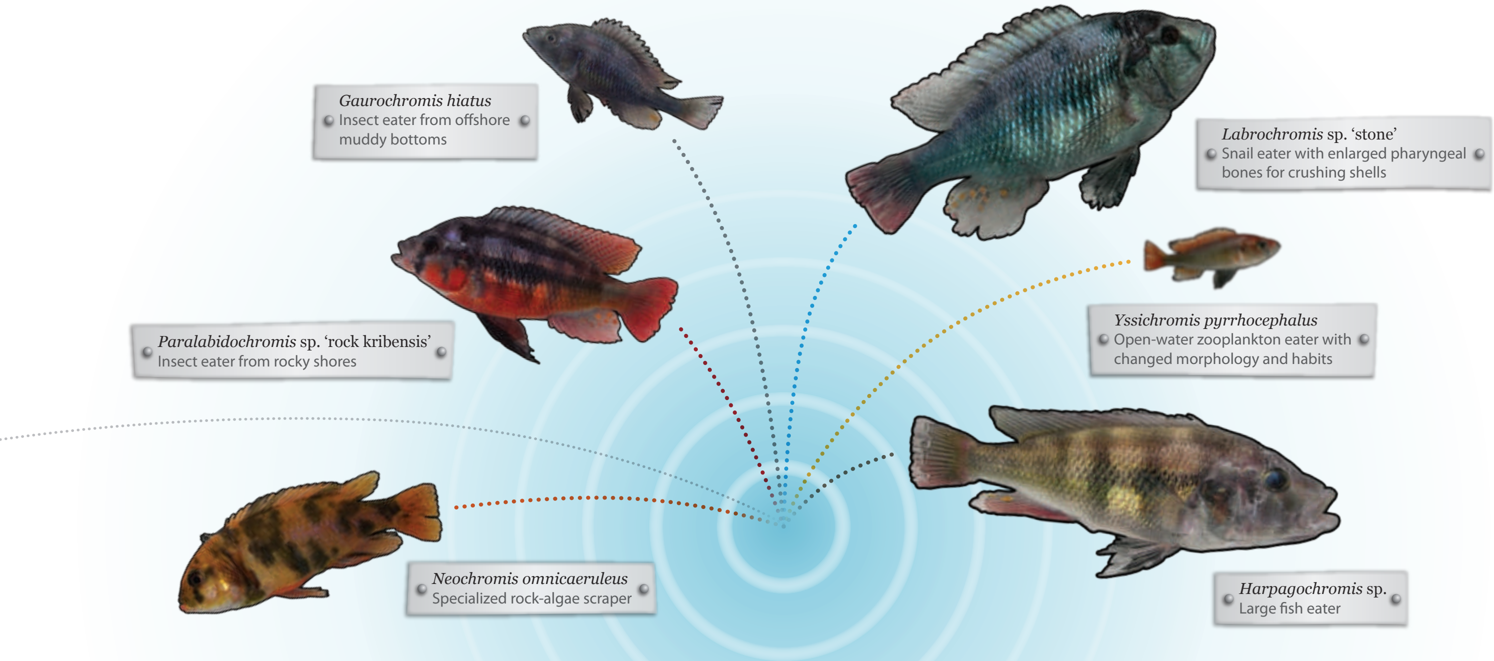

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DREAMPOND REVISITED

A once-threatened population of African fish is now providing a view of evolution in action. **Laura Spinney** asks what Lake Victoria cichlids have revealed about speciation.

Ole Seehausen didn't expect to find much when he dropped his trawling net into Lake Victoria in 1991. The fish he was studying, called cichlids, had been disappearing from the East African lake for years. So he was astounded when he hauled in dozens of them. Close inspection of their coloration and shapes revealed five distinct species. The graduate student couldn't wait to deliver the news to his supervisor, Frans Witte, at Leiden University in the Netherlands. "The quality of the phone line was so horrible that I wasn't sure he had understood that we had caught cichlids offshore again," he recalls.

