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Disparity pattern of unionoid bivalves from Lake Malawi (East-Africa): a case study for adaptive strategies to heterogeneous environment

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Abstract

The shell shape of many unionoid bivalves is known to be highly variable in order to cope with the heterogeneity and instability of freshwater environments. Along environmental gradients shell shape of many species is changing fairly consistently. In this case study the disparity pattern of three species of unionoid bivalves from Lake Malawi (*Nyassunio nyassaensis*, *Chambardia nyassaensis*, *Mutela alata*) is studied along one environmental transect in order to better understand potential adaptive strategies of the species to heterogeneous environment. Using Fourier shape analysis, the shell morphology of about 2,500 unionoids is analysed. The morphometric data are processed by multivariate statistical analyses. The disparity of *Nyassunio nyassaensis* is high and shell shape is changing consistently along the environmental gradient: in offshore habitats, the shells of this species are more swollen and triangular than in nearshore habitats. Disparity and shell shape differences are lower in *Chambardia nyassaensis* and *Mutela alata*. It is suggested, that the three species developed different adaptations to cope with environmental fluctuations: (1) a high level of phenotypic plasticity allows bivalves to adapt the shell shape to variable environmental conditions, as it is mainly the case for *Nyassunio nyassaensis*; (2) other key features such as fused mantle margins help *Chambardia nyassaensis* and *Mutela alata* to survive environmental fluctuations. More transects need to be sampled and more data in particular on growth pattern and migration behaviour of the bivalves need to be collected to test the hypotheses.

Key Words

Introduction

Unionoid bivalves are generally known as highly variable in shell shape. A lot of work has been done in the past to elaborate on the reasons for this variability. It is consensus that the environment has a major influence on shell shape (Jordan, 1881; Ortman 1920; Haas 1922; Altnöder 1926; Baker 1928; Agrell 1949; Green 1972; Eagar 1978; Balla & Walker 1991; Savazzi & Peyi 1992; Watters 1994; Walker et al. 2001; Scholz 2003). Several key observations have been made describing the shape-environment relation. Based on such observations, Ortman (1920) has formulated the "Law of Stream Distribution" (Ortman 1920), also known as the "Big River Effect" (Watters 1994). According to this

law, unionoid bivalves in downstream sections of big rivers, like the present Mississippi River, have less streamlined shells with stronger ornamentation compared to their conspecifics in the headwater section of the same river. Ortman (1920) was not able to give a sufficient explanation for this observation. The reasons for this are (1) that not all species studied by him follow the law and (2) that he was not able to detect the environmental factors responsible for the observed changes in shell shape (Ortman 1920). Watters (1994) identified the downstream features of unionoids as devices to facilitate anchoring under strong but constant river currents, whereas headwater features help the bivalves to rebury if dislodged under fluctuating current conditions (e.g. floods). This serves as an adaptive ex-

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planation for the "Law of Stream Distribution": the high shape variability (disparity) of unionoid bivalves is an expression of a high level of phenotypic plasticity, which is an adaptation for organisms living under heterogeneous, ephemeral, and unstable environmental conditions (DeWitt et al. 1998; Komers 1997; Edelaar 2000; DeWitt & Langerhans 2004). However, it is still debatable why not all species follow the law.

Quantitative studies of unionoid bivalves from Lake Malawi, East Africa, indicate that the "Law of Stream Distribution" is obviously not only valid for big rivers, but also for big lakes. In such lakes, bivalve habitats near the shore are characterised by headwater morphotypes while downstream morphotypes are found in offshore habitats (Scholz 2003). However, it is not studied in detail yet which Lake Malawi unionoids follow the "Law of Stream Distribution" and is the focus of the present case study. The shell shape and its variability (disparity) of the Lake Malawi unionoids is analysed quantitatively along one environmental transect. If a taxon follows the law, the disparity of this taxon is expected to be higher with headwater characters developed in nearshore habitats and downstream features in offshore habitats. If a taxon does not follow the law, it may not develop different shell shapes under changing environmental conditions. The disparity of this taxon is then expected to be low. If high disparity is considered to be an expression of a high level of phenotypic plasticity, which is an adaptation for organisms in freshwater settings, other mechanisms may be developed in these taxa to survive the heterogenous conditions in freshwater environments. This is discussed in this case study. The limitations of the case study are also discussed to show the importance for future studies in order to fully understand the evolution and distribution of unionoid bivalves in big lakes.

Ecological framework

Lake Malawi, formerly known as Lake Nyasa, is the southernmost lake in the East African Rift System (Fig. 1). The oldest known lake sediments are within the Chiwondo Beds in the Karonga region and are 4.5 to 4.0 million years old (Schrenk et al. 1992, 1993, 1995). From that time, Lake Malawi extended to the south during the progressive rifting process (Johnson & Ng'ang'a 1990). Today, the lake is approximately 560 km long, 75 km wide, 700 m deep, and, with the volume of about 8,400 km, the fifth largest lake in the world (Hutchinson 1957; Eccles 1974).

Fluctuations of the lake level in the past 25,000 years are very important to the ecology of Lake Malawi. Several low-stands are documented and described by Finney & Johnson (1991) and Owen et al. (1990). The most recent major lake level low-stand was between 1500 and 1860. During this time, the lake level was 150 m lower than today, as indicated by sand deposits in 150 m water depth. Within less than 250 years, the

whole present shallow water part of the lake was colonised by organisms, including unionoid bivalves.

