



Intraspecific diversity of threespine stickleback (*Gasterosteus aculeatus*) populations in eastern Canada

Grant E. Haines 

Received: 11 April 2022 / Accepted: 18 October 2022
© The Author(s), under exclusive licence to Springer Nature B.V. 2022

Abstract The threespine stickleback (*Gasterosteus aculeatus*) is a small, mesopredatory fish that is widespread in coastal regions of the northern hemisphere. Although studied extensively as a model organism in evolutionary biology, behavioral ecology, genomics, and numerous related subfields, this research relies heavily on populations from the Pacific coastal regions of North America and Asia, and those of northern Europe. However, based on the morphology of some western Atlantic populations, the different ecological context, and the evolutionary history of the species, not all of the knowledge gained from Pacific and European lineages is likely to be fully transferrable to the populations of North America's East Coast. Nevertheless, work in eastern Canada does suggest high levels of intraspecific phenotypic diversity and local adaptation, though much of this diversity may be under threat from climate change, altered land use patterns, and introduced species. These factors warrant a research program focused on broad sampling of previously identified populations, identifying previously undocumented populations, determining whether there are unique genetic mechanisms underlying the unusual trait combinations present in the region, and exploring novel community interactions. Such a research program would facilitate future

studies in ecology, conservation, and evolution by documenting phenotypic changes and establish baselines for future work. Because the work on nearshore marine threespine stickleback populations is sparse in the western Atlantic, I focus here on freshwater populations—with the exception of a brief discussion of the “white” stickleback populations of Nova Scotia—but this is not to suggest that nearshore marine populations are not phenotypically diverse.

Keywords Adaptive radiation · Phenotypic diversity · Intraspecific variation · Bottleneck · Parallel evolution · Postglacial radiation

Introduction

Although threespine stickleback (*Gasterosteus aculeatus*) have been studied extensively in research programs focused on a wide variety of biological disciplines, this research has generally been focused on the populations in the Eastern Atlantic and Pacific. Despite some conspicuous patterns of morphological diversity that differ from those in the rest of the world, the threespine stickleback populations of the Western Atlantic basin are relatively understudied. Recent work has clarified some aspects of this clade's evolutionary history, which have presented opportunities to address new questions about the patterns and processes of evolution.

G. E. Haines (✉)
Redpath Museum and Department of Biology, McGill
University, Montréal, Québec, Canada
e-mail: grant.haines@mail.mcgill.ca

At the same time, multiple cases have been documented over the past two decades of local extinction or dramatic adaptive change of evolutionarily distinctive stickleback populations in response to habitat modification or introduced species. Although threespine stickleback are very common as a species, the loss of distinctive locally adapted populations, particularly in the context of broader environmental changes across aquatic habitats, could compromise our ability to understand the evolutionary and ecological implications of Western Atlantic radiation's recent founding and rapid radiation.

Here, I present a review of threespine stickleback diversity within the Western Atlantic clade, focusing in particular on eastern Canada. I first provide an overview of the evolutionary history of this portion of the species' range. This is followed by descriptions of unusual or unexpected phenotypes or patterns of phenotypic variation that are present in the Western Atlantic basin, and descriptions of threats to the intraspecific diversity of threespine sticklebacks in the region. Finally, I suggest directions for future research meant to fill gaps in the literature, assess the extent of contemporary evolutionary change within populations, determine the genetic bases of phenotypes that are inconsistent with expectations from other parts of the world, and better understand the relationships between sticklebacks and their environments in eastern North America.

Evolutionary history and population establishment

Anatomically modern threespine stickleback have lived in the Pacific for at least 13 million years (Bell et al. 2009), and the split between the modern Atlantic and Pacific lineages occurred between 29.5 and 226.6 thousand years ago (Fang et al. 2020b). However, the populations of eastern North America are considerably more recently derived. Molecular data suggest that the divergence of the western Atlantic lineage from lineages in the Barents and Norwegian Seas occurred between 7.1 and 17.1 kya, with divergence of Canadian populations from one another between 4.5 and 12.4 kya (but see appendix; Fang et al. 2018). When fossil data and the deglaciation of the St. Lawrence valley are considered, this window of possible establishment times

is narrowed to a span of approximately 2 thousand years between 10 and 12 kya for southern Ontario and Quebec populations (Dyke 2004; McAllister et al. 1981). In agreement with this estimate, two described fossilized stickleback dated to approximately 10 kya have been found in the Green's Creek Formation just south of the Ottawa River (Dawson 1893; McAllister et al. 1981). At that point in time, the region would have been part of the Champlain Sea, facilitating inland migration from the Atlantic, and within a few hundred years, these populations would become isolated in freshwater by isostatic uplift and draining of the Champlain Sea (McAllister et al. 1981). This approximate timeline is also supported by subfossil remains of large freshwater populations in western Greenland aged to at least 9 kya (Bennike 1997), and molecular dating of divergence times between lake populations in the same region to up to 9.9 kya (Liu et al. 2018). The existence of populations in Greenland during this period indicates that threespine stickleback were present along their hypothesized migration route from Europe in the approximate period of time that they arrived in what is now Canada.

In the roughly 10–12.4 thousand years since becoming established in eastern Canada, threespine sticklebacks have spread across the coastal regions of the Atlantic and Hudson Bay drainages. Populations can be found as far south along the Atlantic coast as the Chesapeake Bay in the USA, north to Baffin Island, west to the northwestern edge of Hudson Bay and inland to Nueltin Lake in Nunavut, and up the Great Lakes to St. Lawrence River Basin to Niagara Falls or Lake Ontario (Lamothe et al. 2021; Lee et al. 1980; McKillop and McKillop 1997; Oliver 1964; Scott and Crossman 1973). Threespine stickleback are typically anadromous—spawning in freshwater and then migrating out to sea—and have established numerous freshwater populations across their eastern North American range. Since the early 1980s, they have also been introduced and become established, possibly through shipping routes or as baitfish, in all the Great Lakes upstream of their historic range (Stedman and Bowen II 1985; U.S. Geological Survey 2021). In the 1950s and 1960s, they were also occasionally recorded in Cayuga Lake in central New York (Carlson et al. 2016). It is unknown whether this population was native and naturally

migrated inland from Lake Ontario by way of the Oswego River system, or whether its migration inland was facilitated by the construction of the Erie Canal network.

The populations in the Hudson Bay region are believed to have become established more recently than those of waterbodies draining into the St. Lawrence. Prior to 8.5 kya, passage into Hudson Bay by stickleback would have been prevented by the Laurentide Ice Sheet, which had melted sufficiently by 8 kya to open the Hudson Strait, south of Baffin Island, but the shores of the bay were not accessible until 7.6 kya (Dyke 2004; Schroeder 2012). The westernmost population in the Eastern North American region—that of Nueltin Lake, which spans the Manitoba-Nunavut border—is now approximately 100 m above sea level, and believed to have been isolated from anadromous populations nearly 7 ky by isostatic rebound (Dyke 2004; Schroeder 2012).

Two brief caveats should accompany these dates of divergence from other clades of threespine stickleback and establishment in the eastern half of North America. The first is that Fang et al.'s (2018) specimens from the region only included five individuals, and none from north of the 48th parallel or Newfoundland. This excludes almost all known North American populations including individuals with low lateral plate morphs. This leaves open the possibility that some of the variation observed further north, and particularly in the Arctic Basin, is a consequence of post-Pleistocene migration from the Pacific made possible by the re-opening of the Bering Strait, as has occurred in other species (Laakkonen et al. 2021). The second caveat is that, while some of the specimens included in Fang et al. (2018) are from parts of Nova Scotia where populations of the highly divergent white morph of threespine stickleback is common, all the specimens included appear to be from the common morph. To establish a more complete history of colonization patterns, higher resolution sampling of populations is necessary. In spite of this uncertainty, it is clear that most threespine stickleback populations have been established on the eastern half of North America for much less time than in Europe or the Pacific. Nevertheless, freshwater populations in this region have extensively, and relatively rapidly, diversified in phenotype.

Unusual populations and phenotypes in Eastern North America

There are several phenotypes that differentiate the better-studied freshwater populations of stickleback in the Pacific and Europe from those of Eastern North America. The most prominent and widespread of these differences is the unusually high frequency of completely plated individuals in freshwater populations of Eastern North America (Figs. 1, 2, and 3). There is also, however, a great deal of diversity between populations that is expressed as variation in color, pelvic reduction, body size, behavior, and ecology.

