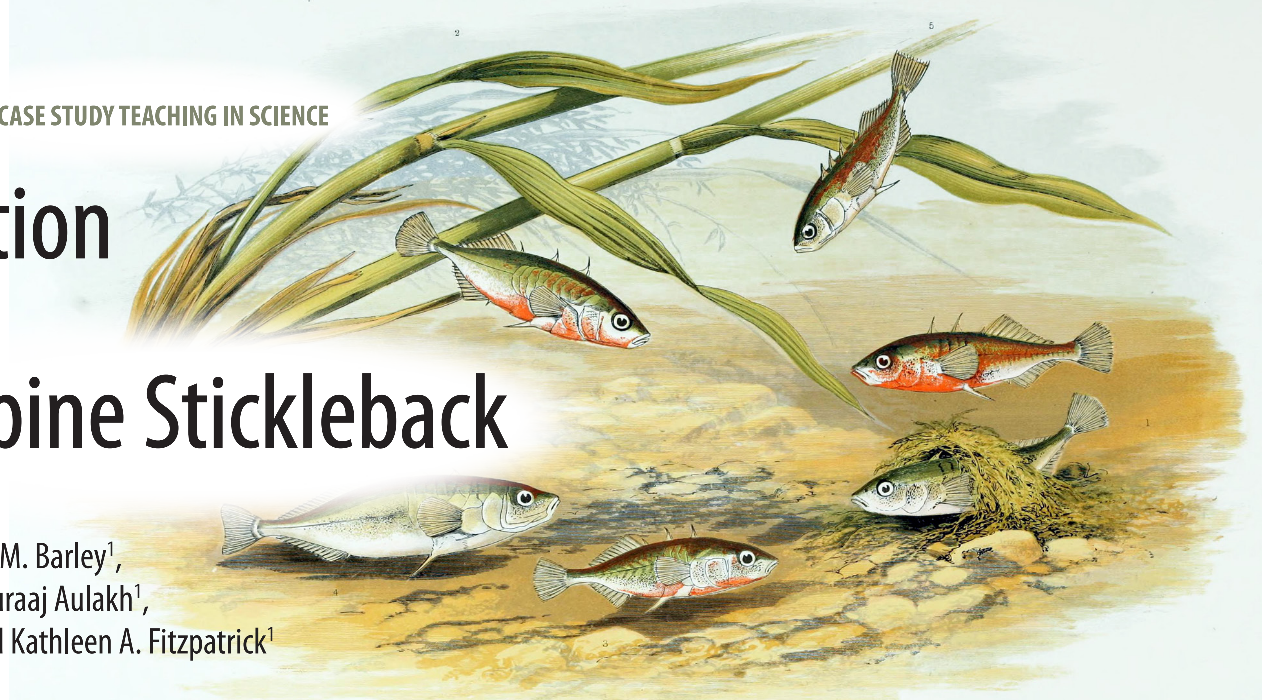
NATIONAL CENTER FOR CASE STUDY TEACHING IN SCIENCE

Speciation *and the* Threespine Stickleback



by
Joan C. Sharp[1], Erin M. Barley[1], Kevin K-W. Lam[1], Suraaj Aulakh[1], Allison Cornell[2], and Kathleen A. Fitzpatrick[1]

Introduction

Watch the following video on allopatric speciation: **<https://youtu.be/TVv7om3WE_M>** (running time: 13:32 min).

This video describes the process of speciation that occurs when a population is split in two by a geographical barrier. After separation, each population accumulates genetic differences through the four mechanisms of genetic divergence (founder effect, genetic drift, mutation, natural selection). If the two populations reunite, there are three possible outcomes: (1) they are a single species, (2) they are separate species, or (3) they are in the process of speciating.

In this case study, we examine a fascinating fish called the threespine stickleback. We focus on Paxton Lake, a lake where two populations of these fish that were once geographically separated came together again. In Part I, we ask *What is the outcome of this reintroduction?*

Part I – Background

Threespine sticklebacks *(Gasterosteus aculeatus)* are minnow-sized fish that live in coastal marine environments throughout Europe, Asia, and North America. Marine threespine sticklebacks are named for the three dorsal spines that help protect them against predators. In addition, they have bony lateral plates to protect their sides and pelvic spines to provide protection on their underside. The dorsal and pelvic spines are held erect by a bony structure called a pelvic girdle. The sides of threespine sticklebacks are well protected with an armor of bony lateral plates. Marine sticklebacks filter-feed on zooplankton, using the long bony gill rakers that line their throats and sieve out small prey from the water that flows into their mouths and over their gills.

In coastal areas, many freshwater lakes and streams are also home to populations of sticklebacks that have become adapted to local freshwater conditions. One such lake is Paxton Lake on Texada Island, British Columbia. Texada is one of the Gulf Islands in the Salish Sea between the British Columbia mainland and Vancouver Island. The origin of the freshwater sticklebacks on Texada Island dates back to glaciation around 13,000 years ago, when the weight of glaciers lowered coastal land relative to sea level and the current Gulf Islands were submerged. As glaciers melted and retreated, the land rebounded and the islands emerged from the ocean, trapping water in lakes that gradually became fresh over time. Throughout the Gulf Islands, freshwater lakes are home to threespine stickleback populations that became trapped and isolated from marine populations as the Gulf Islands formed.