In recent years, lake level fluctuations have a magnitude of less than 5 m. Between 1990 and 2003, the lake level was dropping and rising about 2 m (S.M. Grant, pers. comm., 2000; pers. observation, 2000). During one year, the lake level may fluctuate several decimetres due to evaporation in the dry season and rainfall in the wet season (pers. observation, 2000). These fluctuations are affecting the shallow water habitats near the shore, but not the deep water offshore habitats. As these fluctuations happen within the life time of unionoid bivalves, they are expected to affect the adaptive strategies of the bivalves.
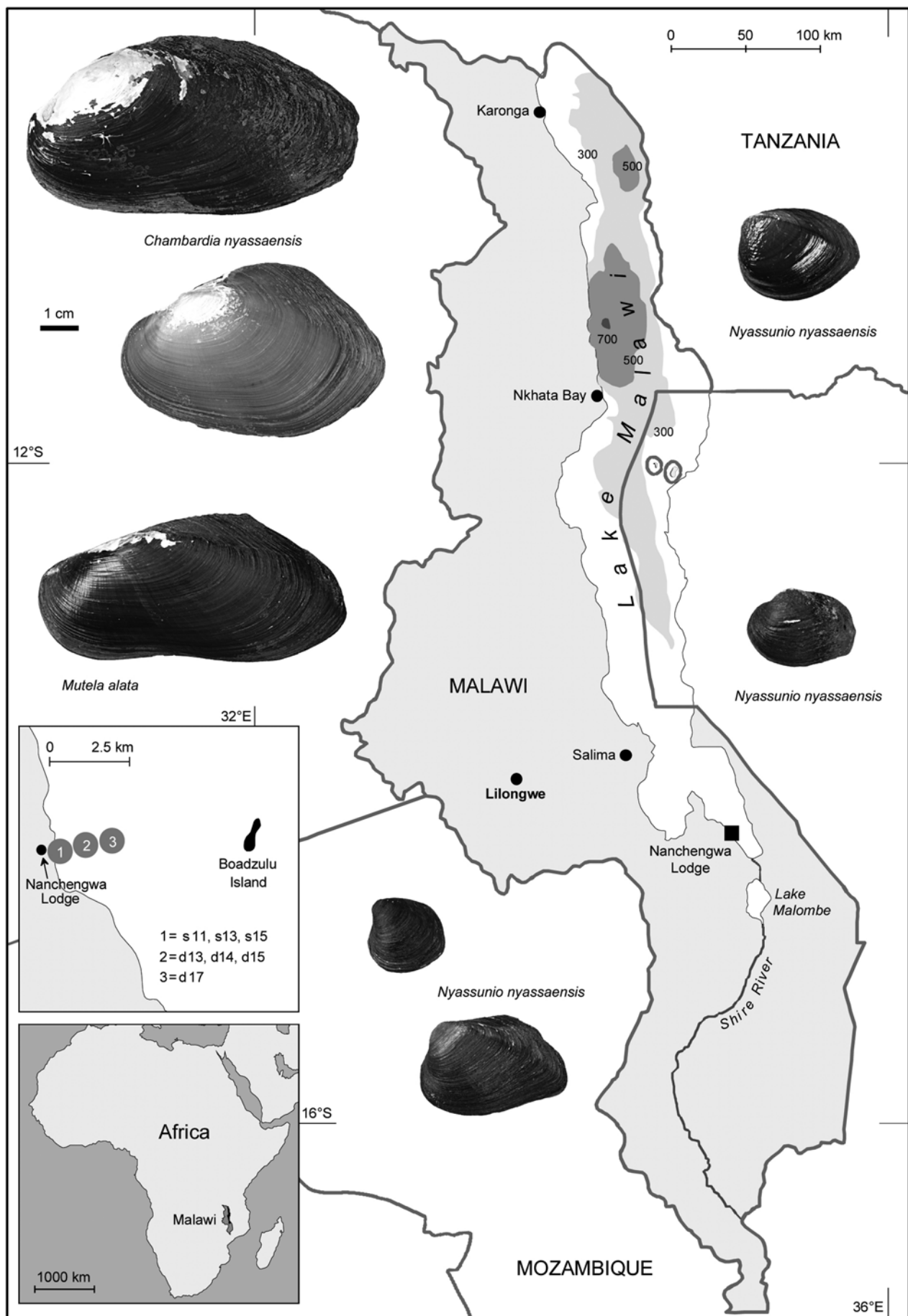
The mentioned lake-level changes in the past are responsible for the uniformity of the lake sediments at all localities sampled for this study: from shallow water down to 18 m in depth, the sediment is sandy, ranging from fine to coarse sand (0.14–0.6 mm mean grain size; see Scholz 2003 for detailed data on sedimentology). Mineralogy and organic content of the samples are also very similar. Therefore, the properties of the sediment, which are considered to be important for the distribution of unionoid bivalves (Tevesz & Carter 1980; Tevesz et al. 1985), have no influence on the studied unionoid bivalves in Lake Malawi.

Very important for the ecology of Lake Malawi are the southeasterly trade winds called Mwera. The winds blow along the axis of the lake, often attaining a speed of 40 km/h, that generate surface waves of 3–4 m height (Eccles 1974). Therefore, Mwera is responsible for turbulent water conditions in nearshore habitats along the western shoreline and controls the physical stability of the habitats. Nearshore habitats in shallow water in open bays are physically very unstable and devoid of unionoid bivalves. Habitats that are sheltered from the southeasterly winds are more stable and allow unionoid bivalves to settle and live. Offshore habitats in deep water below the wave base are considered most stable (Scholz 2003).

Predators have a low importance of bivalve diversity and disparity in Lake Malawi. One cichlid species is known to be the only potential predator of unionoid bivalves in Lake Malawi: *Chilotilapia rhoadesii* (A. Konings, pers. comm., 2001). This fish species has the ability to bite into the shell and suck out the soft parts without crushing the shell completely. However, only shells from the Senga Bay area East of Salima not chosen for this study (see Fig. 1 and material section below) showed high amount of shell injuries that may be attributed to attacks of this fish species (Scholz 2003). Other types of organisms that are known elsewhere as

▶

Figure 1. Map of Malawi illustrating the location of the sampling area and localities along the shore of Lake Malawi considered for this study. Details about the sampling localities are given in Table 1. The three species of unionoid bivalves occurring in the study area are depicted as well.

