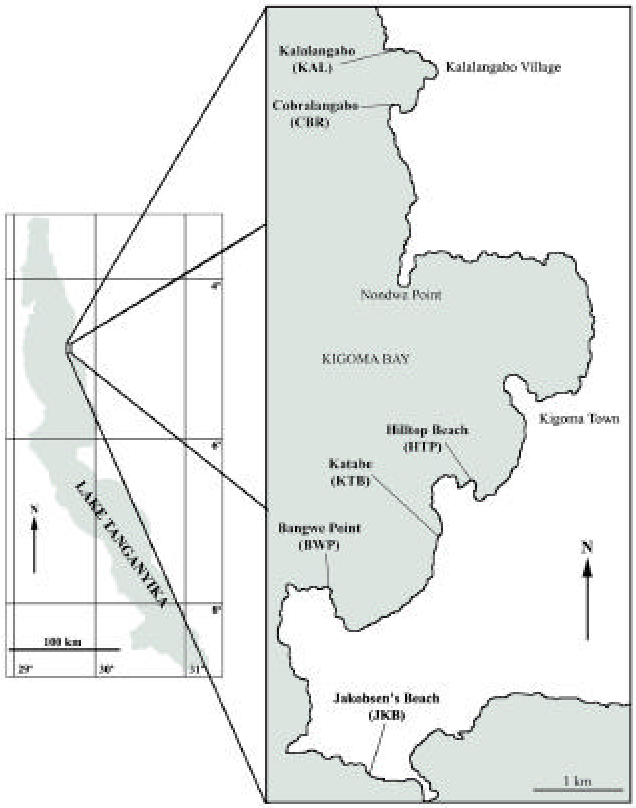


Figure 2. Algal composition of non-attached and attached material at a reference (BWP) and a sedimented (HTP) site.

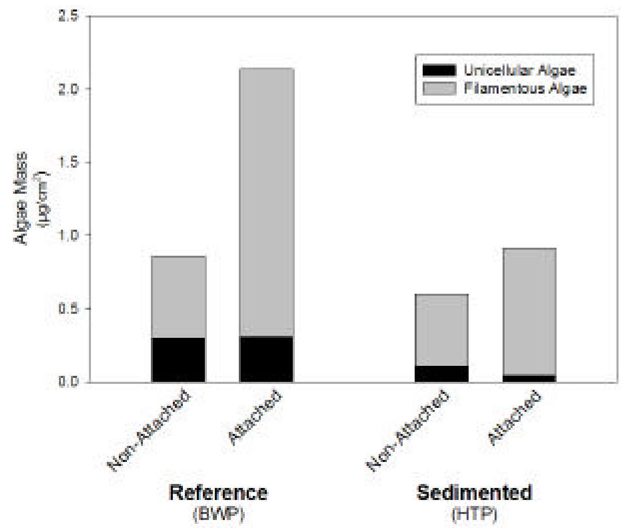


Table 1. Algae biomass, organic matter, and inorganic sediments in non-attached and attached material at 2m depth at reference and sedimented sites in L. Tanganyika. (n = 8/site)

Variable	*Reference* [a]			*Sedimented*		
	Jakobsen's JKB S 04° 54.83' E 29° 36.23'	*Cobralangabo* CBR S 04° 50.61' E 29° 36.46'	*Bangwe Point* BWP S 04° 53.94' E 29° 35.93'	*Hilltop* HTP S 04° 53.33' E 29° 36.90'	*Kalalangabo* KAL S 04° 50.03' E 29° 36.37'	*Katabe* KTB S 04° 53.48' E 29° 36.78'
Non-Attached Material [b]						
Algae Biomass	.241 ± .08	.155 ± .09	.215 ± .07	.120 ± .03	.129 ± .05	.223 ± .09
Organic Matter	.729 ± .13	.288 ± .04	.740 ± .20	.494 ± .09	.713 ± .15	.746 ± .13
Inorganics	.906 ± .27	.808 ± .19	1.14 ± .60	2.51 ± .40	2.55 ± .38	2.04 ± .64
Attached Material [b]						
Algae Biomass	4.02 ± .82	1.28 ± .25	1.69 ± .38	.687 ± .16	2.36 ± .35	1.57 ± .32
Organic Matter	1.57 ± .22	1.18 ± .15	1.96 ± .38	1.18 ± .37	1.28 ± .43	1.05 ± .13
Inorganics	.959 ± .26	1.68 ± .34	1.41 ± .40	3.03 ± .77	3.26 ± .52	3.31 ± 1.1

[a] *Means ± standard errors are reported for each data set.*
[b] *Non-attached and attached material given as µg/cm².*

Figures 3a-d. Relative amounts of filamentous algae, diatomaceous algae, inorganic sediments, and other organic matter (feces, detritus, etc.) in:

3a: Non-attached material from a reference site (BWP).
3b: Attached material from a reference site (BWP).
3c: Non-attached material from a sedimented site (HTP).
3d: Attached material from a sedimented site (HTP).