I. Plate morphs

Threespine stickleback have lateral rows of bony defensive plates beginning just behind the head and proceeding to the end of the caudal peduncle, where the final 5–8 plates are tightly fitted together in a keel (Hagen and Gilbertson 1973). The lateral plates appear in three main morphs, each with some within-morph variation (Fig. 1): the “complete” (C) plate morph includes the keel and an unbroken row of jointed plates continuing along the entire torso;

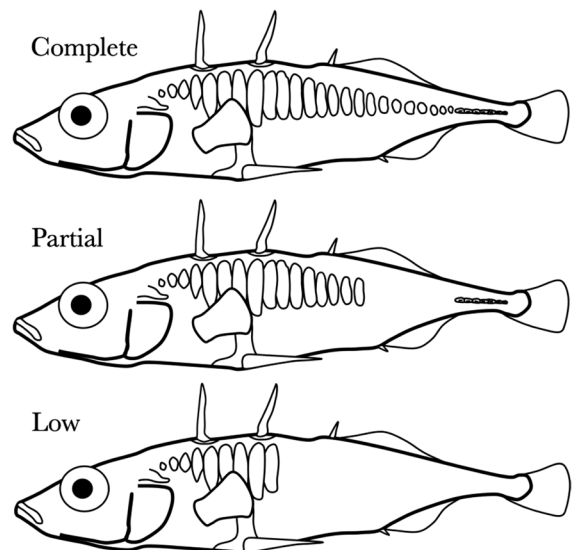


Fig. 1 Threespine sticklebacks with complete (C), partial (P), and low (L) plate morphs. Note the series of small, closely associated plates of the caudal keel in the complete and partial morphs

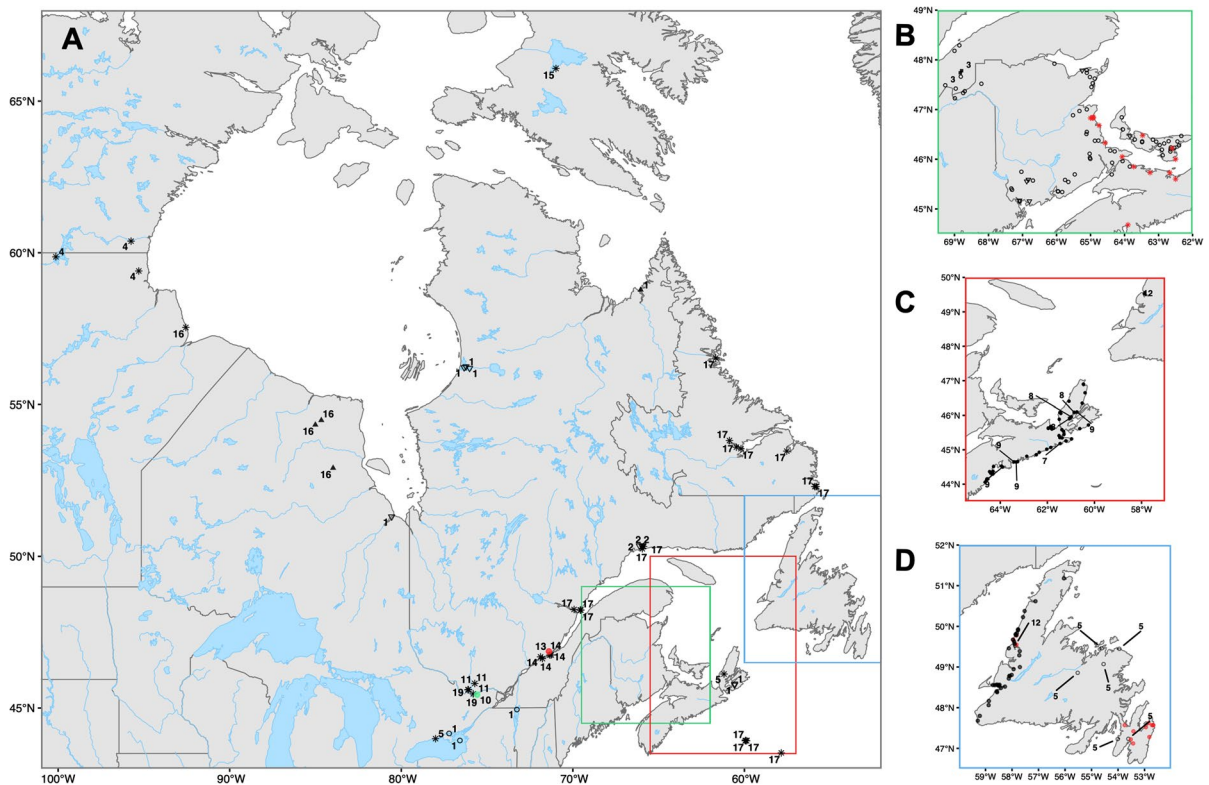


Fig. 2 Some documented populations of threespine stickleback in eastern Canada. Most populations shown are from published works, with the exceptions of two iNaturalist observations (refs. 12 and 13). Many museum specimens that have not been included in published works are known, but are not indicated here due to lack of phenotypic data, and most brackish or marine populations are excluded unless morphologically unusual, or have associated parasite community data (ref. 17). Panels **A** and **B** show freshwater populations, some brackish populations in the Arctic Basin, and a small number of populations in the coastal areas of PEI, NB, and NL that may be brackish based on location, but for which not enough site information was provided to be certain. The green point in panel **A** indicates two fossil specimens from approximately 10 kya, and the red point indicates the barred color morph identified by O. Morissette, respectively. Panel **C** shows only populations of the white color morph of sticklebacks, including an observation of a possible white morph in Newfoundland. All sites in panel **C** are marine or brackish. Panel **D** shows specimens from Newfoundland separately because of the scale of the map. Defensive trait morphs are indicated as follows in panels **A** and **B**: open circle—*C* plate morph most common; open triangle—*P* plate morph most common; closed triangle—*L* plate morph most common; square—majority *P* plate morph and reduced pelvis; star—plate morphs not determinable from information provided or *n* < 20. For the three low plate morph populations in northern Ontario, the most common plate morph was based on mean plate counts for the populations. References are indicated by numeric labels as follows: 1) Hagen and Moodie

(1982) *Can J. Zool.* 60:1032–1042; 2) Coad and Power (1974) *J. Fish. Res. Board Can.* 31:1155–1157; 3) Edge and Coad (1983) *Can. Field-Nat.* 97:334–336; 4) McKillop & McKillop (1997) *Can. Field-Nat.* 111:662–663; 5) Garside & Hamor (1973) *Can. J. Zool.* 51:547–551; 6) Blouin and Hagen (1990) *Biol. J. Lin. Soc.* 39:195–217; 7) Jamieson et al. (1992a) *Can. J. Zool.* 70:956–962; 8) Jamieson et al. (1992b) *Can. J. Zool.* 70:1057–1063; 9) Haley et al. (2019) *Ecol.Evol Res.* 20:145–166; 10) McAllister et al. (1981) *Can. J. Earth Sci.* 18:1356–1364. & Dawson (1893) *The Canadian ice age*; 11) McAllister and Coad (1974) *Fishes of Canada's National Capital Region*; 12) Walsh (2021) *iNaturalist. Observation* 90,757,153; 13) Morissette (2021) *iNaturalist. Observation* 100,646,323; 14) McCairns and Bernatchez (2008) *Mol. Ecol.* 17:3901–3916; 15) Oliver (1964) *Arctic.* 17(2):69–83; 16) Schroeder (2012) *MS Thesis, Univ. of Manitoba*; 17) Poulin et al. (2011) *Ecography* 34:540–551; 18) Scott et al. (2022a) *BioArxiv*; 19) Rubec (1975) *Can. Field-Nat.* 89(4):389–399. All black unlabeled points in panel **B** are from reference 1, and red unlabeled points are from reference 6. The sites of some populations are estimates based on place names due to absence of geographic coordinates or sufficiently detailed maps. To reduce clutter, rivers or streams with multiple sites in their respective original publications are reduced to a single point here. In panel **D**, red points indicate sites in ref. 17, and have documented parasite communities. Solid points were all sampled in a survey conducted for reference 18

the “low” (*L*) plate morph has no keel and typically an average of ~7 plates near the pelvic girdle; the “partial” (*P*) plate morph has a keel, but then a gap before the rest of the plates, which are generally more numerous than in the *L* morph (Hagen and Gilbertson 1972).