Chambardia nyassaensis

1 cm

Mutela alata

12°S

32°E

0   2.5 km

Nanchengwa
Lodge

Boadzulu
Island

1= s 11, s13, s15
2=d13, d14, d15
3=d 17

Africa

Malawi

1000 km

Karonga

TANZANIA

300

500

700

500

Nyassunio nyassaensis

Nkhata Bay

300

MALAWI

Salima

Lilongwe

Nanchengwa
Lodge

Lake
Malombe

Nyassunio nyassaensis

16°S

Nyassunio nyassaensis

Shire River

MOZAMBIQUE

36°E

unionoid predators do not feed on unionoids in Lake Malawi. The crab *Potamonautes lirrangensis* is a scavenger (M. Genner, pers. comm., 2001), the two otter species *Aonyx capensis* and *Lutra maculicollis* are also not molluscivorous (P. Yoxon, pers. comm., 2001). Therefore, populations of unionoid bivalves are not controlled significantly by predators. This is in contrast to other freshwater ecosystems such as the East African Lake Tanganyika and many European and North American waters (Vermeij & Covich 1978; Zahner-Meike & Hanson 2001).

Unionoid bivalves of Lake Malawi

Three species of unionoid bivalves from Lake Malawi are studied herein: *Nyassunio nyassaensis* (Lea, 1864), *Chambardia nyassaensis* (Lea, 1864), and *Mutela alata* (Lea, 1864) (Fig. 1). The first named species belongs to the superfamily Unionoidea, the two latter species belong to the superfamily Etherioidea. All three species are endemic to Lake Malawi.

The bivalves of the Etherioidea differ in some important characters from the Unionoidea. Etherioid bivalves are significantly larger than most African unionoid bivalves. The mean shell length of *Chambardia nyassaensis* and *Mutela alata* is 75.4 mm ($n = 724$) and 72.7 mm ($n = 354$), respectively. The mean shell length of *Nyassunio nyassaensis* is 24.5 mm ($n = 1,386$) (Scholz 2003). The bivalves of the two superfamilies differ also in some anatomical characters and the mode of reproduction. Etherioid bivalves show a variable degree of mantle fusion and simple siphons, which are not present in unionid bivalves (Yonge 1957). Mantle fusion in marine bivalves is advantageous for the burrowing process and facilitates the infaunal life habit of these bivalves (Stanley 1968). The etherioid bivalves differ from *Nyassunio nyassaensis* and all other unionid bivalves by having a different larval type. Instead of glochidia, these bivalves have a lasidium, which develops into a second larval stage in *Mutela*. This second larvae is called haustorium, which allows the young mussel to grow to a larger size (Wächtler et al. 2001).

Material and methods

Material

Between 15 May 2000 and 16 June 2000, altogether seven sites along one transect were sampled along the western shore of Lake Malawi (Fig. 1, Table 1, see also below). All of the localities yielded unionoid bivalves of all species in high abundance and are, therefore, most suitable for quantitative analyses. The samples were taken by snorkeling and SCUBA-diving depending on water depth. The bivalves were collected alive to be sure they are sampled from their life habitat. In addition to bivalves, sediment and water samples were taken and analysed. Water samples were analysed on site with various measuring instruments. A sieving analysis of the sediments was done in the laboratory. Water temperature and depth information were recorded from a diving computer. Other important ecological information, such

Table 1. The seven sampling localities between Nanchengwa Lodge and Boadzulu Island at the SE arm of Lake Malawi (see also Fig. 1). The "s" in the sample column means site investigated by snorkeling, the "d" means site investigated by SCUBA diving. Latitude and longitude values refer to the places in the locality column. The distance values are the approximate distances of the sampling locality from the lake shore. The depth is the average water depth at the sampling locality as recorded from the diving computer. The number of bivalves collected alive at each locality are given in the last three colums: Nn – *Nyassunio nyassaensis*, Cn – *Chambardia nyassaensis*, Ma – *Mutela alata*.

sample	latitude	longitude	distance	depth	Nn	Cn	Ma
s11	14°15′ S	35°08′ E	40 m	3.0 m	50	31	16
s13	14°15′ S	35°08′ E	50 m	2.0 m	23	18	11
s15	14°15′ S	35°08′ E	50 m	2.5 m	28	34	6
d13	14°15′ S	35°08′ E	1,000 m	7.5 m	372	91	50
d14	14°15′ S	35°08′ E	1,000 m	6.7 m	127	24	22
d15	14°15′ S	35°08′ E	1,000 m	7.6 m	147	36	21
d17	14°15′ S	35°08′ E	1,700 m	18.2 m	90	68	34

as macrophyte coverage and fish abundance were also noted. All samples, including shells and associated sediments, were deposited in the Bayerische Staatssammlung Munich. For details on the data and methodology, see Scholz (2003).

Sampling site

Watters (1994) concluded that current or water energy is the major factor responsible for shape changes of unionoid bivalves from headwater to downstream sections of big rivers. Therefore, an important requirement for the sampling transect was a variation in water energy. Wave energy is the most important contributor to the water energy at the lake bottom. The wave energy can only be estimated as both wind energy and wind direction are variable. The wave energy in bays and lagoon protected from the Mwera are supposed to be lower compared to open beaches exposed to the SE. In offshore habitats, water depth determines water energy. In deep water below the wave base, water energy is very low compared to shallow water above or at the wave base.

