PRIMARY RESEARCH PAPER

Depth-dependent abundance of Midas Cichlid fish (*Amphilophus* spp.) in two Nicaraguan crater lakes

Marie Theres Dittmann · Marius Roesti · Adrian Indermaur · Marco Colombo ·
Martin Gschwind · Isabel Keller · Robin Kovac · Marta Barluenga ·
Moritz Muschick · Walter Salzburger

Abstract The Midas Cichlid species complex (*Amphilophus* spp.) in Central America serves as a prominent model system to study sympatric speciation and parallel adaptive radiation, since small arrays of equivalent ecotype morphs have evolved independently in different crater lakes. While the taxonomy and evolutionary history of the different species are well resolved, little is known about basic ecological parameters of Midas Cichlid assemblages. Here, we use a line transect survey to investigate the depth-dependent abundance of *Amphilophus* spp. along the shores of two Nicaraguan crater lakes, Apoyo and Xiloá. We find a considerable higher density of Midas cichlids in Lake Xiloá as compared to Lake Apoyo, especially at the shallowest depth level. This might be due to the higher eutrophication level of Lake Xiloá and associated differences in food availability, and/or the presence of a greater diversity of niches in that lake. In any case, convergent forms evolved despite noticeable differences in size, age, eutrophication level, and carrying capacity. Further, our data provide abundance and density estimates for Midas Cichlid fish, which serve as baseline for future surveys of these ecosystems and are also relevant to past and future modeling of ecological speciation.

Marie Theres Dittmann and Marius Roesti contributed equally to this study.

Handling editor: Christian Sturmbauer

Electronic supplementary material The online version of this article (doi:10.1007/s10750-012-1024-1) contains supplementary material, which is available to authorized users.

M. T. Dittmann · M. Roesti · A. Indermaur ·
M. Colombo · M. Gschwind · I. Keller ·
R. Kovac · M. Muschick · W. Salzburger (✉)
Zoological Institute, University of Basel, Vesalgasse 1,
4051 Basel, Switzerland
e-mail: walter.salzburger@unibas.ch

Present Address:
M. T. Dittmann
Group of Animal Nutrition, Institute of Agricultural
Science, Swiss Federal Institute of Technology,
Universitätsstrasse 2, 8092 Zurich, Switzerland

I. Keller
IFM-Geomar, Evolutionsbiologie, Düstenbrooker Weg
20, 24105 Kiel, Germany

M. Barluenga
Museo Nacional de Ciencias Naturales, CSIC, José
Gutierrez Abascal 2, 28006 Madrid, Spain

Introduction

The species flocks of cichlid fishes in the East African Great Lakes Victoria, Malawi, and Tanganyika are prime model systems in evolutionary biology and, particularly, in research focusing on speciation,

adaptive radiation, and parallel evolution (reviewed in Kocher, 2004; Salzburger, 2009; Sturmbauer et al., 2011). One of the most outstanding features of the East African cichlid assemblages is their species richness, with each of the Great Lakes harboring hundreds of endemic species. The downside of this unparalleled diversity is that these species flocks are notoriously difficult to study in their entirety, which makes it attractive to study simpler cichlid communities in smaller water bodies. In the last years surveys of crater lakes cichlids proved especially fruitful, mostly due to the degree of isolation of their cichlid assemblages (Schliewen et al., 1994; Barluenga & Meyer, 2004; Barluenga et al., 2006). The probably best-studied cichlids in volcanic crater lakes belong to the Midas Cichlid species complex (*Amphilophus* spp.), which is native to Central America. Midas cichlids are abundant in the large lakes of Nicaragua (Lake Nicaragua and Lake Managua) and associated rivers in Nicaragua and northern Costa Rica. Interestingly, Midas Cichlids have also colonized various volcanic crater lakes in the area (Barlow, 1976; Barluenga & Meyer, 2004, 2010), which emerge when calderas of extinct volcanoes of the 'Pacific Ring of Fire' become filled with water.

This study focuses on the *Amphilophus* assemblages in two of these crater lakes, Apoyo and Xiloá, which contain two independent, yet ecologically and morphologically very similar sets of Midas cichlid species (Elmer et al., 2010; Geiger et al., 2010a). The lakes are similar in some aspects, such as their volcanic origin, but they do differ in others (Barlow, 1976; Sussman, 1985; Waid et al., 1999; McKaye et al., 2002; Barluenga & Meyer, 2010): With a surface area of 21.1 km^2 and a maximum depth of 142 m, Lake Apoyo is larger and deeper than Lake Xiloá, which has a surface area of 3.8 km^2 and a maximum depth of 89 m (Table 1). Also, compared to the nutrient-rich Lake Xiloá, Lake Apoyo is oligotrophic. Furthermore, they differ in the number of cichlid species. Crater Lake Apoyo is suggested to harbor six endemic species of the *Amphilophus* complex (Barlow, 1976; Stauffer et al., 2008; Geiger et al., 2010b) (Supplementary Table 1), which most likely go back to a seeding lineage from adjacent Lake Nicaragua (Barluenga et al., 2006); together with *Parachromis managuense* and the recently introduced African species *Oreochromis aureus* and *O. niloticus*, these are the only cichlids found in this lake. In Lake Xiloá three to four endemic species of the *Amphilophus* species complex are described (McKaye et al., 2002;