[1] Department of Biological Sciences, Simon Fraser University, Burnaby, BC.
[2] Department of Biological Sciences, Cedar Crest College, Allentown, PA.

But the story gets more interesting; Paxton Lake is home to not one but two different forms of threespine sticklebacks. The evidence supports a double invasion hypothesis. This proposes that after the first marine population of sticklebacks was trapped and became adapted to local conditions in the lake, additional marine sticklebacks made their way upstream from the ocean into the lake. Paxton Lake is now home to two related but distinct populations of sticklebacks, both descended from a marine ancestor.

In Paxton Lake, the two populations of sticklebacks—limnetic and benthics—are named for the areas of the lake in which they live and feed. Limnetic sticklebacks feed on zooplankton in the limnetic zone, the open waters of the lake near the surface and away from shore. Benthic sticklebacks feed on larger invertebrates in the benthic zone, the muddy lake bottom in the shallow water near the edge of the lake.

Limnetic sticklebacks are slim with narrow mouths. Like their marine ancestors, they have a protective armor of dorsal and pelvic spines, pelvic girdle, and many lateral plates. This armor offers protection from predatory cutthroat trout, which feed on sticklebacks in the limnetic zone of the lake. Their throats contain large numbers of long gill rakers, used by limnetic sticklebacks to filter tiny zooplankton out of the water.

Benthic sticklebacks are stocky fish, with deep bodies and wide mouths. In contrast to their marine ancestors, the benthic fish aren't as well protected. Most have only two dorsal spines instead of the usual three. Most lack pelvic spines and a pelvic girdle and have few lateral plates. They have a relatively small number of short gill rakers and do not filter feed. Instead, they feed on bottom dwelling organisms such as worms, clams, and insect larvae in the muddy shallows of the benthic zone. Their main predators in the benthic zone are large insects such as backswimmers and dragonfly larvae, which capture young sticklebacks by seizing their spines.

Figure 1 shows a limnetic male and a benthic male. Limnetic and benthic sticklebacks live, feed, and face predation in different areas of Paxton Lake. However, males of both types build nests, court females, and care for their eggs side-by-side in the benthic zone of the lake. Sticklebacks have long been studied for their interesting mating behaviors. In springtime, male sticklebacks build nests of vegetation glued together by sticky secretions. A mating male develops bright colors and becomes very aggressive, swimming out to defend his nest from all attackers. A researcher studying the sticklebacks described how the little males would swim up and try to nip at her as she waded into their territories!

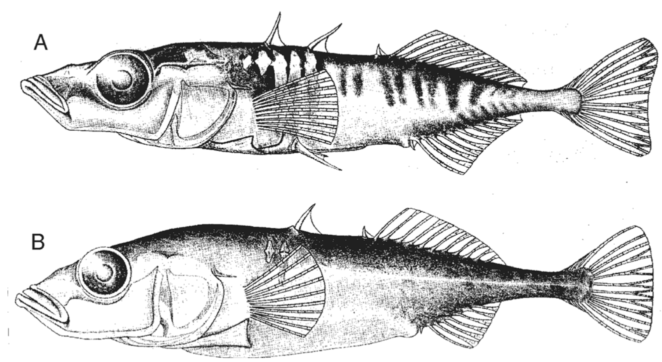


Figure 1. Limnetic male stickleback (top) and benthic male stickleback (bottom). *Image Credit:* Elizabeth Carefoot, Learning and Instructional Development Centre, Simon Fraser University. Used with permission.

When a female stickleback enters a male's territory, he recognizes her by her swollen belly, full of eggs. Instead of attacking, the male courts the female, performing a zigzag dance or nipping at her fins. If the female is receptive, she follows him to his nest. After she enters the nest, the male nudges her to encourage her to spawn. He then enters the nest himself and releases sperm to fertilize the eggs. The male guards the fertilized eggs until they hatch, oxygenating them by fanning the nest with his pectoral fins.

The threespine sticklebacks of Paxton Lake have been studied by researchers at the University of British Columbia (UBC) for over 25 years, first by Dr. Don McPhail and more recently by a research team headed by evolutionary biologist Dr. Dolph Schluter. In this case study, you will design experiments that are similar to those carried out by the UBC researchers and will interpret the data generated from their experiments.

The following video introduces you to Dr. Schluter, the researcher who led much of the research that you will be examining: **<https://youtu.be/FRwqspBKX-I>** (running time: 4:52 min).

Part II – Interaction Between Benthic and Limnetic Sticklebacks

In Part I, you learned about the background and history of Paxton Lake's stickleback fish and specifically about the two distinct populations of sticklebacks that are now in contact. We now ask which of the three outcomes is occurring: (1) benthic and limnetic sticklebacks are one species; (2) benthic and limnetic sticklebacks are separate species; (3) benthic and limnetic sticklebacks are in the process of speciating. Below are data from UBC researchers to help us answer this question.