Another requirement for sampling was the presence of all three species in a reasonable abundance to allow quantitative analyses and a comparison of shell morphology of all species in the same location. Both requirements are difficult to fulfill as habitats exposed to very high water energy are not favourable for unionoid bivalves. Among various examined transects, only one complies with the requirements and was chosen for this case study.

This transect with a consistent gradient of water energy was found in the area between the Nanchengwa Lodge in the year 2000 (the owner of the lodge announced a move of the lodge southwards after 2000) and Boadzulu Island. The small bay of the lodge is reasonably sheltered from wind and waves to allow unionoid bivalves of all species to live in shallow water (s11–15). However, water energy is still higher compared to more offshore sites. Going offshore into deeper water gradually reduces the water energy at the lake bottom (d13–15). In >18 m water depth 1.7 km off the shore, water energy and seasonal fluctuations are minimal and are not affecting the lake bottom bivalve community (d17).

Morphometric analysis

Two different kinds of morphological data were collected for each shell: shell measurements (Fig. 2) and Fourier coefficients of a Four-
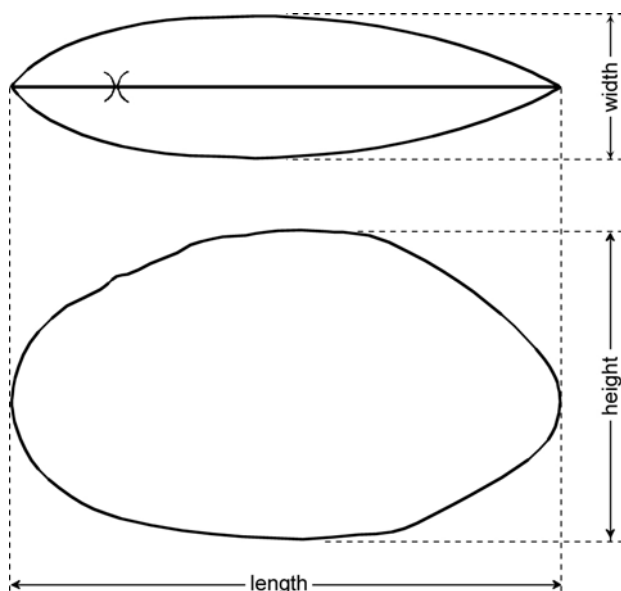
Figure 2. Measurements used for the morphometric analysis in this study.

ier shape analysis. A vernier caliper was used to measure the shells to the nearest 0.5 mm. For the analyses in the present study, the length of the shell was measured as the maximum length of the shell from anterior to posterior (Fig. 2). Shell size was calculated as the arithmetic mean of shell length and shell height (length in mm plus height in mm divided by 2).

The Fourier shape analysis of two-dimensional shell outlines used herein was developed by Crampton & Haines (1996). This analysis uses the entire outline of the shell. Such an approach is superior to classical methods using discrete measurements and multivariate methods based on landmarks for several reasons. Unionoid bivalves are lacking a sufficient number of usable shell characters and landmarks for alternative approaches. In addition, most of the variation in shell shape is included in the shell outline, and it is not possible to quantify this variation without using the information of the entire outline of the shell (Scholz 2003; Scholz & Scholz 2007). Also, different growth stages can be used, making this method useful for incomplete shells and different growth stages of one individual. Finally, the Fourier coefficients contain no shell size information. This facilitates the comparison of morphological differences within and among populations without applying ratios of morphological characters (e.g., length/height). Nevertheless, shell size can be considered by correlating it with the Fourier coefficients (see below). The successful application of this method to variable topics of bivalve biology and palaeontology is illustrated by the studies of Crampton (1996), Crampton & Maxwell (2000), and Scholz (2003).

For the analyses, digital photographs of the shells were taken. All images of the shells were adapted for the digitisation of the shell outline, using Adobe® Photoshop® 6.0. The outline of each shell was digitised using the program tpsDig (Rohlf 1998). These digitised outlines were the basis for the Fourier shape analysis, using the program Hangle (Crampton & Haines 1996). Before calculating the Fourier coefficients, a smoothing normalisation of 10 is applied to the basic data to reduce the high-frequency pixel noise from the automatic digitisation process. If the data are not normalised, distortions and corruptions of the results will occur during the Fourier analysis and subsequent statistic analyses (see Haines & Crampton 2000). To normalise the outlines for starting position, Hmatch (Crampton & Haines 1996) was used. The normalisation is strongly recommended by Haines & Crampton (2000) for organisms that are difficult to align consistently during the digitisation process. This is true for the studied unionoid bivalves with their highly variable shell shape. Normalisation for

starting position is also necessary when homologous landmarks cannot be identified with adequate precision. The umbo of the unionoid bivalves is the only available landmark, but it is broadly rounded and therefore not identifiable precisely (i.e., relocated with adequate precision). During the Fourier shape analysis, altogether 24 Fourier coefficients for the first 12 harmonics were calculated. The number of the harmonics is based on preliminary studies with different numbers of harmonics. The first harmonic (two Fourier coefficients) is removed, thereafter, by the program because it contains no shape information.

Multivariate data analysis

Most multivariate data analyses were processed using PAST version 2.13 (Hammer et al. 2001). Only for the analyses of the disparity, R2.12.1 was used (R Foundation for Statistical Computing, 16 Dec 2010).

Two different approaches were taken to analyse the two components of the "Law of Stream Distribution". The first component of the law predicts that the obesity (i.e. degree of shell inflation) is decreasing with increasing current stability, i.e. specimens in offshore habitats are more swollen than their conspecifics in nearshore habitats. The obesity was calculated as the width-size ratio of the shells. Ortman (1920) suggested to use the width-length ratio for the obesity, but the height of the shells is an important component of the shell size that should be considered. Boxplots were created to illustrate the differences in obesity across the samples and Kruskal-Wallis tests were carried out to test for the significance of the differences.