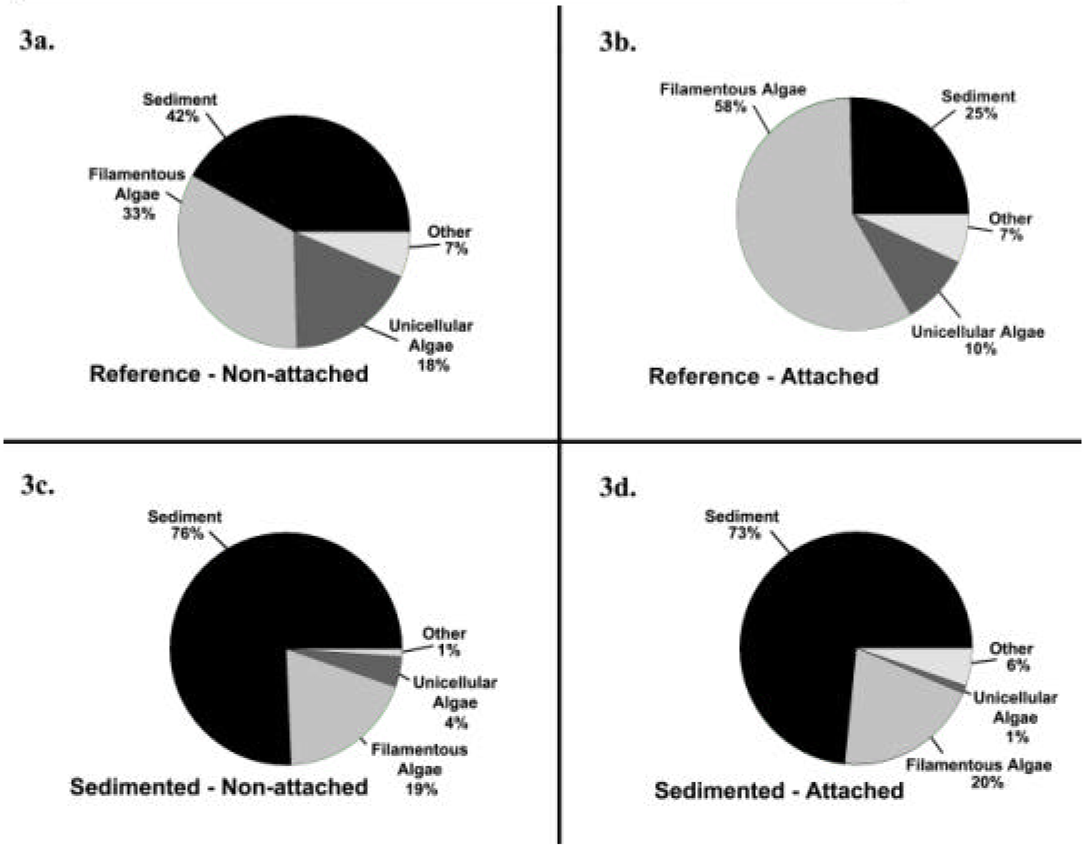


Figure 4. Population density of the herbivorous cichlids *T. brichardi* and *P. polyodon* at reference and sedimented sites. No significant differences are observed. (n = 32/site)

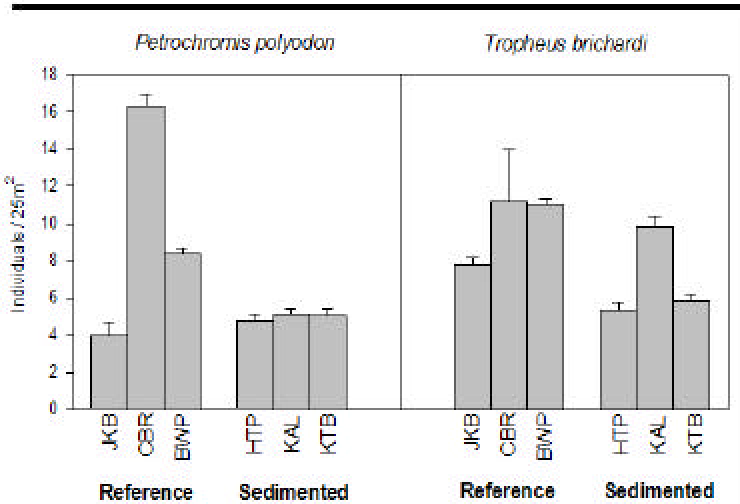


Table 2. Average values and results of nested ANOVA of *T. brichardi* and *P. polyodon* behavioral observations (n = 16/species/site).