Table 1 General descriptors of size, depth, age, visibility, fish density, and population size of the crater lakes Apoyo and Xiloá

	Apoyo	Xiloá
Surface area (km^2)	21.1[a]	3.8[a]
Maximum depth (m)	142[a]	89[a]
Age (year)	<23.000[a]	ca. 10.000[a]
Secchi depth (m)	5–7	3
Cichlid density along shore (individuals per 10 m transect)	11.3	19.9
Total number of *Amphilophus* spp. along shore (estimated)	83.000	66.000

[a] Barluenga & Meyer (2010)

Stauffer & McKaye, 2002) (Supplementary Table 1), which derive from the close-by Lake Managua stocks (Barluenga & Meyer, 2010). In addition to the Midas Cichlid fish, Lake Xiloá is inhabited by eight additional cichlid species, which either migrated naturally from nearby Lake Managua, or were introduced by humans, as might be the case for *Parachromis managuense* (Kullander & Hartel, 1997).

Here, we present a comparative study of cichlid abundance and density estimates in the two Central American calderas Lake Apoyo and Lake Xiloá. The set-up consisting of two rather similar crater lakes seeded independently by more or less the same ancestral line that subsequently radiated in parallel appears ideal to disentangle the biotic and abiotic factors influencing parallel adaptive radiation, particularly in its early stages. Many adaptive radiations appear to proceed in discrete stages starting with an initial diversification into macrohabitats (Streelman & Danley, 2003; Gavrilets & Losos, 2009), which—in fishes—is often associated with differentiation along the benthic-limnetic (pelagic) axis (Schluter & McPhail, 1992; Gíslason et al., 1999; Barluenga et al., 2006; Rutschmann et al., 2011). That independent adaptive radiations of the same group of organisms in similar ecological settings often result in similar morphologies is generally taken as strong evidence for natural selection (and the importance of ecology in speciation) (see Schluter & Nagel, 1995; Losos et al., 1998). On the other hand, the degree of similarity observed in convergent species pairs of cichlids has led some authors to question whether natural selection alone is sufficient to produce such matching morphologies, or whether genetic or developmental constraints have

contributed to the evolution of convergent forms (see, e.g., Brakefield, 2006). Even in the genomic era it is difficult to determine the relative contribution of natural selection and developmental channeling to parallel evolution. One possibility is to apply genetic and genomic experiments (reviewed in: Brakefield, 2006; Arendt & Reznick, 2008). In addition, one should inspect parallel radiations with respect to key ecological parameters. Under the assumption that ecology is the driving force behind parallel adaptive radiation, it is expected that not only the outcome of the radiations should be the same, but that the radiations should also follow the same steps and should show the same (ecological) characteristics. In the case of the parallel radiations of the Midas Cichlid in crater lakes Apoyo

and Xiloá, the outcome in form of morphologically equivalent species is obviously quite similar (Fig. 1) and there is evidence that the radiations progressed in a similar fashion (Barluenga et al., 2006; Barluenga & Meyer, 2010; Elmer et al., 2010). It is not known, however, whether the communities in the seemingly similar crater lakes Apoyo and Xiloá are also similar in terms of ecological parameters such as fish densities and depth distributions.

