continuum in stickleback. As someone with a lifelong affliction of organizing things in tidy little boxes, I was pushed "outside the box" by the main premise of their paper, which is that speciation in stickleback can occur in a variety of forms ranging from panmixia to complete reproductive isolation and that some populations can transition among forms. However, as I immersed myself in the ecology of the early stages of stickleback speciation over those two summers and envisioned how population interactions fluctuate as ephemeral channels open and close, I found myself returning to this paper to make sense of what I had observed firsthand and to inform interpretations of our data and learned that the process of speciation in stickleback mirrors the dynamic and complex landscapes in which the populations evolve.

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The Established Researcher

Twelve years before Emily found herself slogging through the mud and dodging angry nesting birds on remote islands in Alaska, I found myself basking in the pleasant sunshine and being entertained by baby shore birds endlessly circumnavigating a tiny island on Vancouver Island. My island was not nearly so remote as Emily's, but it was remote enough—being situated at the end of a very rough 4-wheel drive road—that I did not see another person while camping there for 6 weeks. I had come to be at this idyllic site for my new postdoctoral work on threespine stickleback.

Near the end of my PhD at the University of Washington, where I studied the reproductive energetics of salmon in Alaska, I was seeking a postdoc that would allow me to study my new passion—the "fist-fight" between natural selection and gene flow that shapes and modifies adaptive population divergence. That new excitement for studying the forces shaping rapid adaptation, when I had originally been focused on salmon biology, was the direct outcome of reading "The Beak of the Finch" by Jonathan Weiner, which my mother had bought for me for Christmas in 1995. During that holiday in frigid Edmonton, Alberta, Canada, I had spent several days huddled over a heater vent being mentally transported to the hot and dry slopes of Daphne Major in Galapagos, where Peter and Rosemary Grant studied the rapid evolution of Darwin's finches. Ever since that fateful reading, my academic efforts were increasingly directed toward studying the forces shaping rapid evolution—but in what study system?

For personal reasons, I needed my postdoc to be close to Seattle. Fortunately, as a Canadian citizen, I was eligible for an NSERC grant—and so off I drove to the University of British Columbia (UBC) to ask professors what would be the optimal system in which to study how adaption was shaped by selection and gene flow. I spoke to Dolph Schluter, Don McPhail, and—finally—Rick Taylor, who suggested that lake–stream stickleback population pairs would be the best system for my work. And he was right. I wrote my postdoctoral application, received the fellowship, and duly headed off for several summers of intensive field work on Vancouver Island, not the least on that small island on that small lake at the end of that 4-wheel drive road.

Stickleback are mega-famous now but, when I started my postdoc in 1998, not that many people worked on them—so my research was conducted mostly alone, albeit with helpful input from students, postdocs, and profs at UBC. Hence, my first big exposure to a diversity of other stickleback researchers was the "Stickleback Behavior and Evolution" meeting held the following year at UBC. I presented my research on how high gene flow between lake and stream populations was constraining their adaptive divergence, and then I received a crucial question from Beren Robinson, who was in the audience having finished a postdoc on stickleback not that long before. "Can't it be the other way around," he asked "where increasing adaptive divergence constrains gene flow – as in ecological speciation." This simple question, reinforced by UBC being the hive of research on ecological speciation at the time, precipitated a series of new studies when I became a professor at McGill University in 2001. Specifically, I set out to understand not just how gene flow constrains adaptive divergence but also the reverse—how adaptive divergence constrains gene flow.

The trouble was—I just couldn't find it. No matter how hard I looked at lake–stream stickleback, I simply could not find the same signatures of reproductive barriers that other researchers, including my friends and colleagues, were finding in their various other stickleback systems. And it was stressful. I can vividly remember lying in bed, unable to sleep from the guilt of having given my first few students and postdocs projects that generated only negative results. Each experiment they conducted failed to find a reproductive barrier, leading to other "better" experiments that also failed to find barriers, and so on and so on—with no end in sight. But on that night, staring up at the unsympathetic ceiling, a little switch somehow clicked over in my head: "Wait, perhaps our data and experiments are actually good; and, instead, our lake-stream system is just somehow fundamentally different from the other stickleback systems."

That very abrupt (in fact, nearly instantaneous) shift, from believing my experiments were somehow "wrong" because they failed to mirror previous work to instead believing in our data and thus questioning the generality of previous work, completely restructured how I thought and worked about the problem thenceforth. Immediately, the important questions were clearly: "In a given case of divergent environments, just how far do the populations get toward speciation," and "What got them that far and why haven't they gotten further?" That is, speciation is a continuum from nothing at all to the whole shebang, and different systems are arrayed at different positions on that continuum—and for different reasons. We were suddenly liberated to completely change the way we thought about speciation. All of a sudden my research, papers, and seminars became much more fun and interesting.

Andrew Hendry spent 6 weeks camping on this small island conducting his postdoctoral research on threespine stickleback. Visible in the lake are stickleback enclosures in the limnetic and benthic environments. Photo credit: Andrew Hendry.

Along with my newest postdoc, Daniel Berner, who was bringing this speciation continuum perspective to our lake–stream system, I sought out a couple of stickleback research friends whose work spanned opposite ends of the continuum. Katie Peichel, then a researcher at the Fred Hutchinson Cancer Research Centre, studied—among many things—highly divergent stickleback species who are reproductively incompatible—all the way at one end of the continuum. Dan Bolnick, then a professor at the University of Texas at Austin, studied—among many things—continuous phenotypic variation within stickleback populations that showed no evidence of reproductive isolation—all the way at the other end of the continuum. With my laboratory somewhere in the middle of this continuum, we had a great time trying to fit everything together into a somewhat coherent whole. I am very glad that Emily found the resulting paper helpful; it certainly was for us.

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