Species *Variable*	*Mean*		*Significance (F, p)* [a, b]	
	Reference	*Sedimented*	*Among Categories (Reference v. Sedimented)*	*Among Sites Within Categories*
Tropheus brichardi				
Grazing Frequency[c]	1522	1159	8.74, < 0.1	0.03, ≥ 0.5
Total Aggressions[d]	17	52	**23.3, < 0.02**	0.05, ≥ 0.5
Chasing Conspecifics	8	32	**11.9, < 0.05**	0.10 ≥ 0.5
Chasing *T. brichardi*	1	1	0.08, ≥ 0.5	0.04, ≥ 0.5
Chasing Other Species	8	19	4.04, < 0.5	0.06, ≥ 0.5
Total Victimizations	14	34	**172, < 0.001**	0.01, ≥ 0.5
Chased by Conspecifics	7	24	**26.5, < 0.02**	0.03, ≥ 0.5
Chased by *T. brichardi*	2	1	0.18, ≥ 0.5	0.09, ≥ 0.5
Chased by Other Species	5	9	0.71, ≥ 0.5	0.15, ≥ 0.5
Petrochromis polyodon				
Grazing Frequency[c]	688	253	**38.7, < 0.01**	0.07, ≥ 0.5
Total Aggressions[d]	22	36	3.36, < 0.5	0.09, ≥ 0.5
Chasing Conspecifics	12	18	1.85, < 0.5	0.05, ≥ 0.5
Chasing *T. brichardi*	2	1	0, ≥ 0.5	0.04, ≥ 0.5
Chasing Other Species	8	17	1.79, ≥ 0.5	0.15, ≥ 0.5
Total Victimizations	10	24	3.61, < 0.5	0.14, ≥ 0.5
Chased by Conspecifics	7	15	4.49, < 0.2	0.05, ≥ 0.5
Chased by *T. brichardi*	1	1	0, ≥ 0.5	0.13, ≥ 0.5
Chased by Other Species	2	8	1.50, ≥ 0.5	0.19, ≥ 0.5

[a] *Among categories (n, df)=(2, 1); among sites within categories (n, df)=(3, 4)*
[b] *Significant p values (≤ 0.05) are indicated in bold.*
[c] *Grazing frequency given as bites/hr.*
[d] *All agonistic interactions given as chases/hr.*

Table 3. Average values of standardized gut length for *T. brichardi* and *P. polyodon* (n = 8/species/site).

Category *Site*	*T. brichardi*	*P. polyodon*
Reference		
JKB	4.9	8.8
CBR	4.2	7.9
BWP	4.4	9.1
Sedimented		
HTP	4.5	7.9
KAL	4.2	8.4
KTB	4.1	7.6

Table 4. Nested ANOVA results of *T. brichardi* and *P. polyodon* stomach contents (n = 8/species/site).

Stomach Contents	*Significance (F, p)*[a, b]	
	Among Categories (Reference v. Sedimented)	*Among Sites Within Categories*
Tropheus brichardi		
Total Stomach Contents	4.73, < 0.2	0.03, ≥ 0.5
Organic Content	2.66, < 0.5	0.08, ≥ 0.5
Inorganic Content	**27,4, < 0.02**	0.02 ≥ 0.5
Petrochromis polyodon	0.08, ≥ 0.5	0.04, ≥ 0.5
Total Stomach Contents	3.12, < 0.5	0.05, ≥ 0.5
Organic Content	**55.3, < 0.002**	0.01, ≥ 0.5
Inorganic Content	**14.3, < 0.05**	0.07, ≥ 0.5

[a] *Among categories (n, df)=(2, 1); among sites w/in cat. (n, df)=(3, 4)*
[b] *Significant p values (< 0.05) are indicated in bold.*

Figure 5. Stomach content (organic, inorganic, and total) of *T. brichardi* and *P. polyodon* vs. % total organics in all benthic material.

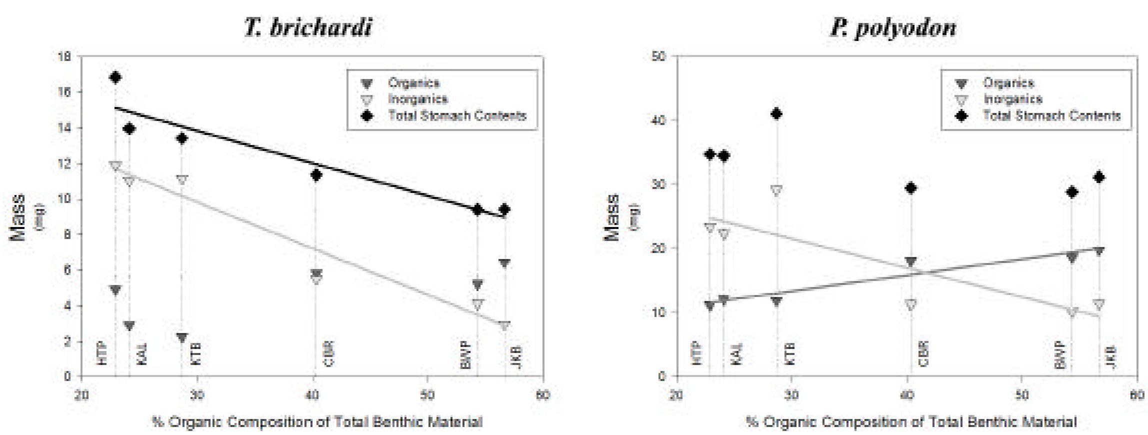


Table 5. Predicted and observed average percent inorganic stomach content (n = 8/species/site).

Category	*T. brichardi*		*P. polyodon*	
	Predicted	*Observed*	*Predicted*	*Observed*
Reference	25%	40%	42%	36%
Sedimented	73%	75%	76%	66%