The second component of the "Law of Stream Distribution" predicts a change in shell shape, i.e. elongate shells occur in nearshore habitats where wave energy is high and water energy conditions are fluctuating and trigonal shells occur in offshore habitats where water energy is low and constant. Principal component analyses (PCA) of the Fourier coefficients were carried out for the various groups to investigate the morphospace occupation pattern in more detail. Shell outlines were created to illustrate the shell shape changes in the morphospace.

The disparity of one species is calculated as the bootstrap sum of variances (SOV; $n = 1,000$) of the first four principal components (PC) of a principal component analysis (PCA) of the Fourier coefficients accounting for 82.3 % of the total variance of the sample (Ciampaglio et al. 2001; Foote 1993). In addition, the 95 % confidence intervals of the variance measures are given. The variance measure was chosen out of other methods for the calculation of morphological disparity, as it is not sensitive to sample size (Ciampaglio et al. 2001).
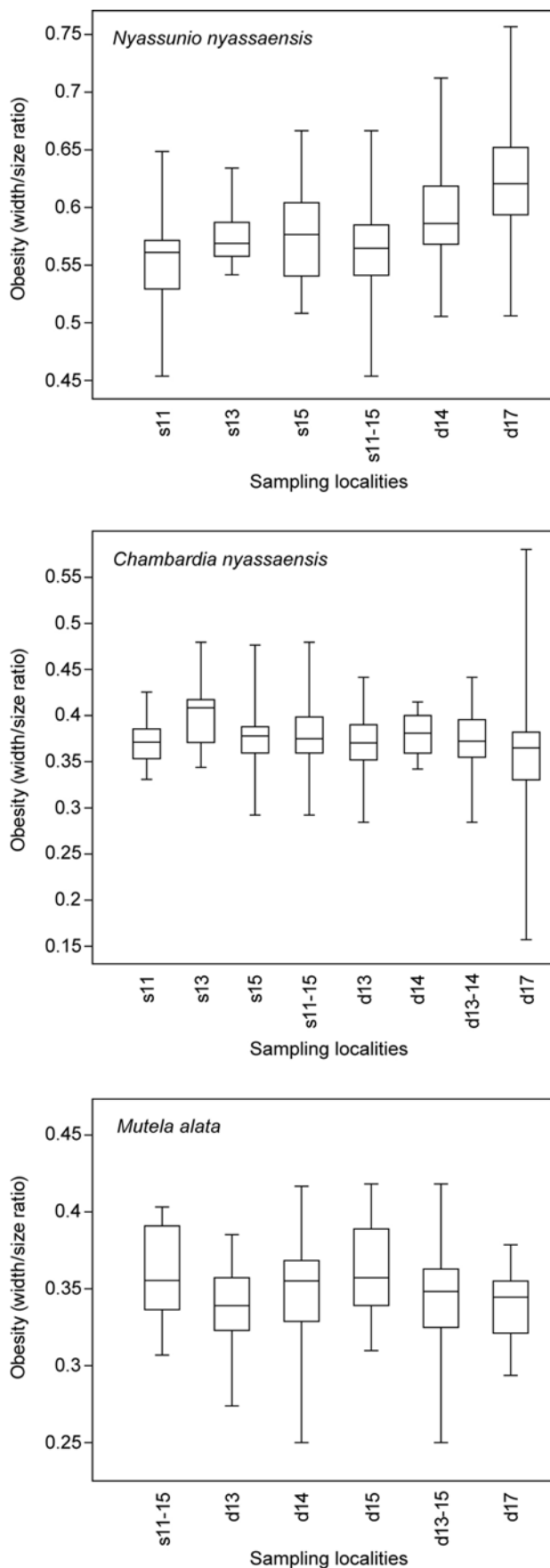
Results

Nyassunio nyassaensis follows the "Law of Stream Distribution" in all respects (including obesity). The shells are significantly ($p < 0.001$) more swollen (high value for obesity) in offshore habitats than in habitats near

Table 2. Results of the Kruskal-Wallis test: $p = 0.0017$, $H = 19.31$. The table gives the results of the pairwise Mann-Whitney comparisons, Bonferroni uncorrected in the upper right triangle, Bonferroni corrected in the lower left triangle (* = not significant).

	s11	s13	s15	d14	d17
s11	0	0.01	0.04	< 0.0001	< 0.0001
s13	0.1009*	0	0.4677*	0.0678*	< 0.0001
s15	0.4014*	1*	0	0.0192	< 0.0001
d14	< 0.0001	0.6783*	0.1923*	0	< 0.0001
d17	< 0.0001	0.0002	< 0.0001	< 0.0001	0

Figure 3. Boxplots of the obesity across the sampling localities for all three species. In addition to the individual samples, small samples are grouped and depicted as well.

Table 3. Results of the Kruskal-Wallis test: $p = 0.0017$, $H = 19.31$. The table gives the results of the pairwise Mann-Whitney comparisons, Bonferroni uncorrected in the upper right triangle, Bonferroni corrected in the lower left triangle (* = not significant).

	s11	s13	s15	d13	d14	d17
s11	0	0.0171	0.466*	0.9084*	0.2073*	0.0994*
s13	0.2561*	0	0.0434	0.006	0.1558*	0.0005
s15	1*	0.651*	0	0.6376*	0.4781*	0.0234
d13	1*	0.0901*	1*	0	0.172*	0.0223
d14	1*	1*	1*	1*	0	0.0104
d17	1*	0.0071	0.3512*	0.3342*	0.1563*	0

Table 4. Results of the Kruskal-Wallis test: $p = 0.007$, $H = 14.09$. The table gives the results of the pairwise Mann-Whitney comparisons, Bonferroni uncorrected in the upper right triangle, Bonferroni corrected in the lower left triangle (* = not significant).

|	s11−15	d13	d14	d15	d17
s11−15	0	0.0067	0.5591*	0.6776*	0.0165
d13	0.0668*	0	0.0519*	0.0177	0.9481*
d14	1*	0.5191*	0	0.5844*	0.0554*
d15	1*	0.177*	1*	0	0.0196
d17	0.1647*	1*	0.554*	0.1956*	0

the shore (Table 2, Fig. 3). The obesity differences of the two etheriod species are in most cases not significant ($p > 0.05$; Tables 3 and 4; see also Fig. 3).