In this study, we applied transect surveys to record the abundance of *Amphilophus* spp. in crater lakes Apoyo and Xiloá. Applying SCUBA diving and snorkeling, fish were counted at different locations and depth levels to provide data on densities of cichlids in both lakes. We hypothesized that the
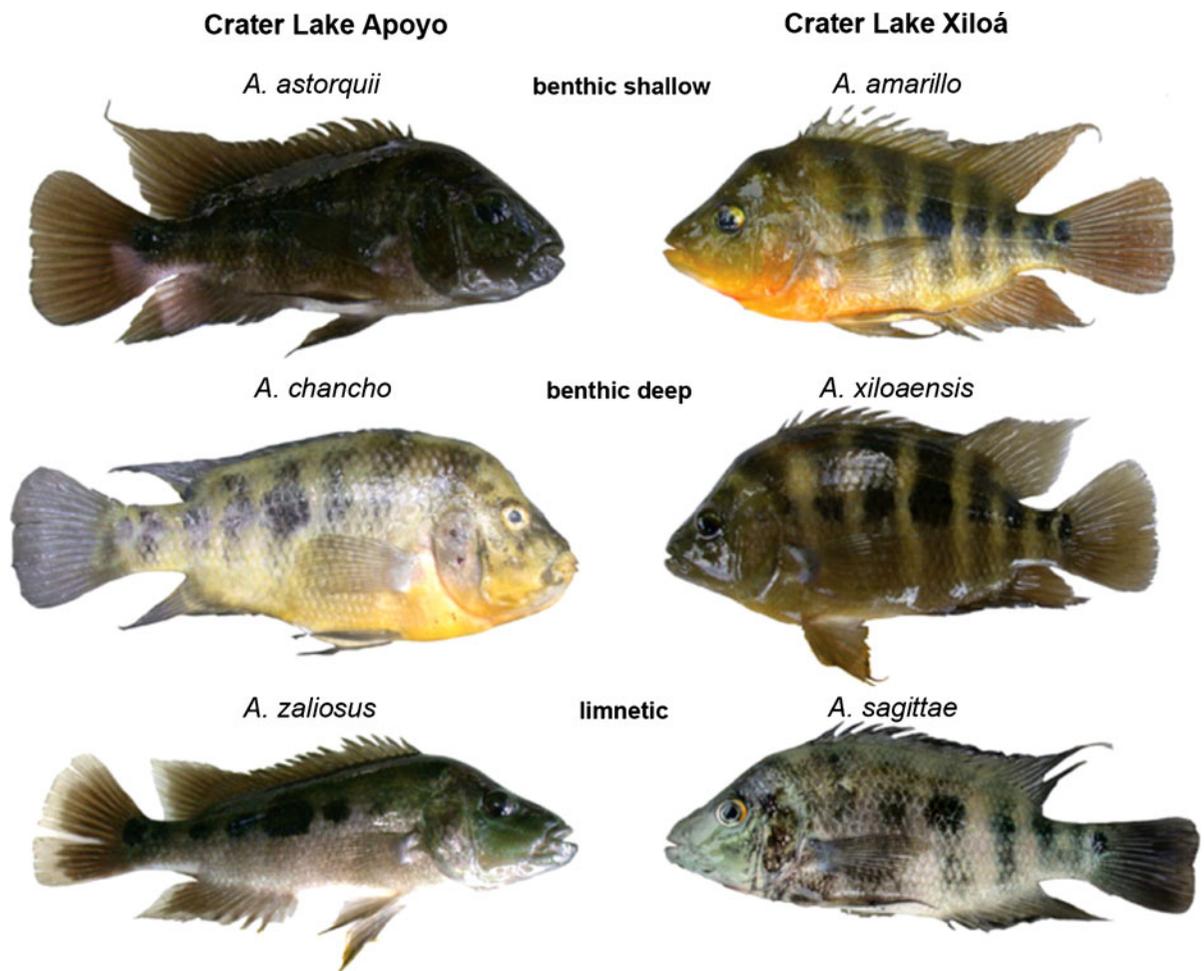

Fig. 1 Convergent phenotypes that evolved independently in the two Nicaraguan crater lakes Apoyo and Xiloá. Three species pairs are shown: benthic species using the shallow areas of the lakes; benthic species using the deeper areas of the lakes; and limnetic species inhabiting the open water column

density and distribution of Midas cichlids should be rather similar in both crater lakes due to their similar mode of origin and structure. In addition, this study aims to add ecological data in the form of abundance estimates for *Amphilophus* spp. to theoretical studies on sympatric and/or ecological speciation. Gavrilets et al. (2007), for example, investigated under which biological conditions rapid colonization of a new niche followed by sympatric or parapatric speciation in Lake Apoyo is theoretically possible. However, in their models, Gavrilets et al. (2007) were lacking empirical data on several important biological parameters (including abundance estimates). Finally, knowledge of the natural abundance of a population, species, or species group is fundamental not only to biological research but also to the management of wildlife populations. This is important in the case of crater lakes Apoyo and Xiloá, too, where cichlid fishes make up the main fraction of the ichthyofauna and provide a valuable food resource for local people (Schuster, 1957; Lin, 1961; Barlow, 1976). Importantly, through the recent introduction of African tilapiine cichlid species (*Oreochromis* spp.), the endemic cichlids of Lake Apoyo are thought to be threatened (McKaye et al., 1995; McCrary et al., 2001; Barluenga & Meyer, 2004), calling for an evaluation of the conservation status of the endemic faunas in the two crater lakes. Our data should, thus, provide important baseline references, with which upcoming impacts on the native cichlid abundance can be assessed.