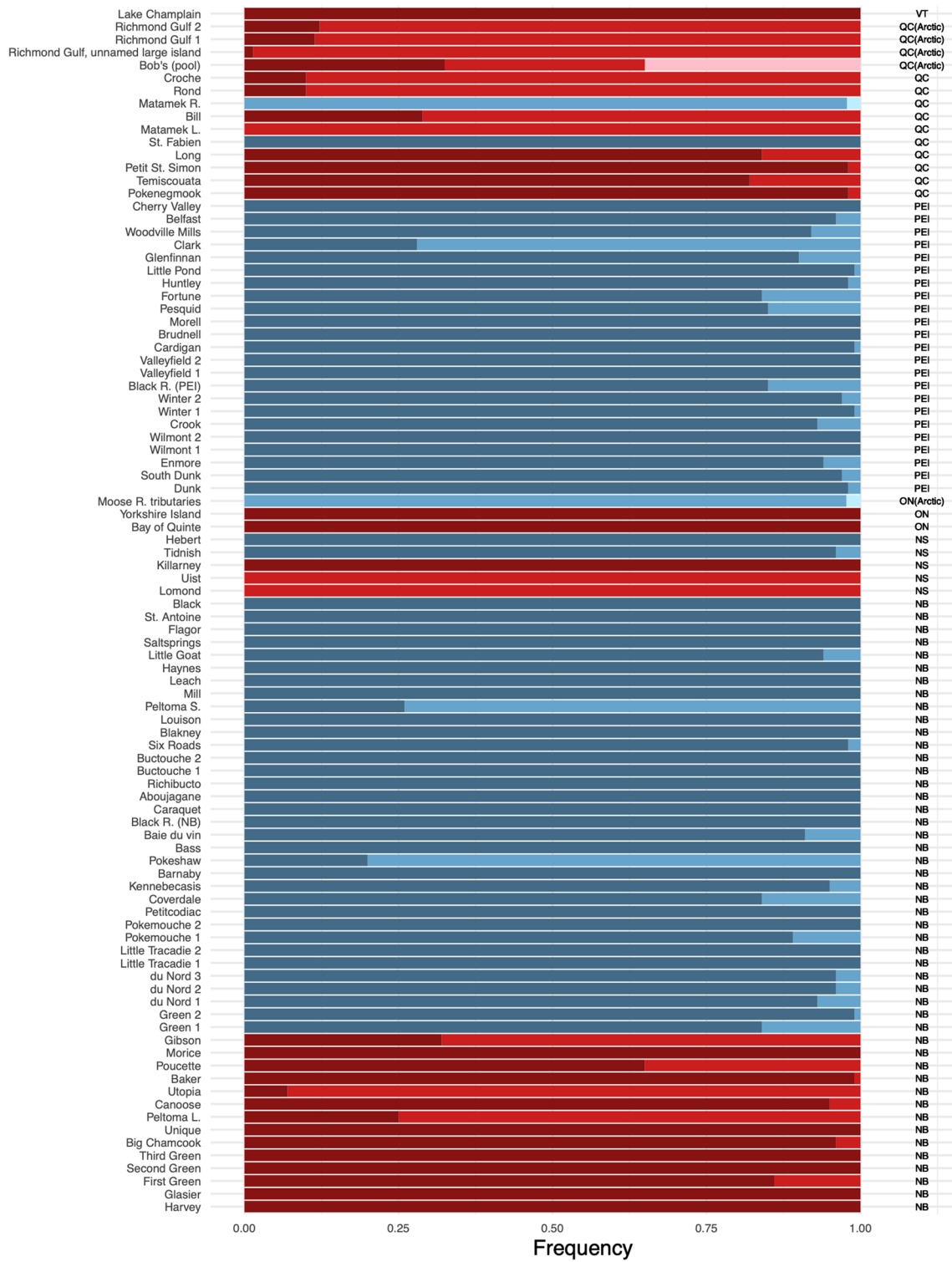
Although freshwater *C* morph populations do occur on occasion, in most parts of the world, a well-documented and widespread pattern of parallel evolution occurs when populations with marine ancestors become isolated in freshwater, where the *C* morph, which is nearly monomorphic in the ocean, is selected against and mostly replaced by *L* morph (Barrett et al. 2008). This shift has occurred remarkably quickly in numerous instances, even over the course of one or a few decades (Bell et al. 2004; Gelmond et al. 2009; Klepaker 1993; Lescaak et al. 2015). The adaptation of low-platedness in freshwater habitats has made high-frequency *C* morph freshwater populations a relative rarity globally (Hagen and Gilbertson 1972; Klepaker 1995). In eastern Canada, however, such populations are remarkably common.

In an extensive survey conducted by Hagen and Moodie (1982), the typical pattern of plate morph frequencies in freshwater was completely inverted. This work focused on Prince Edward Island, New Brunswick, and the Gaspésie and Bas-Saint-Laurent regions of Québec, but also included sites in northern Nova Scotia, two on Lake Ontario, and one on the Vermont side of Lake Champlain. They found not a single freshwater population in which the majority of individuals exhibited the *L* morph, but in lakes alone, they identified 19 populations with a *C* morph majority (Fig. 2). There are also numerous freshwater streams and rivers, and brackish habitats on both the St. Lawrence and Bay of Fundy sides of QC and NB, respectively, where high *C* morph frequencies are maintained, although it is more difficult to determine whether the freshwater stream and river localities are isolated from anadromous populations (Delbeek and Williams 1987; Hagen and Moodie 1982). Hagen and Moodie (1982), however, argue that freshwater resident and anadromous *C* morph populations can be differentiated by the size and robustness of the lateral plates, which is congruent with my own observations, but difficult to establish as general rule. It may also be possible in future studies to use parasite communities (Bell et al. 2016; Poulin et al. 2011) or stable isotope

data (Jones et al. 2013) to determine whether it likely that these populations are anadromous.

The pattern of complete platedness in Atlantic Canada freshwater populations is particularly remarkable because the extant lake populations of western Greenland—the probable sister lineage to the eastern N. American threespine sticklebacks—exhibits the same pattern of *L* morph predominance seen in most of the rest of the world (Liu et al. 2018). Hagen and Moodie (1982) proposed that *C* plate morphs may be favored by the extreme winters in the northwest Atlantic, but the data from Greenland are a compelling case to the contrary (Liu et al. 2018). This East Coast deviation from the typical patterns of plate morph parallelism in fresh water was also observed by McCairns and Bernatchez (2012). However, their study sites were confined to the St. Lawrence estuary and its tributaries, so their hypotheses for the maintenance of *C* monomorphism assumed this trend was specific to the St. Lawrence watershed, and not as widespread as others have demonstrated (McCairns and Bernatchez 2012). Parallel adaptation in freshwater habitats—including reduction of plate counts—is predicted to be constrained in the western Atlantic by founder effects that have resulted in less standing genetic variation at adaptive loci (Fang et al. 2020a).

Another, even more unusual trend in plate frequencies among western Atlantic threespine stickleback populations is the number of populations, including several in the Arctic drainage basin identified from museum collections, in which the *P* morph is the most common, or even only, plate morph present (Figs. 2 and 3; Coad and Power 1974; Edge and Coad 1983; Hagen and Moodie 1982). This is remarkable because the genetic basis of most variation between the three major plate morphs is a single gene, *Eda*, which generally produces *C*- or *L*-plated individuals when homozygous for their respective alleles, but produces partially plated heterozygotes (Colosimo et al. 2005; Colosimo et al. 2004). The low-plated allele on North America’s East Coast (based on fish from a polymorphic population in Jamaica Pond, Massachusetts, but see the issues with this population below) is descended from the one that appears on its West Coast (Colosimo et al. 2005), but under this single-locus model of inheritance and in the absence of implausibly strong selection, no more than 50% of individuals in any population should be partially plated, let alone 100%. Hagen and Moodie (1982) did



◀ **Fig. 3** Plate morph frequencies in populations with $n > 20$ reported by Hagen and Moodie (1982), Edge and Coad (1983), and Coad and Power (1974) for freshwater lake (red scale) and river/stream (blue scale) populations. Lake and river populations are further partitioned as to plate morph with lake-L, lake-P, and lake-C referring to lake low, lake partial, and lake complete plate morphs, respectively. Similarly, river low, river partial, and river complete plate morphs are designated river-L, river-P, and river-C, respectively. Region or province of the site is noted along the right side of the figure, including whether the site is in the Arctic basin. All included populations are from freshwater locations, with the exception of the Richmond Gulf populations, which are from brackish water sites. This body of water is now known as Lake Tasiujaq (Commission de toponymie 2016), and sites are only referred to as “Richmond Gulf” to maintain clarity with respect to the source publication. Although many of these sites are inaccessible to migration from the ocean, it is unfortunately not possible to determine if some populations are or could be anadromous with the information provided in the source publications. Note that Lac Croche and Rond morph frequencies were pooled together when initially reported, and frequencies represented in the figure only include the Edge and Coad (1983) data, not data from any specimens that have been collected subsequently

reference six populations on the West Coast that have high frequencies of partial plate morphs. But these lakes have open connections to the ocean (Hagen and Gilbertson 1972; Kynard and Curry 1976; Moodie and Reimchen 1976), meaning they are likely mixed resident-anadromous populations in which the anadromous adults were unrepresented due to the timing or location of sampling (Ishikawa and Kitano 2020). Some of the East Coast high-frequency *P* populations are open to migration permanently or possibly seasonally, but those of QC and NS appear isolated from anadromous populations by the absence of passable outlet streams to marine or estuarine habitats. A potential genetic locus for further investigation into the basis of plate morphs is the *Edar*, which encodes the *Eda* receptor. One allele at *Edar* is associated with the production of a *C* phenotype (instead of the usual *P* phenotype) in *Eda* heterozygotes (Laurentino et al. 2022), which would not explain the absence of the *L* morph in most of eastern North America, but does suggest that genes in the *Eda* pathway other than *Eda* itself may play important roles in plate determination in this region.

The *L* plate morph, the most globally common plate morph for stickleback in freshwater, appears to be nearly absent in eastern North American populations south of Newfoundland, where it is present at

least on the island’s west coast (Scott et al. 2022a), or further upstream on the St. Lawrence Basin than the Matamek River, near Sept-Iles, QC, where a single low-plated individual has been collected (Coad and Power 1974). The apparent exception to this tendency is a population with all three plate morphs in Jamaica Pond in Olmstead Park near Boston, Massachusetts (Colosimo et al. 2005), which is the only known exclusively freshwater population in that state (Hartel et al. 2002; NHESP). The Jamaica Pond population is believed to be the southernmost exclusively freshwater population on the East Coast, although it has been isolated from the Charles River estuary only since the late nineteenth century (Hartel et al. 2002; NHESP). It is also in a portion of the park that was originally intended to be an exhibit of marine species, and it is possible that the population was introduced (Scudder 1893; U.S. Geological Survey 2021). Although there are also numerous landlocked threespine stickleback populations in Maine, most published records of these populations are from multi-species surveys, and rarely indicate plate morphs (Bowes et al. 1999; Fuller and Cooper 1946; Maine IF&W 2022). The geographic distribution of plate morphs in Eastern Canada suggests either distinct Northern and Southern lineages, ongoing gene flow from Greenland to the Canadian Arctic and Newfoundland and Labrador, or the secondary trans-Arctic migration from the Pacific during the Holocene that I have proposed for stickleback in the previous section. None of these possible histories would explain the origin of the *L* plate morph in Jamaica Pond, however.