Seehausen's catch suggested a reversal of more than two decades of declining population and collapsing biodiversity. Lake Victoria, the world's second-largest freshwater lake, had been home to no fewer than 500 species of cichlid. The fish displayed such a variety of colours, shapes and adaptations that evolutionary biologist Tijs Goldschmidt, formerly at Leiden University, dubbed the lake 'Darwin's dreampond'. In one of the most spectacular demonstrations of what is known as adaptive radiation, cichlids are thought to have diversified from a handful of species in as few as 15,000 years — essentially a new species every 30 years. But that menagerie was all but obliterated when humans introduced a much larger predator, Nile perch (*Lates niloticus*), into the lake in the 1960s and then flocked to its shores to harvest them.

Now, scientists such as Seehausen, at present a professor of ecology at the University of Bern and the Swiss Federal Institute of Aquatic Science and Technology in Kastanienbaum, have documented the cichlids' return and are capitalizing on the opportunity to watch a new radiation unfold. The researchers are starting to see how different environments shape the dynamics of speciation. And they are finding that hybridization between species may be a crucial step in generating the remarkable diversity that comes with adaptive radiation. This may help scientists to understand the timescales at which speciation occurs.

Collapse and regrowth

Lake Victoria has dried up and been refilled several times in its 400,000-year history. Ancestors of today's cichlids arrived there after the last such cycle, roughly 15,000 years ago, possibly from neighbouring Lake Edward or Lake Kivu. Those founding cichlids exploited a wide range of niches, each of which encouraged specialized adaptation. Species numbers exploded. Around 15 major cichlid 'guilds' — each with many sub-specializations — have been identified in Lake Victoria, from streamlined open-water hunters to slope-headed algae scrapers. "It is, by far, the fastest large-scale adaptive radiation known," says Seehausen.

In 1979, when Witte and his group began studying the cichlids in the Mwanza Gulf of Lake Victoria (see 'Great lakes of East Africa'), they were catching 1,000 or more in 10 minutes of experimental trawling, representing, on average, 100 species. But by this time their numbers were already falling. The lake was changing.

Whether for sport or to increase the amount of protein in the local diet, Nile perch were added to the lake in the early 1960s. A fecund and voracious predator, the fish grows to almost two metres in length and is a more attractive food source for humans than small and bony cichlids. Within a few decades, Nile-perch numbers expanded rapidly, along with a fishing industry.

In a cautionary parable on globalization, film-maker Hubert Sauper chronicled the growth of slum-like 'fish cities' around filleting factories at Lake Victoria that were sending much of their produce to the developed world. In homage to Goldschmidt, he called his film, released in 2004, *Darwin's Nightmare*. Although his conclusions have been controversial, the effects of development on Lake Victoria are undeniable. An influx of nutrients, mainly due to deforestation, industrialization and human pollution, fed large algal blooms that in turn fed oxygen-devouring bacteria. Over time, the water grew murkier and less able to sustain life — a process known as eutrophication.

Owing to predation, eutrophication or both, cichlids had all but vanished from Witte's

nets by the late 1980s. Researchers trawling in open waters were lucky to find any. Hence Seehausen's excitement in 1991. Today, Witte's data indicate that the biomass of cichlids in the lake has returned to 1979 levels, and that biodiversity is increasing.

Genetic analyses and simple observation show that the cichlid population structure has changed markedly. Of the 20 species in the average catch, says Seehausen, two or three are species that seem to have survived the population crash unchanged. Another two or three look like new species, and are probably hybrids of old ones. But most fall in-between: they may have different colours or shapes, occupy different habitats or eat different foods, but genetically they aren't different enough from their predecessors to be termed new species. Crucially, old, new and in-between remain close enough to interbreed.

"It is, by far, the fastest large-scale adaptive radiation known."

Blind dates

Hybridization tends to reduce genetic diversity. Breeding between species is, indeed, antithetical to the reproductive isolation often deemed necessary for speciation. But this homogenizing step could be a precursor to adaptive radiation. In 2002, by comparing nuclear and mitochondrial DNA sequences, Walter Salzburger, an evolutionary biologist at the University of Basel in Switzerland, showed that two ancient cichlid species from the oldest of Africa's Great Lakes, Lake Tanganyika, may have hybridized roughly 100,000 years ago, producing a new species[1]. Salzburger speculates that some radical change in the lake environment brought the two parental species together.