Materials and methods

Study area and period

Field work was carried out in the two crater lakes Apoyo and Xiloá in Nicaragua, Central America, in September 2009. Diving was performed during the day by almost invariably good weather conditions. At the time of the study, water temperatures ranged between 29 and 31°C on all surveyed depth levels in both lakes. Transect sites were chosen randomly in both lakes, balanced, however, for different geographical locations within each lake (Supplementary Table 2). As crater lakes have a relatively homogenous habitat structure, the transects are representative of the habitat composition in each lake.

Transect surveys

We used fish counts along line transects to compare the depth-dependent abundance and density of *Amphilophus* spp. between the two lakes. Six transects were studied in the larger Lake Apoyo and four transects in the smaller Lake Xiloá. The start and end coordinates of each transect were taken with a handheld GPS from a boat (Supplementary Table 2). Depth levels at 10, 15, and 20 m were covered for each transects by a SCUBA diving buddy pair, whereas the 5 m depth level was covered by snorkelers (whenever the visibility was sufficient).

Transect length was determined by the distance covered during 10–15 min of diving (depending on the available air). Diving pace was moderate but varied between transects according to visibility and the quantity of fish that had to be counted, leading to variation in the lengths of the different transects. After having covered a transect one way, buddy pairs remained at their set depth level for 10 min to leave enough time for the fish to restore an undisturbed distribution. The end of each transect was marked with a buoy, which enabled the recording of the GPS coordinates. Buddy pairs then returned along the line transect back to the starting point. Diving was performed at 2 m above the substrate whereby dive buddies were swimming beside each other, individually counting all *Amphilophus* spp. individuals larger than ca. 5 cm within a visual field of about 4 m distance and 2 m to either side of the transect line. Snorkelers covering the 5 m depth used the same method and tried to remain at a depth of 3 m as much as possible. Owing to the difficulty to clearly identify species in sub-adult or non-breeding life stages underwater and the ongoing debate and steady changes in species classification, the overall number of *Amphilophus* spp. individuals was counted and no attempts were made to distinguish species, hybrids, or morphotypes (e.g., Barlow, 1976; McKaye et al., 2002; Bunje et al., 2007; Stauffer et al., 2008). In this visual survey a minimal bias among and within observers is expected due to individual survey differences (Thompson & Mapstone, 1997). To remove such potential confounding effects, observers alternated between different depth levels and in buddy pair partners at consecutive transects. The total number of dives over all transects was 36 (including each two persons diving back and forth), resulting in 144 single transect records.

In addition, Secchi depth measurements were taken from a boat to determine the water transparency at several random locations in both lakes.

Data analysis

To determine the average number of *Amphilophus* spp. individuals for every transect at each depth level separately, we averaged the fish counts by the two buddy team partners including the replicates from diving back and forth (Supplementary Table 3). We then calculated the average numbers of individuals per 10 m transect length for each depth level for every transect (Fig. 2), which we tested for normal distribution by applying a Shapiro–Wilk test. Using this data we tested for an overall difference in the density of *Amphilophus* spp. between lakes using Mann–Whitney U tests. We further applied a linear mixed model (LMM, LME4 package, Bates et al., 2011) to test for a difference in number and depth-distribution of individuals between the lakes by including the number of individuals counted per 10 m as the dependent variable, and lake and depth level as predictors. Assumptions of the LMM were visually checked. Since we assumed a potential difference in the depth-distribution of individuals between lakes, we included the interaction of lake and depth in the model. Furthermore, to correct for dependence in our data, we included transect as random factor. To further explore the data for effects not captured by the LMM, we applied separate Mann–Whitney U Tests for each depth level to test for depth-dependent differences in fish abundance between lakes. To roughly estimate the

total number of Midas cichlids for both lakes, the numbers of fish per 10 m were extrapolated to the total circumference of the lake. This was calculated by summing up the average number of individuals at all four depth levels (Suppl. Table 3) multiplied by the circumference of the lake. All analyses was performed using R 2.9.2 (R Foundation for Statistical Computing, Vienna, Austria).

Results

The average number of *Amphilophus* spp. individuals per 10 m transect length in Apoyo across all transects and depth levels was 11.3 (min = 0, max = 37, SD = 9.5), which did not differ significantly from Lake Xiloá with 19.9 fish per 10 m transect length (min = 3, max = 55, SD = 15.7) (Mann–Whitney U test, $N = 36$, $p = 0.112$). The LMM did not reveal a significant interaction between lake and depth ($t = 0.1692$, $p = 0.169$) (Fig. 2). However, testing for single depth levels between the lakes revealed a marginally significant difference at the 5 m depth level (Mann–Whitney U test, $N = 10$, $W = 18$, $p = 0.050$). The pairwise comparison of numbers of fish per 10 m transect at the other depth levels exhibited no significant difference between the lakes (Mann–Whitney U test, 10 m: $N = 10$, $p = 0.394$; 15 m: $N = 10$, $p = 0.796$; 20 m: $N = 8$, $p = 0.180$).