II. Pelvic complex

In threespine sticklebacks, the pelvic complex includes the defensive spines formed by fused pelvic fin rays which are supported by an external pelvic girdle. This structure increases survival in interactions with predatory fishes (Reimchen 1991). Reduction of the pelvic complex does occur rarely in some freshwater populations, beginning with loss of the pelvic spines, and occasionally proceeding to the loss of the entire pelvic girdle that supports them (Bell 1987). This phenotype is regulated by a genetic mechanism that is particularly prone to mutation (Chan et al. 2010; Xie et al. 2019), making independent *de novo* mutations in freshwater more likely for pelvic reduction than

the reciprocal transportation of *L* lateral plate morph alleles between the ocean and freshwater (Roberts Kingman et al. 2021; Schluter and Conte 2009).

However, even in the absence of native predators, reduction of the pelvis occurs only in populations with low calcium concentrations (Bell et al. 1993; but see also Reimchen et al. 2013). At least four populations—three in Parc National du Lac-Témiscouata (in Lacs Rond, Croche, and Sutherland) all either partially or completely plated (Edge and Coad 1983), and one (Narrows Pond) in western Newfoundland that is predominantly low-plated (Scott et al. 2022b)—have unusual reduction of the pelvic complex in the presence of high calcium availability. The geology of Parc National du Lac-Témiscouata is karstic (Ministère du Développement durable de l'Environnement et des Parcs 2008), and in a survey in June 2022, I found that the pH values at two of these lakes are 7.74 (Croche) and 8.15 (Rond), with conductivities of 107.4 and 92.2 $\mu\text{S}/\text{cm}$, respectively (ProQuatro Multiparameter Meter, YSI). Additionally, these appear to be the only documented populations of *C*- or *P*-plated, reduced pelvis populations in the wild (but see Cresko et al. 2004 for production of such individuals from lab crosses). Thus, the patterns of selection and genetic constraints resulting in the maintenance of this combination of phenotypes in lacs Rond, Croche, and Sutherland remain obscure and require further investigation. The Narrows Pond site, too, sits atop a narrow band of calcium-rich geology (DeGrace 1974), and additionally contains brook trout (*Salvelinus fontinalis*), a predator of stickleback (Scott et al. 2022b), making the reduction of this anti-predator trait all the more unusual.

III. Color, size, and behavior

Finally, there are several populations with unusual non-armor related morphological phenotypes. These include coastal marine populations of small-bodied “white” stickleback on the Atlantic coast of NS and Bras d'Or Lake, NS, which have iridescent white nuptial coloration in males, reduced parental care, and reversed sexual dimorphism of brain size compared to “common” threespine stickleback (Blouw and Hagen 1990; Haley et al. 2019; Jamieson et al. 1992a, 1992b; Samuk et al. 2014). These populations may mate assortatively, reinforcing isolation from the common threespine stickleback populations (but see

Corney 2021 for a contrary result), then lay eggs on filamentous algae, and disperse the embryos, allowing them to sink into the algae mats (Blouw 1996; Blouw and Hagen 1990; Haley et al. 2019). In spite of some gene flow between sympatric common and white stickleback populations, the white stickleback do represent a distinct lineage of threespine stickleback (Samuk 2016), but the exact timing and causes of their divergence from common threespine stickleback remains obscure.

A male stickleback that is very similar in appearance to the known white stickleback populations has been recorded on iNaturalist in Neddy Harbour, NF (Fig. 4B; Walsh 2021), and further investigation in this location may be worthwhile to determine if it is part of a population that is genetically and ecologically similar to the NS white sticklebacks. The Neddy

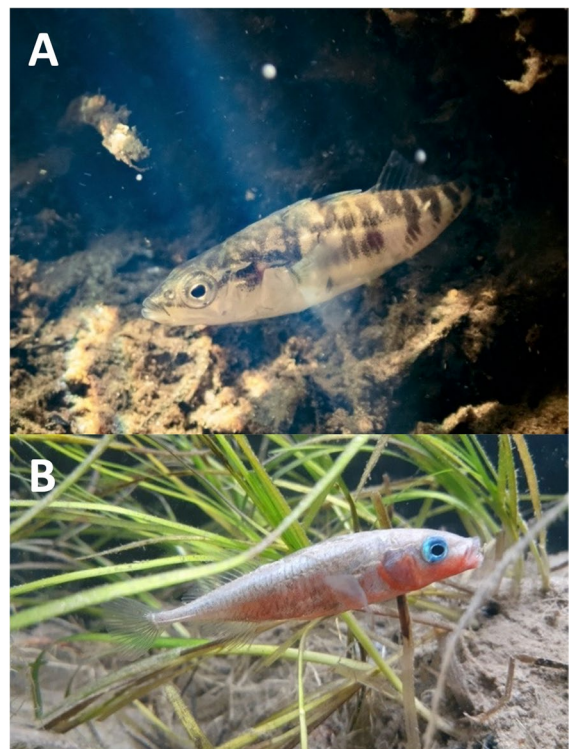


Fig. 4 Coloration in understudied populations of threespine stickleback. Panel **A** shows an individual from a population near Québec city with pale coloration and prominent barred pattern. Image ©Olivier Morissette, used under CC-BY-NC license. Panel **B** shows a male individual from Bonne Bay, Newfoundland, with similar coloration to the Nova Scotia white stickleback populations. Image ©Tim Walsh, used with permission

Harbour individual was collected in Bonne Bay, in a habitat with abundant filamentous algae, similar to the NS populations, and was being kept in captivity when it underwent its most dramatic color change (D. McIlroy, personal communication). The captive status and timing of color change have resulted in differing opinions as to whether this individual is an example of the white stickleback morph (R. J. Scott and A. Dalziel, personal communications).

Dr. Olivier Morissette of Québec's Ministère des Forêts, de la Faune et des Parcs has also observed a population in the Rivière Nelson, a tributary of Québec's Rivière St.-Charles, which has very pale coloration with bold vertical bars or alternating blotches spanning the lateral line (Fig. 4A; Morissette 2021). Freshwater populations have been documented with similar barring on the Pacific Coast of North America, and at least three genetic regions associated with this pattern in juveniles have been identified (Greenwood et al. 2011), but it is unknown whether the coloration of the population in Rivière Nelson shares this genetic basis. Although such color patterns are sometimes reduced in adults (Kim and Velando 2015), the Rivière Nelson individuals observed are adults that have maintained prominent markings. Barring patterns in stickleback caused by melanophore concentration are associated with anti-predator behavior (Kim and Velando 2015), and are favored in selection experiments with cutthroat trout (*Oncorhynchus clarki*) predators, especially in waters with low turbidity (Gygax et al. 2018). Notably, the Rivière Nelson stickleback are sympatric with brook trout, an East Coast native salmonid (Morissette, personal communication). Whether barring patterns also serve an antipredatory function against East Coast native salmonid potential predators arctic char, lake trout, brook trout, Atlantic salmon, whitefish, and grayling (*Salvelinus alpinus*, *S. namaycush*, *S. fontinalis*, *Salmo salar*, *Coregonus* spp. and *Prosopium cylindrafomis*, and *Thymallus arcticus*, respectively) is an of avenue eco-evo research with potential implications for the impacts of stocking non-locally adapted salmonid strains on the fish community, and environmental changes that affect ambient light conditions and water visibility.

The Lac-Témiscouata population, in addition to having high C plate morph frequency, has very large fish (adult mean = 67.05 ± 5.87 mm; LaCasse and Aubin-Horth 2012), not far from the 75-mm threshold

used to designate the Drizzle and Mayer Lake sticklebacks of Haida Gwaii as "Giant" for purpose of SARA protection (COSEWIC 2013). The Lac-Témiscouata population is also strikingly similar in body shape to the Mayer Lake population (Spoljaric and Reimchen 2007), and has a superficially similar habitat (a large lake with several likely predatory species). Near Lac-Témiscouata, the karstic geology has also resulted in some water-filled caverns, and there are second-hand reports that these may contain small populations of stickleback with some accompanying cave adaptations, although research is needed to confirm their phenotypic differentiation from nearby populations (M. Grégoire, personal communication).

Threats to intraspecific diversity and responses to environmental change

Intraspecific differences in phenotype between populations have environmental effects that are often as large as the impacts of different species (Des Roches et al. 2018). Morphological and consequent functional differences between populations shape communities and influence ecological function (Mimura et al. 2017), and in stickleback, trait shifts have been shown to influence the composition of their invertebrate prey communities (Schmid et al. 2019). Intraspecific diversity in such a widespread species as threespine stickleback should therefore be an important consideration for conservation practitioners and other environmental scientists whose work involves measuring, forecasting, and mitigating changes in ecological functions. The threats facing individual populations of threespine stickleback (and other native species) in eastern Canada are similar to those on the West Coast, but potentially more challenging for conservation practitioners because so much less is known about the ecology and evolution of East Coast populations. Environmental change and invasive species have the potential to be particularly destructive to both locally adapted specialist phenotypes, and whole populations that are unable to adapt to their presence.