Survival of Benthic, Limnetic, and Hybrid Sticklebacks

Method: Artificially fertilized eggs from benthics, limnetics, and hybrids were reared in the laboratory.

Results: **Table 1. Survival of fertilized eggs to hatching.**

Form	*Total # of Eggs*	*Survivors / Egg #*	*% Survival*
Benthics	682	662/682	97%
F1 hybrids	659	626/659	95%
Limnetics	599	575/599	96%
F2 hybrids	525	504/525	96%

Source: McPhail, J.D. 1992. Ecology and evolution of sympatric sticklebacks (Gasterosteus): evidence for a species pair in Paxton Lake, Texada Island, British Columbia. *Canadian Journal of Zoology* 70: 361–9.

Questions

1. What can we conclude from the data in Table 1?

2. What is the difference between F1 and F2 crosses, and why are both crosses necessary?

Proportions of Benthic, Limnetic, and Hybrid Stickleback in Paxton Lake

Method: Large numbers of fish were captured from Paxton Lake during the summers of 1969, 1979, and 1986. Table 2 shows the proportions of benthic, limnetic, and hybrid fish captured from the lake each year.

Results: **Table 2. Proportions (and numbers) of benthic, limnetic, and hybrid sticklebacks in summer trap samples.**

Year	*Total*	*Benthics*	*Limnetics*	*Hybrids*
1	1057	0.50 (528)	0.48 (509)	0.019 (20)
2	962	0.50 (479)	0.49 (473)	0.010 (10)
3	994	0.49 (491)	0.49 (489)	0.014 (14)

Source: McPhail, J.D. 1992. Ecology and evolution of sympatric sticklebacks (Gasterosteus): evidence for a species pair in Paxton Lake, Texada Island, British Columbia. *Canadian Journal of Zoology* 70: 361–9.

Question

3. What can we conclude from the data in Table 2?

Morphology of Benthic, Limnetic, and Hybrid Sticklebacks

Table 3. Comparison of anatomical differences between laboratory-reared benthic, limnetic, and F2 hybrid sticklebacks.

Form	*Benthic*	*Limnetic*	*F2 Hybrids*
Average body depth:	10.6 mm	8.8 mm	9.7 mm
Percentage of population with two (vs. three) dorsal spines:	56%	2%	46%
Percentage of population without pelvic girdle:	81%	0.2%	37%
Average number of gill rakers:	18.7	23.8	20.6
Average gill raker length:	0.8 mm	1.5 mm	1.2 mm
Average jaw width:	3.7 mm	2.5 mm	3.2 mm
Average number of lateral plates:	0.7	11	6.9

Source: McPhail, J.D. 1992. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): evidence for a species pair in Paxton Lake, Texada Island, British Columbia. *Canadian Journal of Zoology* 70: 361–9.

Questions

4. What can we conclude from the data in Table 3?

5. Given the data from Tables 1–3, which of the three possible outcomes from renewed contact between isolated populations best describes the interaction between benthic and limnetic sticklebacks? In other words, do they form one species, separate species, or are they in the process of speciating?

Part III – Experimental Data and Summary

In Part II, you saw that although benthic and limnetic fish can interbreed, interbreeding is rare under natural conditions. We now further investigate this process by asking: *If benthic and limnetic sticklebacks are capable of producing viable and fertile hybrids, why are there so few hybrid sticklebacks in Paxton Lake?*

Your task is to propose one (or more) hypotheses, and then design one (or more) sets of observations or experiments that would generate data to help you test your hypotheses. These observations or experiments could involve captive fish in aquaria or wild fish in Paxton Lake. Work in a group to develop your ideas. Then describe your observations or experiments to an instructor, who will provide you with related data from similar research carried out by UBC researchers.

Hypothesis and proposed methods:

Observations/Experiments:

Questions

1. Assume that conditions in Paxton Lake, including the availability of benthos and zooplankton and the number and type of predators in the benthic and limnetic zones, remain unchanged. If you returned to Paxton Lake in a thousand years and collected data about the mating choices of benthic and limnetic sticklebacks and the proportions of benthic, limnetic, and hybrid sticklebacks in the lake, what would you expect to find? Explain your answer.

2. In the 1970s, Enos Lake on Vancouver Island in British Columbia was found to contain populations of benthic and limnetic sticklebacks, similar to those in Paxton Lake. In the late 1990s, non-native crayfish used as bait by people fishing for trout escaped and established a large population in Enos Lake. These crayfish feed in the benthic zone, where they eat aquatic plants, insects, snails, and tadpoles. They have grazed down the benthic vegetation, which used to be lush. The benthic zone is now very silty, with low water clarity, because the crayfish stir up the sandy bottom as they move about and look for prey. Researchers have collected data about the proportions of benthic, limnetic, and hybrid sticklebacks in Enos Lake, following the crayfish invasion. What do you predict the researchers found, and why?