Extrapolating the average number of *Amphilophus* spp. individuals of all transects and depth levels to the total circumference in both lakes (Apoyo approx. 18.2 km; Xiloá approx. 8.3 km) revealed a similar

Fig. 2 Average number of *Amphilophus* spp. individuals per 10 m transect at each depth level for Lake Xiloá and Lake Apoyo. "*" denotes a marginally significant difference in cichlid fish density between the lakes (Mann–Whitney U test, $N = 10$, $p = 0.050$)
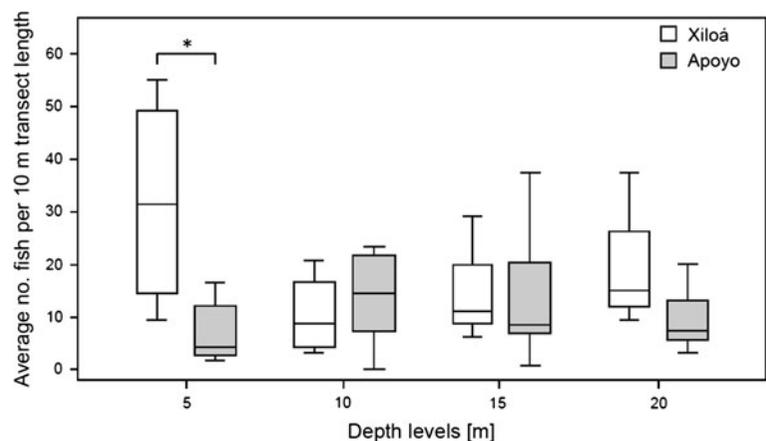
total number of fish in both lakes along the shoreline: ca. 83.000 individuals (13.000 to 150.000) in Lake Apoyo and ca. 66.000 individuals (13.000 to 120.000) in Lake Xiloá.

The Secchi depth, measured randomly several times in both lakes, ranged between 5 and 7 m in Lake Apoyo, compared to an approximately constant Secchi depth of 3 m in Lake Xiloá.

Discussion

Benefits of fish abundance estimates are diverse. The comparison of fish abundances between comparable ecosystems (e.g., between lakes) that differ in only few and well-defined ecological factors, allows to draw general conclusions on the possible impact of these factors on fish abundances and the composition and evolution of communities. This is especially the case when members of the same lineage radiated in parallel. Furthermore, in conservation biology and wildlife management, for example, changes in abundance of a fish species or population in a specific area may give an estimate for its "ecological health". This allows to define appropriate conservation strategies as well as to evaluate the (long-term) effects of habitat or species-specific conservation actions (Cheal & Thompson, 1997; Witmer, 2005). To estimate the impact of naturally induced (e.g., by a hurricane) or human-induced (e.g., by industrial fishery) changes on fish abundance, a baseline abundance needs to be established against which future levels of impact can be assessed (Jennings & Blanchard, 2004; Silvano et al., 2009). Then, abundance estimates are valuable to evaluate the relative importance and status of a fish species in an ecosystem, such as in a predator–prey relationship in the food web. Finally, mathematical modeling in fields such as evolutionary biology provides more accurate, theoretical insights into biological processes. Most often, however, theoretical approaches lack data from empirical work such as abundance estimates that would allow to make biologically reasonable assumptions and to apply mathematical models to particular case studies (see, e.g., Gavrilets et al., 2007).

The above reasons have been the motivation for this comparative study of Midas cichlid fish (*Amphilophus* spp.) abundance and density estimates in the two comparable Nicaraguan crater lakes, Apoyo and

Xiloá. Despite the lack of statistical significance, our data reveal an almost twofold higher density of cichlid fish along the shoreline in Lake Xiloá as compared to Lake Apoyo. At a depth of 5 m, we found a more than fourfold higher density of Midas cichlids in Lake Xiloá (Fig. 2). Overall, however, as a consequence of the higher density of fish in the smaller lake Xiloá, the absolute numbers of *Amphilophus* spp. are relatively similar in both lakes—at least along the shore habitat covered by our survey.