On several occasions, threespine stickleback populations have been driven to extinction by the introduction of invasive species, including populations of particular ecological and scientific interest. The most notable of these extinctions are two of the benthic-limnetic "species" pairs of British Columbia which

occupied distinct planktivorous and benthivorous ecological niches and rarely hybridized. Both populations in one of these species pairs were driven to extinction in Hadley Lake, BC, by the introduced brown bullhead catfish (*Ameiurus nebulosus*), now the only species in the lake (Hatfield 2001). Most famously, the Enos Lake, BC species pair went extinct as separate populations and merged into a single, generalist hybrid population following the introduction of the signal crayfish (*Pascifasticus lenisculus*; Taylor et al. 2006). Although similar benthic-limnetic pairs have not been documented in the western Atlantic clade, common marine and white stickleback populations do occur in sympatry and are particularly susceptible to ecological disruptions (Haley et al. 2019), and introductions may threaten the survival of other populations altogether. Local extinctions driven by introduced species pose a particular threat to populations with reduced antipredator armor. In 2002, the stickleback of Prator Lake, Alaska, a relatively rare reduced pelvis population was driven to extinction by the invasive—and voracious—northern pike (*Esox lucius*; Patankar et al. 2006). This extinction was also a near miss for the similarly weakly armored stickleback population of nearby Bear Paw Lake, which happens to be the source population of the first threespine stickleback to have its whole genome sequenced (Jones et al. 2012; Patankar et al. 2006).

The preceding are only some of the most remarkable examples of local extinctions resulting from the establishment of invasive species, but many more have resulted either from introduced species or efforts to limit their spread (e.g., rotenone treatment; Dunker et al. 2020; Haught and von Hippel 2011; Massengill et al. 2020). Within Québec, pike introductions have caused the extinction of a small, isolated population of threespine stickleback in Lac Ramsay in Gatineau Park, along with the lake's populations of Allegheny pearl dace (*Margariscus margarita*) and brook stickleback (*Culea inconstans*; Vachon et al. 2005). In fact, throughout Gatineau Park, small lakes with introduced piscivores have fewer smaller-bodied fish species, and five of the park's small-bodied species—including threespine and brook stickleback—are now only found where there are no introduced predators (Chapleau et al. 1997). Two of these introduced species were the largemouth and smallmouth bass (*Micropterus salmoides* and *M. dolomieu*, respectively), and other centrarchids have also been widely

introduced and are likely to be important predators of stickleback. Smallmouth bass (*Micropterus dolomieu*) have already been associated with changes in defensive traits in British Columbia (Kienzle 2018), and in Nova Scotian lakes, introduced smallmouth bass and chain pickerel (*Esox niger*) populations appear to be negatively associated with threespine stickleback presence (A. Dalziel, personal communication).

In addition to local extinctions, there is some evidence that introduced and invasive species are inducing adaptive changes in some populations in the eastern Canada. In Lacs Rond and Croche, the sites of the reduced-pelvis populations in Parc National du Lac-Témiscouata, brook trout (*S. fontinalis*) were introduced to both lakes for the purposes of sportfishing and have been present since at least 1973 (Edge and Coad 1983). Creek chub (*Semilotus atromaculatus*) and northern redbelly dace (*Chrosomus eos*)—presumably both introduced as live bait—are now also present (personal obs.) in addition to the native fathead minnow (*Pimephales promelas*; Edge and Coad 1983). Since the initial assessment of these populations' morphologies from samples taken in 1980–1981, the frequency of pelvic reduction in Lac Rond had declined from 100% ($n=82$), to 61% ($n=11$) in 2010 (Edge and Coad 1983; LaCasse and Aubin-Horth 2012), and 57% ($n=7$) in 2022 (Haines, this study). The decline of pelvic reduction in Lac Croche has been even more extensive, dropping from 97% ($n=38$) in 1980–1981 (Edge and Coad 1983) to 7% ($n=41$) in 2022 (Haines, this study). This decline in frequency of reduced pelvises is likely a response to predation in a previously predator-free habitat.

Beyond their effects on particular native populations, invasive species cause community biodiversity changes that could influence species interactions and ecological function in the long term. Further south in the Appalachians, invasive species have caused declines in endemic species and homogenization of community composition between habitats (Sleezer et al. 2021). This could pose particular problems for sticklebacks and salmonids, most of which have a propensity for extreme local adaptation (Arostegui and Quinn 2019; Chaverie et al. 2016; Dynes et al. 1999; Muir et al. 2016)—including a series of sympatric dwarf-normal population pairs of lake whitefish occupying the lakes of the St. John River system (Landry et al. 2007). The zebra and quagga mussels (*Dreissena polymorpha* and *D. rostriformis*) that have invaded

many habitats in and around the Great Lakes have unknown effects on threespine stickleback. However, following their introduction to Lake Huron, the mussels have reduced zooplankton abundance, causing numerous population declines of forage fish species, including the threespine stickleback's ecologically similar confamilial species, the ninespine stickleback (*Pungitius pungitius*; Roseman and Riley 2009).

Environmental change, too, can modulate the ecological and evolutionary relationships between sticklebacks and their environments. Des Roches et al. (2019) showed that in systems where precipitation and flow rates are strongly linked, warmer, drier climate led to increases in frequencies of *L* plate morphs. In an abrupt change in the opposite direction, the stickleback population of Lake Washington, Washington experienced a rapid increase in body size and frequency of *C* plate morphs, likely because increased water clarity resulting from the opening of a canal left stickleback more vulnerable to salmonid predation (Kitano et al. 2008). Use of surrounding lands has also caused local extinctions by altering habitat morphology (Wootton 2010), or caused adaptive morphological responses to loss of connections with marine habitats (Kristjánsson et al. 2002, 2005). In cases of adaptive responses to environmental change like these, it is important to consider that morphological traits are correlated with behavior (De Winter et al. 2016; LaCasse and Aubin-Horth 2012) and function (Bergstrom 2002). Eutrophication of lakes in Gatineau Park between the mid-nineteenth and mid-twentieth centuries, likely the consequence of a combination of deforestation, excess nutrients leaching from pit latrines, and smallmouth bass introductions, resulted in extirpation of salmonid species from some lakes (Rubec 1975), potentially initiating lake-wide trophic cascades. Environment-induced adaptive change can therefore not only result in change to a stickleback population, but the whole way it interacts with its habitat. Such changes could have large ecological impacts in systems with few other fish species.

It is important to stress here that, while some knowledge from West Coast or European systems may be transferable, the general paucity of ecological and evolutionary work on threespine stickleback in eastern North American systems means we do not know *how much* will be transferable. Although the primary fish predators of stickleback on the West Coast and

Europe are salmonids, they are not the same species as on the East Coast, where we have, e.g., lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*). Non-salmonid predators (e.g., topminnows, *Fundulus* spp.—which are possible predators in early stickleback life stages (Kneib 1986); American eel, *Anguilla rostrata*; and centrarchid basses and sunfishes) may also be relatively more important on the East Coast than the West Coast. While there are some survey records of fish communities in lakes with sticklebacks (Rubec 1975; Tessier 2008), and these records are particularly rich in some regions of eastern North America, (e.g., Maine; Bowes et al. 1999; Fuller and Cooper 1946; Havird et al. 2011; Lake Stewards of Maine 2022), few datasets describing communities and their specific relevance to stickleback exist for the east coast. Notable exceptions here are the parasite community data of Hanek and Threlfall (1970), which was later expanded upon by Poulin et al. (2011), and the prey selectivity analyses of Delbeek and Williams (1988). One particularly interesting quirk of the threespine stickleback's range on the East Coast is that it overlaps substantially with the ranges of four other stickleback species: the congeneric blackspotted stickleback (*Gasterosteus wheatlandi*), ninespine stickleback (*Pungitius pungitius*), fourspine stickleback (*Apeltes quadracus*), and brook stickleback (*C. inconstans*; Scott and Crossman 1973), and at some sites all four of the species that are tolerant of brackish water (threespine, ninespine, fourspine, and blackspotted) are known to occur in sympatry (Craig and FitzGerald 1982; McCleave et al. 2018). On the West Coast, in comparison, only the ninespine stickleback co-occurs with the threespine. This overlap in ranges, particularly in Maine, the Canadian Maritime provinces, and the St. Lawrence River Valley, has great potential as a system for competition, character displacement, and comparative eco-evo studies, but also potentially decreases the specificity with which we can describe relationships between threespine stickleback, their environments, and the communities with which they interact. A further distinction from the other regions with threespine stickleback, particularly North America's Pacific coast, is the environmental difference caused by more extreme seasonal temperature swings on the East Coast (Kottek et al. 2006) that led Hagen and Moodie (1982) to hypothesize climate was responsible for the pattern of high *C* and *P* plate frequencies. If the

Table 1 Outstanding questions and lines of investigation for further research, based on the information synthesized in this review

Phylogenetics and evolutionary history	Resolution of the phylogeography and colonization history of threespine stickleback in the western Atlantic at the level of major drainage basins and regions
	Have the northern portions of the threespine stickleback range in eastern North America experienced gene flow from the Pacific or European lineages?
	What was the cause and timing of the divergence of the white stickleback from common marine stickleback, and to what extent are genetically distinct?
Genetics	What is the genetic basis of the east coast partial plate morph, and does it involve genes in the <i>Eda</i> pathway that are not <i>Eda</i> , itself?
	Does the barred pattern seen on some East Coast stickleback share a genetic basis with the similar patterns observed on the West Coast?
Ecology	Do stocked sportfish impose consistent and predictable selection pressures on traits associated with swimming, defense, and coloration, especially at the expense of highly specialized, locally adapted phenotypes?
	In what way do the selective landscapes in the three reduced-pelvis populations differs from similar populations in other parts of the world, such that high frequencies of pelvic reduction can be maintained even in the presence of high calcium concentrations?
	Does the more intense seasonality of temperature fluctuations on the east coast of North America, relative to the west coast and Europe, result in differing pressures on morphological or life history traits?
	Can any broad-scale associations between ecology and phenotype be identified using specimens in museum collections or existing community data?
Conservation	Identify any specialized, locally adapted populations that could warrant conservation measures
	Are there any broad trends in phenotype, population size, or other aspects of stickleback biology that have undergone recent changes resulting from land use change, species introductions, or climate change?
	Do antipredator phenotypes result in differing ecological interactions between stocked and wild lineages of predator species?
Evolutionary processes	Has the reduction of standing genetic diversity resulting from this lineage's colonization history resulted in greater phenotypic plasticity in the western Atlantic region than in the rest of the species' range? If so, how does this affect local adaptation?
	Do the species assemblages of the east coast of North America modulate the parallelism of adaptations to predators, relative to Europe and the Pacific? If so, how and to what extent?

extremes of the east coast's climate are responsible for stabilizing selection, this could impose constraints on future adaptations to new conditions. Finally, the recency of the entire radiation relative to those in the eastern Atlantic and Pacific may mean that a reduced availability of genetic variation could limit adaptive potential to novel changes (Barrett and Schluter 2008).