The shell outline of *Nyassunio nyassaensis* also follows the "Law of Stream Distribution". In offshore habitats (d17) more shells are short and high, whereas elongate shells dominate in nearshore habitats (Fig. 4). These changes in shell shape are reflected on the two first principal components. Comparing the morphospace within a sampling area and between sampling areas, it is also obvious that within one area (d13 vs d14 vs d15) the difference of the morphospace occupation is smaller (Fig. 4A) compared to the morphospace occupation difference between areas (s11−15 vs d13−15 vs d17) (Fig. 4B).

In the morphospace of *Chambardia nyassaensis*, the "Law of Stream Distribution" is evident on PC2 explaining only 18.8% of the total variance. Here elongate shells are present in the nearshore habitats and

▶

Figure 4. PCA of the Fourier coefficients with the 95 % confidence ellipses for the individual groups. Some shell outlines are depicted to illustrate the shell morphology in the different areas of the morphospace. A, B – Morphospace occupation of *Nyassunio nyassaensis* for all specimens under study; C, D – Morphospace occupation of *Chambardia nyassaensis* for all specimens under study; E, F – Morphospace occupation of *Mutela alata* for all specimens under study. A, C, E – 95 % ellipses for the three samples d13, d14 and d15; B, D, F – 95 % ellipses for s11−15, d13−15, d17.
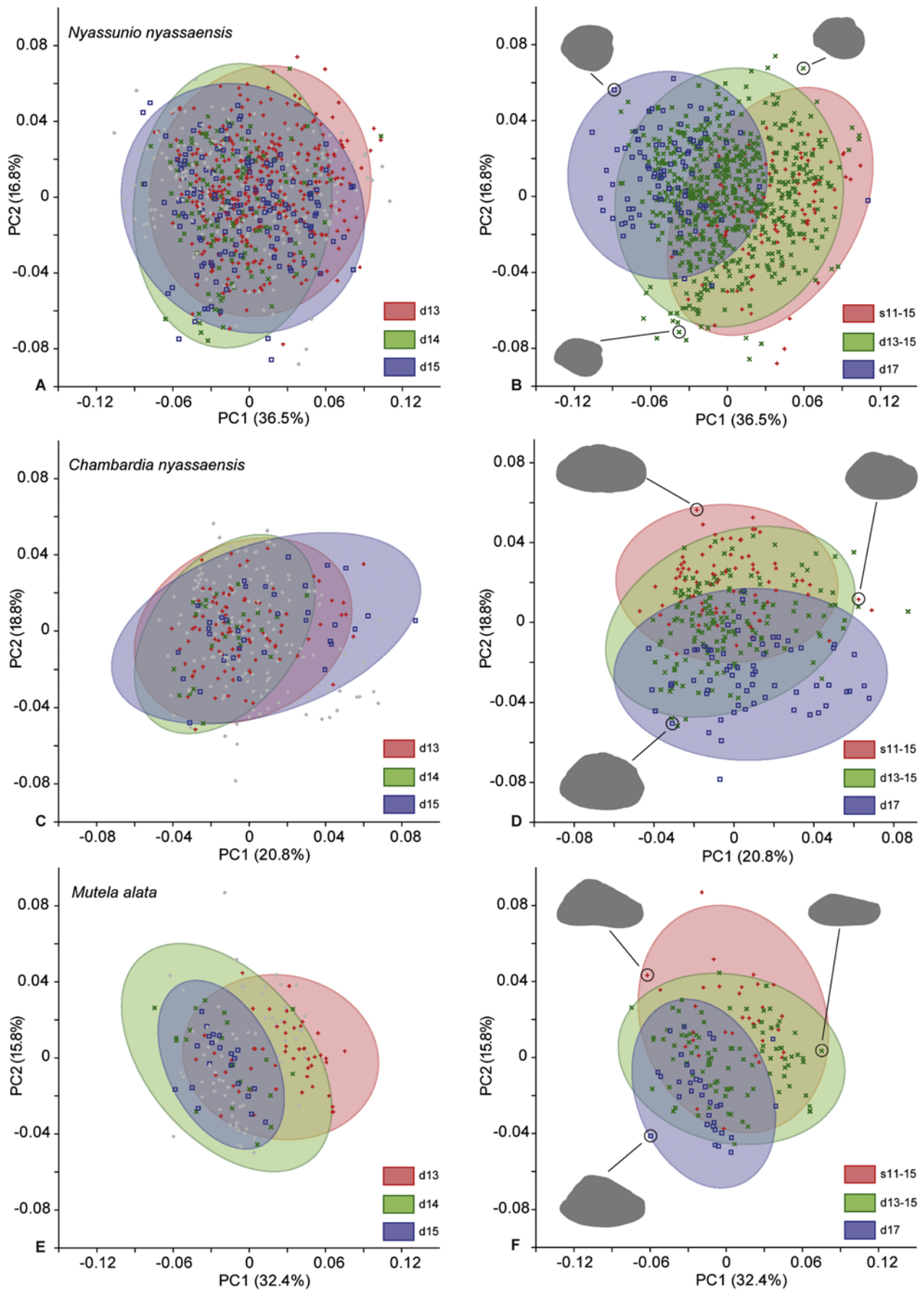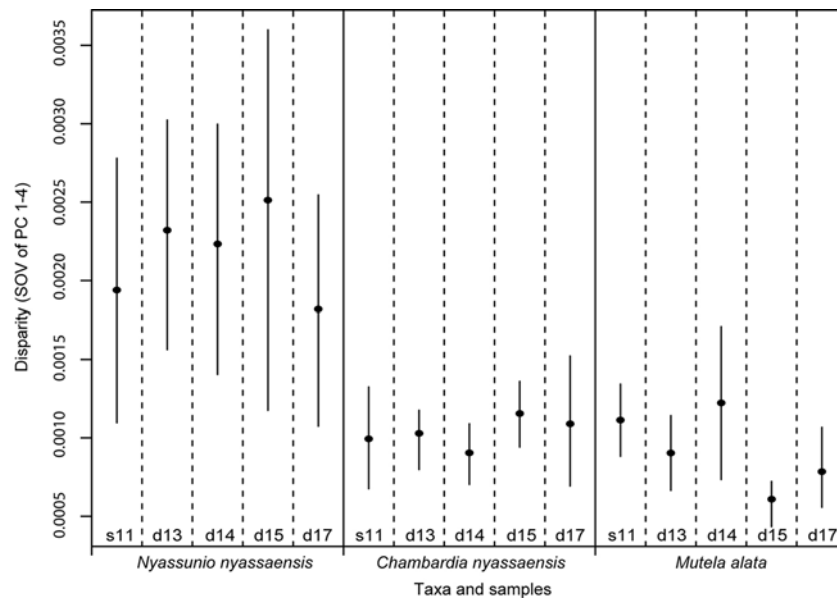
Figure 5. Morphologic disparity expressed as the bootstrap sum of variance of the first four PC of the PCA of the Fourier coefficients. The 95 % confidence limits are given as well.