Differences in food availability could explain the different densities of *Amphilophus* spp. between the two crater lakes. Indeed, the two lakes differ in their level of eutrophication: Lake Apoyo is an oligotrophic environment, whereas Lake Xiloá is relatively more eutrophic. But why would higher fish densities then only be found at shallow areas and not throughout Lake Xiloá? Eutrophication leads to a considerable reduction of ambient light at deeper waters (e.g. Koch, 2001), which can restrict photosynthesis to the shallow waters where sufficient ambient light is available for primary production (see Secchi depth in Table 1). This can directly (e.g., algae-feeders) or indirectly (e.g., through the food web) lead to higher fish densities in the shallow area. Higher fish densities in more turbid waters may also be explained by the reduced performance of predators, such as birds, which under turbid conditions have more difficulties to spot fish. It has previously been shown that reduced visibility can influence color-recognition in cichlids, and, hence, may have an impact on intraspecific (and interspecific) species recognition and communication (see, e.g., Seehausen, 1997, 2008). Whether this is also the case in Nicaraguan crater lakes remains to be tested.

An alternative explanation for the higher density of cichlids in Lake Xiloá could be the availability of ecologically more diverse niches in this lake, e.g., in the shallow area where differences in the densities of *Amphilophus* spp. are greatest. This could also explain the higher variance in fish counts at the 5 m depth level in Lake Xiloá compared to the other depth levels. Perhaps it is a combination of both factors, eutrophication and habitat complexity, that leads to higher fish densities in Lake Xiloá. A more thorough analysis of the habitat structure would be necessary to clarify this point. Furthermore, there is no knowledge on fish densities in deeper and open waters, which would allow a comprehensive comparison of both lakes. Such fish counts at deeper waters seem particularly

interesting, since we observed a distinct and clear water layer below a depth of 35 m in Lake Xiloá.

Crater lakes Apoyo and Xiloá are inhabited by a similar set of convergent *Amphilophus* ecotype morphs (Fig. 1) making the Midas Cichlid complex an ideal system to study parallel evolution (see, e.g., McKaye et al., 2002; Barluenga et al., 2006; Elmer et al., 2010). While taxonomy, morphology, and evolutionary history of the species complex is largely resolved (see Barluenga et al., 2006; Barluenga & Meyer, 2010; Elmer et al., 2010; Geiger et al., 2010a, b), little is known about basic ecological parameters such as the relative densities of the different species. Our study is the first to provide such data. We uncover a rather similar overall number of *Amphilophus* spp. individuals in both lakes, but also account differences in densities, especially in the shallow area (see above). Interestingly, the shallow areas of Lake Xiloá are not only characterized by larger densities of Midas cichlids, but also by the presence of additional cichlid species (see Supplementary Table 1). It remains unclear whether these never arrived in Lake Apoyo (e.g., because of the larger distance to a large lake), or whether these could not establish themselves there (e.g., because of the eutrophic situation). In any case, convergent phenotypes evolved in both crater lakes despite noticeable differences in size and age of the respective lake (see Table 1), in community structure (the presence/absence of other cichlid species; Supplementary Table 1), and in fish densities (Fig. 2). This corroborates the view that the initial steps of ecological speciation in fish species flocks follow similar pathways in form of a splitting into benthic and limnetic types (see, e.g., Schluter & McPhail, 1992; Salzburger, 2009), which does not seem to be dependent on phylogenetic background and parameters such as size or age of a lake or level of eutrophication. Apparently, it is enough that a benthic-limnetic axis is present in a lake (see Barluenga et al., 2006).

The Midas cichlid fauna from Lake Apoyo represents one of the most famous examples for sympatric speciation (Barluenga et al., 2006), and has attracted theoretical modeling work. Gavrilets et al. (2007), for example, investigated whether at all and under which ecological conditions sympatric speciation is likely to have occurred in lake Apoyo. One of the parameters incorporated into the model of Gavrilets et al. (2007) was the carrying capacity (K) of Lake Apoyo. Carrying capacity stands for the maximum number

of individuals that can live in a particular environment given the available nutrients and without causing detrimental effects. Gavrilets et al. (2007) concluded that intermediate carrying capacities ($K = 16.000$) are propensive for sympatric speciation, whereas large carrying capacities ($K = 32.000$–51.200, depending on the model) would rather lead to the evolution of a single, generalistic species. Our estimates of K (ca. 83.000 and ca. 66.000 individuals in Lakes Apoyo and Xiloá, respectively) lie above these numbers, although these estimates refer to counts at four depth levels along the shoreline only and nothing is known about fish densities below 20 m. One also has to consider that Gavrilets et al. (2007) assumed the presence of a single age class (i.e., generation) at a given time. Our counts certainly included members from different age classes, although we lack detailed information on age distribution. Taken together, the carrying capacities assumed by Gavrilets et al. (2007) to model sympatric speciation in Lake Apoyo seem to be slightly—however not substantially—underestimated compared to our findings and it would now be interesting to evaluate what effect this has on available models.