Conclusions and recommendations

Although the threespine stickleback radiation of eastern North America should be of particular interest to evolutionary biologists and ecologists, it has been neglected compared to its counterparts in Northern Europe and the Pacific. It exhibits a great deal of variation between freshwater populations in color, body size, and behavior, despite being a maximum of 12.4

thousand years old—younger than any other threespine stickleback lineage that is so geographically expansive. It is also a notable exception to the global pattern of reduced lateral plate counts in freshwater habitats. Furthermore, the extremely high frequencies of partially plated morphs in some isolated populations suggests the presence of an unknown alternative mechanism to heterozygosity at the *Eda* gene for partial-platedness. Determining the causes of this variation could not only help settle the evolutionary conundrum of plate phenotype determination within this lineage, but also help to anticipate responses to ecological change induced by species introductions or environmental change. Additionally, the ecological interactions between East Coast stickleback and species that do not occur elsewhere remain unexplored or underexplored, and acquiring a more comprehensive knowledge of these relationships is necessary to

understand the selective pressures on this lineage of threespine stickleback, relative to those occurring in other regions. Identifying unusual specialized populations, like the benthic-limnetic pairs of the Georgia Straight (Schluter and McPhail 1992), the giant populations of Haida Gwaii (Gambling and Reimchen 2012; Reimchen 1992), and the unarmored populations of Haida Gwaii and California (Moodie and Reimchen 1973; Reimchen 1984), that should be targeted for conservation actions should also be a priority.

In addition to numerous lines of inquiry that can be pursued based on the information presented in this review (see Table 1 for some examples), efforts to build the literature on threespine sticklebacks in eastern Canada should prioritize four broad research directions: (1) resampling documented populations for previously measured traits to assess whether and how they have changed in the intervening years. For many populations, this can include going back to original specimens—many of which are catalogued in Canadian museums—for additional phenotyping, although genotyping will be difficult for the many formalin-fixed specimens. (2) Sampling likely sites of populations that have not yet been documented. This work could focus on the inland lakes of the St. John River basin (Edge and Coad 1983; Hagen and Moodie 1982), the group of lakes in the Moisie and Matamek River systems (Coad and Power 1974), and the bodies of water surrounding Nuelin Lake (McKillop and McKillop 1997; Schroeder 2012) as these have already been demonstrated to have some stickleback populations, and are likely to have more that are undocumented and isolated from anadromous populations. This exploratory work could further be guided by iNaturalist observations and museum collections, which include documented specimens from the Saguenay River basin, Arctic basin, Labrador, and inland Nunavik, about which little morphological information exists, despite their isolation from other populations. (3) Determining the genetic basis and evolutionary history of the region's plate morphs. Determining the gene or genes responsible for the prevalence of the *P* morph is particularly critical. (4) Elucidating ecological and evolutionary relationships between sticklebacks and other East Coast species, particularly salmonids. Of special interest in this respect are stickleback populations of the St. John River system that are sympatric with lake whitefish population pairs, which may

be sensitive to any changes that affect zooplankton communities (Landry et al. 2007). This will provide a better understanding of the threats to freshwater environments posed by invasive species and environmental changes induced by a changing climate and patterns of development and land use. Demonstrated effects of stickleback ecology and diversity on commercial, recreational, and subsistence fisheries on the East Coast are also likely to generate further interest in research from governments, nonprofits, and communities relying on these resources.

Acknowledgements Many thanks to Andrew Hendry for his comments on this manuscript and his encouragement to expand it from a brief white paper to a review and submit it to this special issue commemorating David Noakes. Dr. Anne Dalziel, Dr. Olivier Morissette, and Alan García-Elfring also provided comments on drafts of this manuscript, which improved it a great deal. Thanks to Rosalie Morin-Nadeau, who has assisted with field work and served as my guide in Parc National du Lac-Témiscouata, Sarah Sanderson, who assisted with field work, and to Michel Grégoire, who brought the park's unusual stickleback populations to the attention of the Hendry Lab and who has supported the lab's work in the park. From Memorial University, thanks to Drs. Duncan McIlroy and Robert J. Scott for providing information about the unusually colored stickleback on display in the Bonne Bay Aquarium and other stickleback populations in the area, and to Tim Walsh, for permission to use his photograph of this individual. For information about the specimens in the southern and western Hudson Bay region, and for providing data on the Manitoba Museum's stickleback collections from this part of the country, thanks to Dr. Randy Mooi.

Funding This work was supported by NSERC grant 77947 and Tri-agency Institutional Programs Secretariat grant 75385, both to Andrew Hendry. No funding was obtained from organizations that may gain or lose financially from the publication of this manuscript.

Declarations

Ethical approval Ethical approval for new sampling in Parc national du Lac-Témiscouata was obtained from McGill University's Animal Care Committee, under Animal Use Protocol 2022–8265. Provincial approval for sampling was obtained from Québec's Ministère des Forêts, de la Faune, et des Parcs under Scientific Permit 20220224–012-01–11-S-P.

Competing interests The author declares no competing interests.

Appendix

The estimates of divergence times and timing of the most recent common ancestor of western Atlantic

populations in this work rely on the phylogenies presented in Fang et al. (2018) and Fang et al. (2020b), the latter of which reanalyzed the data published in the former with revised methods. However, Fang et al. (2020b) does not include updated divergence times for all nodes. Because the divergence time estimate of the W. Atlantic lineage from the E. Atlantic lineage was excluded from the updated paper, the divergence time provided in Fang et al. (2018) is used in this paper.

A third global phylogeny of threespine sticklebacks published Fang et al. (2021) also used the revised methods from Fang et al. (2020b), but was designed to answer questions related to parallel evolution in comparison to ninespine stickleback (*Pungitius pungitius*). The exclusion of some samples to answer these questions resulted in a different tree topology, which placed the W. Atlantic threespine stickleback clade as the sister group of the European clade, rather than nested within it, and pushed the divergence time from European populations to well before the end of the Pleistocene. Because the timing for the W. Atlantic branch of the phylogeny in Fang et al. (2021) seems unlikely in light of the timing of deglaciation and its dependence on omitting some samples from analysis, dates from this phylogeny were not relied on for the this review.

A recent global phylogeny of threespine stickleback using mitochondrial DNA has also been published (Artamonova et al. 2022), but the authors reject the use of molecular dating. Instead, they rely on haplotype network topologies and geological evidence to infer the dispersal path of *G. aculeatus* around the globe. This leads them to the conclusions that the Pacific and Atlantic lineages diverged as much as 30 mya (Artamonova et al. 2022), and the Atlantic lineage arrived in the Black and Mediterranean Seas by dispersing across waterways spanning what is now central Asia. This would make the Atlantic–Pacific lineage split considerably older than the split between *G. aculeatus* and *G. wheatlandi*, and than one fourth of the age of the entire percomorph clade (Near et al. 2012), which includes taxa as diverse as the mackerels, snailfishes, pipefishes, swordfish, flounders, and both freshwater (centrarchid) and ocean (molid) sunfishes. As a consequence, until further evidentiary support is provided for the dispersal hypotheses described by Artamonova et al. (2022), I regard the

dispersal pattern described by Fang et al. (2018) to be more likely.