Although that ancient event can only be guessed at, Seehausen could be observing a contemporary parallel. Eutrophication has reduced visibility in the waters of Lake Victoria, especially near the shore, and female cichlids are less able to distinguish the different hues of breeding males, which is how they choose their mates[2]. Seehausen has found that less-discriminating encounters between species are producing cichlids that are not as genetically diverse, particularly in the more turbid, inshore waters. Where there were once hundreds of different specialists, there are now what he calls "hybrid swarms".

But many of the gene variants that previously promoted the cichlids' prolific adaptation still persist in these swarms. Hybridization has essentially thrown much of the genetic record of the last adaptive radiation into an evolutionary blender, allowing those variants to come together in different combinations.

Seehausen speculates that the lake's coastal bays and gulfs, where the water is murkiest, act as a 'hybridization belt'. Individuals of new genetic make-up are born here and move out into the altered lake. As they do so, they are confronted by the choice of new or vacated niches to exploit, and those specimens best adapted take up residence. Farther from the shore, visibility is better. Seehausen's group has shown that male breeding colours and female mate preferences co-evolve to suit the light conditions[3]. The changes that take place ultimately drive reproductive isolation. Thus, sexual selection reinforces ecological selection, resulting in new species. This seems to happen without the aid of geographical or physical barriers, and might therefore make the cichlids one of very few examples of side-by-side, or sympatric, speciation, says Seehausen.

Learning to get along

That the returning cichlids are better suited to life in the altered lake is supported by evidence that they are now resisting the predator. What is puzzling, says Seehausen, is that many returning species seem to have increased rather than decreased habitat overlap with Nile perch. Take *Yssichromis pyrrhocephalus*, one species that has returned with modifications. Before the population crashed, Witte found that this fish fed on zooplankton floating in the water. In 2008, his analyses of its stomach contents suggested that it was rooting up organisms from the lake bed[4]. Perhaps to cope with the lower oxygen levels at that depth, the surface area of its gills has increased. But Nile perch are abundant at the same depth. Seehausen can't explain why the two are now cohabitating successfully, when they couldn't 20 years ago.

Better genetic tools might help researchers track the genes that are driving morphological and behavioural adaptation. For now, they are hampered by the limited genetic maps at their disposal, which have marked out only a fraction of the 30,000 or more genes in the cichlid genome. The genes that can be tracked using well-established markers may not be the ones that are driving adaptation. Moreover, because the different species have diverged from each other so recently, in evolutionary terms their DNA is similar. The sequences that differentiate them may not be those that can be tracked by existing markers, making it hard to identify distinct species. That could change once the cichlid genome has been fully sequenced — a project being undertaken by an international research group led by the US National Institutes of Health based in Bethesda, Maryland, and the Broad Institute in Cambridge, Massachusetts.

Armed with a complete sequence, researchers will be able to select more sensitive markers of speciation, and feed the resulting data about the relationships between species into mathematical models to calculate when they diverged from each other. Such work may help to predict how long it will take for the current radiation to return cichlids to their former diversity in Lake Victoria. "Even though we have good reasons to believe that evolution can be fast, this is likely going to take centuries, if not millennia," says Seehausen.

What caused the cichlids' return is uncertain, but it is probably a combination of fishing pressures on the Nile perch and some measures taken to reduce pollution in the lake, coupled with the cichlids' own capacity for adaptation. Nobody is complacent about the recovery, however. Oliva Mkumbo, a senior scientist at the Lake Victoria Fisheries Organization in Jinja, Uganda, says that the water quality may have stopped deteriorating, thanks in part to the construction of new sewage works, but deforestation and erosion are still major problems. As Seehausen puts it, eutrophication could still "close the show", resulting in an even more catastrophic collapse of cichlid biomass and diversity. ■

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