short shells offshore. The morphologic changes along PC1 are most probably an ontogenetic pattern: large shells have low values for PC1 (dorsally arched, ventrally straight), whereas small shells have high values for PC1 (dorsally straight, ventrally arched) (see Scholz 2003).

The morphospace of *Mutela alata* indicates changes of shell shape from nearshore to offshore habitats along PC2 as well. These changes can also be interpreted being in accordance with the "Law of Stream Distribution". Shells are ventrally straight in nearshore habitats and are ventrally arched in offshore habitats (Fig. 4E, F). Thus nearshore features (facilitate burrowing) are replaced by offshore features (antiscouring devices). *Nyassunio nyassaensis* is more variable (high disparity expressed as bootstrap sum of variance) across all samples compared with the two etherioid species (Fig. 5).

Discussion

Shell morphology of *Nyassunio nyassaensis*

As presented above, *Nyassunio nyassaensis* is the only species following the "Law of Stream Distribution" in all respects. The high disparity can be considered as a consequence of this. Habitat differences are responsible for shape changes in *Nyassunio nyassaensis*. In nearshore habitats, more shells are streamlined (Fig. 4). This form is considered to be an adaptation to high energy habitats facilitating the locomotion in the sediment (Watters 1994; Eagar 1978). In Lake Malawi, high energy habitats are characterised by high wave energy responsible for sediment movements. Wave ripples are developed in these habitats, in particular after periods with strong winds. During the movement of the sedi-

ment, also the small bivalves of *Nyassunio nyassaensis*, which live buried in the sediment with a shallow infaunal life habit, can be exposed and dislodged easily (pers. observation, 2000). Therefore, the ability to react on these environmental conditions by improved locomotion abilities to rebury after exposure is strongly adaptive.

In offshore habitats, more shells are triangular in shell outline (Fig. 4). This is considered to improve the anchoring facilities of the shells, for example (Watters 1994). In transitional habitats between nearshore and offshore habitats, an intermediate and transitional shape is dominant. However, also nearshore and offshore shapes might be present and able to survive. This would serve as an explanation for the higher disparity of the shells in these habitats compared to shells from offshore and nearshore habitats (Fig. 5).

Reciprocal transplant experiments are suggested as a next step in order to better understand the adaptive value of the shell shape of all three species. The usefulness of such experiments is confirmed by several studies. Hinch et al. (1986), for example, tested the degree of phenotypic plasticity in shell shape of North American unionoids by reciprocal transplant experiments. This study has shown that shell shape of unionoids can indeed be adaptively modified under changing environmental conditions.

Reciprocal transplant experiments with regular recapture of shells would also help to analyse and understand the shape changes during the lifetime of the unionoids. This aspect was not studied herein, but is considered an important aspect for future studies. Although size was measured for this study, the size-age relationship is not known. The full understanding of the growth processes of these bivalves are a requirement for a full understanding of the disparity pattern.

These experiments would also allow a better understanding of the migration pattern of these bivalves. It would be important to know how many bivalves can be recaptured in the same area and if it is possible to relocate specimens elsewhere. This would give an insight into the potential for mixing of populations over time.

It has to be mentioned that another unionid species is described from Lake Malawi, i.e. *Coelatura hypsiprymna* (Martens, 1897; Scholz & Glaubrecht 2004). Based on previous morphological studies, it is assumed that this species is not present at the localities selected for this study and thus was not available for study (Scholz 2003). However, molecular studies are required to analyse the unionid diversity in Lake Malawi to also help with the interpretation of disparity pattern of shells.

Shell morphology of *Chambardia nyassaensis*

Shell shape of *Chambardia nyassaensis* is variable but less variable than *Nyassunio nyassaensis*. The observed shape changes seem to have an ontogenetic and an ecophenotypical component. The ontogenetic component is discussed in detail by Scholz (2003), which is summarised below.