References

- Arostegui MC, Quinn TP (2019) Reliance on lakes by salmon, trout and charr (*Oncorhynchus*, *Salmo* and *Salvelinus*): An evaluation of spawning habitats, rearing strategies and trophic polymorphisms. *Fish Fish* 20:775–794. <https://doi.org/10.1111/faf.12377>
- Artamonova VS et al (2022) Round-the-world voyage of the threespine stickleback (*Gasterosteus aculeatus*): phylogeographic data covering the entire species range. *Water* 14:2484. <https://doi.org/10.3390/w14162484>
- Barrett RDH, Schluter D (2008) Adaptation from standing genetic variation. *Trends Ecol Evol* 23:38–44. <https://doi.org/10.1016/j.tree.2007.09.008>
- Barrett RDH, Rogers SM, Schluter D (2008) Natural selection on a major armor gene in threespine stickleback. *Science* 322:255–257. <https://doi.org/10.1126/science.1159978>
- Bell MA (1987) Interacting evolutionary constraints in pelvic reduction of threespine sticklebacks, *Gasterosteus aculeatus* (Pisces, Gasterosteidae). *Biol J Linn Soc* 31:347–382. <https://doi.org/10.1111/j.1095-8312.1987.tb01998.x>
- Bell MA, Ortí G, Walker JA, Koenings JP (1993) Evolution of pelvic reduction in threespine stickleback fish: a test of competing hypotheses. *Evolution* 47:906–914. <https://doi.org/10.2307/2410193>
- Bell MA, Aguirre WE, Buck NJ (2004) Twelve years of contemporary armor evolution in a threespine stickleback population. *Evolution* 58:814–824. <https://doi.org/10.1111/j.0014-3820.2004.tb00414.x>
- Bell MA, Stewart JD, Park PJ (2009) The world's oldest fossil threespine stickleback fish. *Copeia* 2009:256–265. <https://doi.org/10.1643/CG-08-059>
- Bell MA et al (2016) Reintroduction of threespine stickleback into Cheney and Scout Lakes, Alaska. *Evol Ecol Res* 17:157–178
- Bennike O (1997) Quaternary vertebrates from Greenland: a review. *Quat Sci Rev* 16:899–909. [https://doi.org/10.1016/S0277-3791\(97\)00002-4](https://doi.org/10.1016/S0277-3791(97)00002-4)
- Bergstrom CA (2002) Fast-start swimming performance and reduction in lateral plate number in threespine stickleback. *Can J Zool* 80:207–213. <https://doi.org/10.1139/Z01-226>
- Blouw DM (1996) Evolution of offspring desertion in a stickleback fish. *Ecoscience* 3:18–24. <https://doi.org/10.1080/11956860.1996.11682310>
- Blouw DM, Hagen DW (1990) Breeding ecology and evidence of reproductive isolation of a widespread stickleback fish (Gasterosteidae) in Nova Scotia, Canada. *Biol J Linn Soc* 39:195–217. <https://doi.org/10.1111/j.1095-8312.1990.tb00512.x>
- Bowes K, Lê J, Moring JR (1999) Fishes and other aquatic resources of Acadia National Park: a synopsis of published and unpublished information. Boston, Massachusetts. <https://irma.nps.gov/DataStore/DownloadFile/560152>

- Carlson DM, Daniels RA, Wright JJ (2016) Atlas of inland fishes of New York. The New York State Education Department and Department of Environmental Conservation, Albany, NY
- Chan YF et al (2010) Adaptive evolution of pelvic reduction in sticklebacks by recurrent deletion of a Pitx1 enhancer. *Science* 327:302–305. <https://doi.org/10.1126/science.1182213>
- Chapleau F, Findlay CS, Szenasy E (1997) Impact of piscivorous fish introductions on fish species richness of small lakes in Gatineau Park, Québec. *Ecoscience* 4:259–268. <https://doi.org/10.1080/11956860.1997.11682404>
- Chaverie L et al (2016) Multiple generalist morphs of Lake Trout: avoiding constraints on the evolution of intraspecific divergence? *Ecol Evol* 6:7727–7741. <https://doi.org/10.1002/ece3.2506>
- Coad BW, Power G (1974) Meristic variation in the threespine stickleback, *Gasterosteus aculeatus*, in the Matamek River system, Quebec. *J Fish Res Board Can* 31:1155–1157. <https://doi.org/10.1139/f74-135>
- Colosimo PF et al (2004) The genetic architecture of parallel armor plate reduction in threespine sticklebacks. *PLoS Biol* 2:0635. <https://doi.org/10.1371/journal.pbio.0020109>
- Colosimo PF et al (2005) Widespread parallel evolution in sticklebacks by repeated fixation of ectodysplasin alleles. *Science* 307:1928–1933. <https://doi.org/10.1126/science.1107239>
- Commission de toponymie (2016) Lac Tasiujaq. In: toponymie QCd (ed). Quebec Commission de toponymie. https://toponymie.gouv.qc.ca/ct/ToposWeb/fiche.aspx?no_seq=27441
- Corney RH (2021) Mate choice in white and common threespine sticklebacks. MSc Thesis, Saint Mary's University
- COSEWIC (2013) COSEWIC assessment and status report on the giant threespine stickleback *Gasterosteus aculeatus* and the unarmoured threespine stickleback *Gasterosteus aculeatus* in Canada. In: COSEWIC (ed). Ottawa, p xiv + 62. www.registrelep-sararegistry.gc.ca/default_e.cfm
- Craig D, FitzGerald GJ (1982) Reproductive tactics of four sympatric sticklebacks (Gasterosteidae). *Environ Biol Fishes* 7:369–375. <https://doi.org/10.1007/BF00005572>
- Cresko WA et al (2004) Parallel genetic basis for repeated evolution of armor loss in Alaskan threespine stickleback populations. *PNAS* 101:6050–6055. <https://doi.org/10.1073/pnas.0308479101>
- Dawson JW (1893) The Canadian ice age: being notes on the pleistocene geology of Canada, with especial reference to the life of the period and its climatal conditions. William V. Dawson, Montreal
- De Winter G, Martins HR, Trovo RA, Chapman BB (2016) Knights in shining armour are not necessarily bold: defensive morphology correlates negatively with boldness, but positively with activity, in wild threespine stickleback, *Gasterosteus aculeatus*. *Evol Ecol Res* 17:279–290
- DeGrace JR (1974) Limestone resources of Newfoundland and Labrador. John's, Newfoundland. www.gov.nl.ca/iet/files/mines-geoscience-publications-degrace.pdf, Newfoundland Department of Mines and Energy, Mineral Development Division, St
- Delbeek JC, Williams DD (1987) Morphological differences among females of four species of stickleback (Gasterosteidae) from New Brunswick and their possible ecological significance. *Can J Zool* 65:289–295. <https://doi.org/10.1139/z87-045>
- Delbeek JC, Williams DD (1988) Feeding selectivity of four species of sympatric stickleback in brackish-water habitats in eastern Canada. *J Fish Biol* 32:41–62. <https://doi.org/10.1111/j.1095-8649.1988.tb05334.x>
- Des Roches S et al (2018) The ecological importance of intraspecific variation. *Nat Ecol Evol* 2:57–64. <https://doi.org/10.1038/s41559-017-0402-5>
- Des Roches S, Bell MA, Palkovacs EP (2019) Climate-driven habitat change causes evolution in threespine stickleback. *Global Change Biol* 26:14892. <https://doi.org/10.1111/gcb.14892>
- Dunker K et al (2020) A decade in review: Alaska's adaptive management of an invasive apex predator. *Fishes* 5:12. <https://doi.org/10.3390/fishes5020012>
- Dyke AS (2004) An outline of North American deglaciation with emphasis on central and northern Canada. In: Ehlers J, Gibbard PL (eds) Quaternary glaciations – extent and chronology, Part II: North America. Developments in Quaternary Science, 2, vol 2(B). Elsevier B.V., Amsterdam, p 373–424
- Dynes J, Magnan P, Bernatchez L, Rodrigue MA (1999) Genetic and morphological variation between two forms of lacustrine brook charr. *J Fish Biol* 54:955–972. <https://doi.org/10.1111/j.1095-8649.1999.tb00850.x>
- Edge TA, Coad BW (1983) Reduction of the pelvic skeleton in the threespine stickleback, *Gasterosteus aculeatus*, in two lakes of Québec. *Can Field Nat* 97:334–336
- Fang B, Merilä J, Ribeiro F, Alexandre CM, Momigliano P (2018) Worldwide phylogeny of three-spined sticklebacks. *Mol Phylog Evol* 127:613–625. <https://doi.org/10.1016/j.ympev.2018.06.008>
- Fang B, Kempainen P, Momigliano P, Feng X, Merilä J (2020) On the causes of geographically heterogeneous parallel evolution in sticklebacks. *Nat Ecol Evol* 4:1105–1115. <https://doi.org/10.1038/s41559-020-1222-6>
- Fang B, Merilä J, Matschiner M, Momigliano P (2020) Estimating uncertainty in divergence times among three-spined stickleback clades using the multispecies coalescent. *Mol Phylog Evol* 142:106646. <https://doi.org/10.1016/j.ympev.2019.106646>
- Fang B, Kempainen P, Momigliano P, Merilä J (2021) Population structure limits parallel evolution in sticklebacks. *Mol Biol Evol* 38:4205–4221. <https://doi.org/10.1093/molbev/msab144>
- Fuller JL, Cooper GP (1946) Fish survey report no. 7: a biological survey of the lakes and ponds of Mount Desert Island, and the Union and Lower Penobscot River Drainage Systems. Fish Survey Report. Inland Fisheries and Wildlife, Augusta, Maine. https://digitalmaine.com/ifw_docs/63
- Gambling SJ, Reimchen TE (2012) Prolonged life span among endemic *Gasterosteus* populations. *Can J Zool* 90:284–290. <https://doi.org/10.1139/Z11-133>
- Garside E. T., Hamor T. (1973) Meristic variation in the threespine stickleback, *Gasterosteus aculeatus* L., in eastern Canadian waters. *J Zool* 51:547–551. <https://doi.org/10.1139/z73-079>