Although a reproducing population of invasive *Oreochromis* spp. (tilapias) has been reported for Lake Apoyo in previous studies (McKaye et al., 1995; McCrary et al., 2001), we did not observe any tilapiine species during our fieldwork. These African cichlids were reported to feed on stonewort beds (*Chara* spp.) and are likely to account for the temporal elimination of these algae in Lake Apoyo (McKaye et al., 1995; McCrary et al., 2001, Canonico et al., 2005). However, we found extensive stonewort beds in Lake Apoyo. This suggests that tilapia populations might have failed to establish permanently in an oligotrophic environment such as Lake Apoyo.

Conclusions

Our study gives estimates of cichlid fish densities in two crater lakes in Nicaragua, Apoyo and Xiloá. We find that parallel ecotype morphs evolved despite noticeable differences in size, age, eutrophication level, and carrying capacity. We provide ecological data for understanding the carrying capacity of the systems in order to apply it to modeling sympatric/parapatric speciation. Furthermore, it sets baseline abundance estimates for cichlid fish in Nicaraguan

crater lakes, to which future ecological health assessments of these lakes can be compared.

References

Arendt, J. & D. Reznick, 2008. Convergence and parallelism reconsidered: what have we learned about the genetics of adaptation? Trends in Ecology & Evolution 23: 26–32.

Barlow, G. W., 1976. The Midas cichlid in Nicaragua. In Thorson, T. B. (ed.), Investigations of the Ichthyofauna of Nicaraguan Lakes, University of Nebraska-Lincoln: 333–358.

Barluenga, M. & A. Meyer, 2004. The Midas cichlid species complex: incipient sympatric speciation in Nicaraguan cichlid fishes. Molecular Ecology 13: 2061–2076.

Barluenga, M. & A. Meyer, 2010. Phylogeography, colonization and population history of the Midas cichlid species complex (Amphilophus spp.) in the Nicaraguan crater lakes. BMC Evolutionary Biology 10: 326.

Barluenga, M., K. N. Stölting, W. Salzburger, M. Muschick & A. Meyer, 2006. Sympatric speciation in Nicaraguan Crater Lake cichlid fish. Nature 439: 719–723.

Bates, D., M. Mächler & B. Bolker, 2011. LME4: linear mixed-effects model using S4 classes. R package, v. 0.999375-40. http://cran.r-project.org.

Brakefield, P. M., 2006. Evo-devo and constraints on selection. Trends in Ecology & Evolution 21: 362–368.

Bunje, P. M., M. Barluenga & A. Meyer, 2007. Sampling genetic diversity in the sympatrically and allopatrically speciating Midas cichlid species complex over a 16 year time series. Bmc Evolutionary Biology 7: 25.

Canonico, G. C., A. Arthington, J. K. McCrary & M. L. Thieme, 2005. The effects of introduced tilapias on native biodiversity. Aquatic Conservation: Marine and Freshwater Ecosystems 15: 463–483.

Cheal, A. J. & A. A. Thompson, 1997. Comparing visual counts of coral reef fish: implications of transect width and species selection. Marine Ecology Progress Series 158: 241–248.

Elmer, K. R., H. Kusche, T. K. Lehtonen & A. Meyer, 2010. Local variation and parallel evolution: morphological and genetic diversity across a species complex of Neotropical Crater Lake cichlid fishes. Philosophical Transactions of the Royal Society London B 365: 1763–1782.

Gavrilets, S., A. Vose, M. Barluenga, W. Salzburger & A. Meyer, 2007. Case studies and mathematical models of ecological speciation. 1. Cichlids in a crater lake. Molecular Ecology 16: 2893–2909.

Gavrilets, S. & J. B. Losos, 2009. Adaptive radiation: contrasting theory with data. Science 323: 732–737.

Geiger, M. F., J. K. McCrary & U. K. Schliewen, 2010a. Not a simple case – A first comprehensive phylogenetic hypothesis for the Midas cichlid complex in Nicaragua (Teleostei: Cichlidae: Amphilophus). Molecular Phylogenetics and Evolution 56: 1011–1024.

Geiger, M. F., J. K. McCrary & J. R. Stauffer, 2010b. Description of two new species of the Midas cichlid complex (Teleostei: Cichlidae) from Lake Apoyo, Nicaragua. Proceedings of the Biological Society of Washington 123: 159–173.

Gíslason, D., M. M. Ferguson, S. Skúlason & S. S. Snorrason, 1999. Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic charr (Salvelinus alpinus). Canadian Journal of Fisheries and Aquatic Sciences 56: 2229–2234.

Jennings, S. & J. Blanchard, 2004. Fish abundance with no fishing: predictions based on macroecological theory. Journal of Animal Ecology 73: 632–642.

Koch, E. W., 2001. Beyond light: physical, geological and geochemical parameters as possible submersed aquatic vegetation habitat requirements. Estuaries 24: 1–17.