Small shells are characterised by a straight dorsal margin and an arched ventral margin. The straight dorsal margin saves the permanent function of the ligament and leads to a straightening of the posterior margin. When buried completely, this is an effective antiscouring device (Watters 1994). It reduces the risk of being exposed from wave energy and also reduces the risk of being dislodged by waves. It can be assumed that juvenile and young bivalves of *Chambardia nyassaensis* live well protected and deeply buried in the sediment, what seems to be typical for unionoid bivalves (Matteson 1955; Yeager et al. 1994).

Large shells of *Chambardia nyassaensis* are characterised by an arched dorsal margin. Associated with this dorsal arching is a straight ventral margin. This is considered to improve the ability of the bivalve to extrude the foot out of the shell and with it the anchoring facilities of the bivalves (Eagar 1978). This is adaptive as adult individuals usually live semi-infaunal with a significant part of the shell exposed to the open water. This life habit increases the susceptibility to scouring by wave action (Stanley 1977). The improved anchoring abilities provided by the arched morphotype and the high shell size counteracts the increased scouring and helps the bivalves to withstand high wave energy even in nearshore habitats.

The ecophenotypic component is summarised in PC2 in Figure 4. *Chambardia nyassaensis* is quite abundant in nearshore habitats (Scholz 2003) and thus benefits from the elongate headwater shape to rebury quickly or move back into deeper water if the habitat is subject to desiccation. If the bivalve is exposed to dry conditions, a tight seal of the valves is advantageous. The partially fused mantle helps *Chambardia nyassaensis* to survive dry conditions. Actually, *Chambardia nyassaensis* is able to survive for several weeks and even several month without water. One bivalve from Kande Beach survived five weeks without water (pers. observation, 2000). Other representatives of Chambardia from Lake Tanganyika survived for a period of 12.5 months without water (Dance 1958). This way the bivalve can even survive a dry season and wait until water comes back in the rainy season.

Shell morphology of *Mutela alata*

The shell shape variability of *Mutela alata* is comparable with the variability of *Chambardia nyassaensis*. The most obvious shape changes affect the height of the posterior wing. Shells with a more rectangular shell outline are characterised by a low wing, whereas wedge-shaped shells are characterised by a high wing. The straight posterior margin that is typical for most shells is an effective antiscouring device. The straight or concave ventral margin works as an anchoring device because of the improved facilities to extrude the foot. The anteroventral shell gap further helps the bivalve to extrude the foot without even opening the valves. In addition, a posterior gap is developed, which permits the work of the inhalent and exhalent openings while the valves are closed. While these shell gaps are typical for the genus *Mutela*, the fusion of the mantle margins is typical for all Etherioidea. *Mutela alata* shows a very strong developed mantle fusion also in the posterior part of the bivalve. Simple siphons are developed here that facilitate the work of the inhalent and exhalent openings when buried in the sediment. Mantle fusion on the other side supports the function of the foot and thus facilitates infaunal life for bivalves (Stanley 1968). This charactersuite allows *Mutela alata* to be well adapted to a continuous infaunal life in offshore deep water environments of Lake Malawi. The shell gaps and exposed mantle margins are not suitable for nearshore habitats that are subject to desiccation.

Chambardia nyassaensis has no shell gaps so the mantle fusions is supporting the tight seal of the valves. Therefore, it closes the valves tightly when exposed to dry conditions. In contrast, *Mutela alata* starts with foot extrusion just after being exposed to dry conditions to rebury quickly (pers. observation, 2000). The exposed mantle along the shell gaps makes this species vulnerable to dry out and die. Thus these bivalves have a different habitat preference compared to *Chambardia nyassaensis* and avoid habitats that are vulnerable to desiccation.

Conclusions

The three species of unionoid bivalves from Lake Malawi exhibit a diverse set of adaptations to cope with the variability and instability of freshwater ecosystems.

Nyassunio nyassaensis follows the "Law of Stream Distribution" in all respect, with elongate and slender shells in nearshore habitats and triangular and swollen shells in offshore habitats. The disparity of shell shape of this species is very high arguing for a very high level of phenotypic plasticity. *Chambardia nyassaensis* and *Mutela alata* are less plastic than *Nyassunio nyassaensis*, but still show a considerable variability in shell morphology. Depending on the environmental conditions, either antiscouring devices or burrowing devices are better developed. In addition to phenotypic plasticity, other adaptations are developed in these two species to survive the heterogeneous freshwater environments. The large size and partial mantle fusion in particular allow both species to develop different habitat preferences. *Chambardia nyassaensis* has adaptations to dry conditions and is able to live in nearshore environments. *Mutela alata* has adaptations for stable conditions in deep offshore habitats.

All these habitat preferences are not exclusive as all species also live in the same habitats next to each other. Also the shape features described above are not exclusive and only allow the specimens to live in a certain environment. Shell shape is always a trade-off to cope with the temporal and spatial variability of freshwater habitats. Much more work is required to better understand this shell shape variability and its relationship to environmental variability. Reciprocal transplant experiments in natural environments would be required to study the influence of changing environmental conditions. Regular recapture sessions would be necessary to analyse the growth rate and pattern of these bivalves to better understand the ontogenetic shape changes and different requirements of juvenile and adult shells. Laboratory experiments are necessary to study different environmental factors separately, e.g. constant current vs. waves. All these experiments would give a much better framework and dataset to test the hypotheses for adaptive strategies of unionoid bivalves developed herein: (1) a high level of phenotypic plasticity allows bivalves to adapt the shell shape to variable environmental conditions, as it is mainly the case for *Nyassunio nyassaensis*; (2) a low level of phenotypic plasticity allows bivalves to grow larger and use other key features such as fused mantle margins to survive under fluctuating environmental conditions, as it is mainly the case for *Chambardia nyassaensis* and *Mutela alata*. The further study of these aspects is necessary to answer evolutionary, biogeographical, and ecological questions.

Acknowledgements

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