Kocher, T. D., 2004. Adaptive evolution and explosive speciation: the cichlid fish model. Nature Reviews Genetics 5: 288–298.

Kullander, S. & K. E. Hartel, 1997. The systematic status of cichlid genera described by Louis Agassiz in 1859: Amphilophus, Baiodon, Hypsophrys and Parachromis (Teleostei: Cichlidae). Ichthyological Explorations of Freshwaters 7: 193–202.

Lin, S. Y., 1961. Informe al goberino de Nicaragua sobre el desarrollo de un proyecto de pesquerías continentals en dicho país. Informe F. A. O. 1347: 1–21.

Losos, J. B., T. R. Jackman, A. Larson, K. Queiroz & L. Rodriguez-Schettino, 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279: 2115–2118.

McCrary, J. K., E. P. van den Berghe, K. R. McKaye & L. J. Lopez Perez, 2001. Tilapia cultivation: a threat to native species in Nicaragua. Encuentro 58: 9–19.

McKaye, K. R., J. D. Ryan, J. R. Stauffer, L. J. Lopez Perez & E. P. van den Berghe, 1995. African tilapia in Lake Nicaragua: ecosystem in transition. BioScience 45: 406–411.

McKaye, K. R., J. R. Stauffer, E. P. van den Berghe, R. Vivas, L. J. Lopez Perez, J. K. McCrary, R. Waid, A. Konings, W. J. Lee & T. D. Kocher, 2002. Behavioral, morphological and genetic evidence of divergence of the Midas Cichlid species complex in two Nicaraguan crater lakes. Cuadernos de Investigación de la UCA 12: 19–47.

Rutschmann, S., M. Matschiner, M. Damerau, M. Muschick, M. F. Lehmann, R. Hanel & W. Salzburger, 2011. Parallel ecological diversification in Antarctic notothenioid fishes as evidence for adaptive radiation. Molecular Ecology 20: 4707–4721.

Salzburger, W., 2009. The interaction of sexually and naturally selected traits in the adaptive radiations of cichlid fishes. Molecular Ecology 18: 169–185.

Schliewen, U. K., D. Tautz & S. Paabo, 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. Nature 368: 629–632.

Schluter, D. & J. D. McPhail, 1992. Ecological character displacement and speciation in sticklebacks. American Naturalist 140: 85–108.

Schluter, D. & L. Nagel, 1995. Parallel speciation by natural selection. American Naturalist 140: 292–301.

Schuster, W. H., 1957. Informe al goberino de Nicaragua sobre fomento de la pesca contonental. Informe F. A. O. 607: 1–13.

Seehausen, O., 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science 277: 1808–1811.

Seehausen, O., Y. Terai, I. S. Magalhaes, K. L. Carleton, H. D. J. Mrosso, R. Miyagi, I. van der Sluijs, et al., 2008. Speciation through sensory drive in cichlid fish. Nature 455: 620–626.

Silvano, R. A. M., M. Ramires & J. Zuanon, 2009. Effects of fisheries management on fish communities in the floodplain lakes of a Brazilian Amazonian Reserve. Ecology of Freshwater Fish 18: 156–166.

Stauffer, J. R. & K. R. McKaye, 2002. Descriptions of three new species of cichlid fishes (Teleostei: Cichlidae) from Lake Xiloá, Nicaragua. Cuadernos de Investigacíon de la Universidad Centroamericana 12: 1–18.

Stauffer, J. R., J. K. McCrary & K. E. Black, 2008. Three new species of cichlid fishes (Teleostei: Cichlidae) from Lake Apoyo, Nicaragua. Proceedings of the Biological Society Washington 121: 117–129.

Streelman, J. T. & P. D. Danley, 2003. The stages of vertebrate evolutionary radiation. Trends in Ecology & Evolution 18: 126–131.

Sturmbauer, C., M. Husemann & P. D. Danley, 2011. Explosive speciaiton and adaptive radiation of East African cichlid fishes. In Zachos, F. E. & J. C. Habel (eds.), Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas. Springer: 333–362.

Sussman, D., 1985. Apoyo caldera, Nicaragua: a major quaternary silicic eruptive center. Journal of Volcanology and Geothermal Research 24: 249–282.

Thompson, A. A. & B. D. Mapstone, 1997. Observer effects and training in underwater visual surveys of reef fishes. Marine Ecology Progress Series 154: 53–63.

Waid, R. M., R. L. Raesly, K. R. McKaye & J. K. McCrary, 1999. Zoogeografía íctica de lagunas cratéricas de Nicaragua. Encuentro 51: 65–80.

Witmer, G. W., 2005. Wildlife population monitoring: some practical considerations. Wildlife Research 32: 259.