- Gelmond O, Hippel FAV, Christy MS (2009) Rapid ecological speciation in three-spined stickleback *Gasterosteus aculeatus* from Middleton Island, Alaska: the roles of selection and geographic isolation. *J Fish Biol* 75:2037–2051. <https://doi.org/10.1111/j.1095-8649.2009.02417.x>
- Greenwood AK et al (2011) The genetic basis of divergent pigmentation patterns in juvenile threespine stickleback. *Heredity* 107:155–166. <https://doi.org/10.1038/hdy.2011.1>
- Gygax M, Rentsch AK, Rudman SM, Rennison D (2018) Differential predation alters pigmentation in threespine stickleback (*Gasterosteus aculeatus*). *J Evol Biol* 31:1589–1598. <https://doi.org/10.1111/jeb.13354>
- Hagen DW, Gilbertson LG (1972) Geographic variation and environmental selection in *Gasterosteus aculeatus* L. in the Pacific Northwest. *American Evolution* 26:32–51. <https://doi.org/10.2307/2406981>
- Hagen DW, Gilbertson LG (1973) The genetics of plate morphs in freshwater threespine sticklebacks. *Heredity* 31:75–84. <https://doi.org/10.1038/hdy.1973.59>
- Hagen DW, Moodie GEE (1982) Polymorphism for plate morphs in *Gasterosteus aculeatus* on the east coast of Canada and an hypothesis for their global distribution. *Can J Zool* 60:1032–1042. <https://doi.org/10.1139/z82-144>
- Haley AL, Dalziel AC, Weir LK (2019) A comparison of nuptial coloration and breeding behaviour in white and common marine threespine stickleback (*Gasterosteus aculeatus*) ecotypes. *Evol Ecol Res* 20:145–166
- Hanek G, Threlfall W (1970) Parasites of the threespine stickleback (*Gasterosteus aculeatus*) in Newfoundland and Labrador. *J Fish Res Board Can* 27:901–907. <https://doi.org/10.1139/f70-096>
- Hartel KE, Halliwell DB, Launer AE (2002) Threespine stickleback. In: Hartel KE, Halliwell DB, Launer AE (eds) *Inland fishes of Massachusetts*. Massachusetts Audubon Society, Natural History of New England Series, pp 223–225
- Hatfield T (2001) Status of the stickleback species pair, *Gasterosteus* spp., in Hadley Lake, Lasqueti Island, British Columbia. *Can Field-Nat* 115:579–583
- Haught S, von Hippel FA (2011) Invasive pike establishment in Cook Inlet Basin lakes, Alaska: diet, native fish abundance and lake environment. *Biol Invasions* 13:2103–2114. <https://doi.org/10.1007/s10530-011-0029-4>
- Havird JC, Parker JK, Connery B (2011) Fishes of the streams of Acadia National Park, Maine. *Northeast Nat* 18:217–228
- Ishikawa A, Kitano J (2020) Diversity in reproductive seasonality in the three-spined stickleback, *Gasterosteus aculeatus*. *J Exp Biol* 223:jeb208975. <https://doi.org/10.1242/jeb.208975>
- Jamieson IG, Blouw DM, Colgan PW (1992) Field observations on the reproductive biology of a newly discovered stickleback (*Gasterosteus*). *Can J Zool* 70:1057–1063. <https://doi.org/10.1139/z92-148>
- Jamieson IG, Blouw DM, Colgan PW (1992) Parental care as a constraint on male mating success in fishes: a comparative study of threespine and white sticklebacks. *Can J Zool* 70:956–962. <https://doi.org/10.1139/z92-136>
- Jones FC et al (2012) The genomic basis of adaptive evolution in threespine sticklebacks. *Nature* 484:55–61. <https://doi.org/10.1038/nature10944>
- Jones AW, Palkovacs EP, Post DM (2013) Recent parallel divergence in body shape and diet source of alewife life history forms. *Evol Ecol* 27:1175–1187. <https://doi.org/10.1007/s10682-013-9650-2>
- Kienzle HM (2018) Impacts of non-native species on the morphology of threespine stickleback (*Gasterosteus aculeatus*). MSc Thesis, University of Calgary
- Kim S-Y, Velando A (2015) Phenotypic integration between antipredator behavior and camouflage pattern in juvenile sticklebacks. *Evolution* 69:830–838. <https://doi.org/10.1111/evo.12600>
- Kitano J et al (2008) Reverse evolution of armor plates in the threespine stickleback. *Curr Biol* 18:769–774. <https://doi.org/10.1016/j.cub.2008.04.027>
- Klepaker T (1993) Morphological changes in a marine population of threespined stickleback, *Gasterosteus aculeatus*, recently isolated in fresh water. *Can J Zool* 71:1251–1258. <https://doi.org/10.1139/z93-171>
- Klepaker T (1995) Postglacial evolution in lateral plate morphs in Norwegian freshwater populations of the threespine stickleback (*Gasterosteus aculeatus*). *Can J Zool* 73:898–906. <https://doi.org/10.1139/z95-105>
- Kneib RT (1986) The role of *Fundulus heteroclitus* in salt marsh trophic dynamics. *Am Zool* 26:259–269. <https://doi.org/10.1093/icb/26.1.259>
- Kottek M, Greiser J, Beck C, Rudolph B, Rubel F (2006) World map of the Köppen-Geiger climate classification updated. *Meteorol Z* 15:259–263. <https://doi.org/10.1127/0941-2948/2006/0130>
- Kristjánsson BK, Skúlason S, Noakes D (2002) Rapid divergence in a recently isolated population of threespine stickleback (*Gasterosteus aculeatus*). *Evol Ecol Res* 4:1–14
- Kristjánsson BK, Skúlason S, Noakes DLG (2005) Unusual number of pectoral fin rays in an Icelandic population of threespine stickleback (*Gasterosteus aculeatus*) recently isolated in freshwater. *Evol Ecol* 18:379–384. <https://doi.org/10.1007/s10682-004-2679-5>
- Kynard B, Curry K (1976) Meristic variation in the threespine stickleback, *Gasterosteus aculeatus*, from Auke Lake, Alaska. *Copeia* 1976:811–813. <https://doi.org/10.2307/1443471>
- Laakkonen HM, Hardman M, Strelkov P, Väinölä R (2021) Cycles of trans-Arctic dispersal and vicariance, and diversification of the amphiboreal marine fauna. *J Evol Biol* 34:73–96. <https://doi.org/10.1111/jeb.13674>
- LaCasse J, Aubin-Horth N (2012) A test of the coupling of predator defense morphology and behavior variation in two threespine stickleback populations. *Curr Zool* 58:53–65. <https://doi.org/10.1093/czoolo/58.1.53>
- Lake Survey Maps (2022) Maine Department of Inland Fisheries & Wildlife. <https://www.maine.gov/ifw/fishing-boating/fishing/lake-survey-maps/index.html>
- Lake Stewards of Maine (2022) Lakes of Maine. <https://lakesofmaine.org>
- Lamothe KA, Hubbard JAG, Drake DAR (2021) Freshwater fish functional and taxonomic diversity above and below Niagara Falls. *Environ Biol Fishes* 104:637–649. <https://doi.org/10.1007/s10641-020-01044-w>

- Landry L, Vincent WF, Bernatchez L (2007) Parallel evolution of lake whitefish dwarf ecotypes in association with limnological features of their adaptive landscape. *J Evol Biol* 20:971–984. <https://doi.org/10.1111/j.1420-9101.2007.01304.x>
- Laurentino TG, Boileau N, Ronco F, Berner D (2022) The ectodysplasin-a receptor is a candidate gene for lateral plate number variation in stickleback fish. *G3* 12:jkac077. <https://doi.org/10.1093/g3journal/jkac077>
- Lee DS, Gilbert CR, Hocutt CH, Jenkins RE, McAllister DE, Stauffer Jr. JR (1980) Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh, NC, USA
- Lescap EA et al (2015) Evolution of stickleback in 50 years on earthquake-uplifted islands. *PNAS* 112:E7204–E7212. <https://doi.org/10.1073/pnas.1512020112>
- Liu S, Ferchaud A-L, Grønkvær P, Nygaard R, Hansen MM (2018) Genomic parallelism and lack thereof in contrasting systems of three-spined sticklebacks. *Mol Ecol* 27:4725–4743. <https://doi.org/10.1111/mec.14782>
- Massengill R, Begich RN, Dunker K (2020) Operational Plan: Kenai Peninsula nonnative fish control, monitoring, and native fish restoration Regional Operation Plan. Alaska Department of Fish and Game, Anchorage, Alaska.
- McAllister DE, Cumbaa SL, Harington CR (1981) Pleistocene fishes (*Coregonus*, *Osmerus*, *Microgadus*, *Gasterosteus*) from Green Creek, Ontario, Canada. *Can J Earth Sci/rev Can Sci Terre* 18:1356–1364. <https://doi.org/10.1139/e81-125>
- McAllister DE, Coad BW (1974) *Gasterosteus aculeatus* Linnaeus; Threespine stickleback / Épinoche à trois épines. In: Stevenson JC (ed) Fishes of Canada's national capital region. Miscellaneous special publication. Department of the environment, fisheries and marine service, Ottawa, p 178–179
- McCairns RJS, Bernatchez L (2008) Landscape genetic analyses reveal cryptic population structure and putative selection gradients in a large-scale estuarine environment. *Mol Ecol* 17:3901–3916. <https://doi.org/10.1111/j.1365-294X.2008.03884.x>
- McCairns RSJ, Bernatchez L (2012) Plasticity and heritability of morphological variation within and between parapatric stickleback demes. *J Evol Biol* 25:1097–1112. <https://doi.org/10.1111/j.1420-9101.2012.02496.x>
- McCleave JD, Zydlewski GB, Vieser JD (2018) Biology of four sympatric sticklebacks in Cobscook Bay, Maine, a boreal, macrotidal bay. *Environ Biol Fishes* 101:1443–1465. <https://doi.org/10.1007/s10641-018-0791-6>
- McKillop WB, McKillop WM (1997) Distribution records for the threespine stickleback, *Gasterosteus aculeatus* Linnaeus (Pisces: Gasterosteidae), in Manitoba. *Can Field-Nat* 111:662–663
- Mimura M et al (2017) Understanding and monitoring the consequences of human impacts on intraspecific variation. *Evol Appl* 10:121–139. <https://doi.org/10.1111/eva.12436>
- Ministère du Développement durable de l'Environnement et des Parcs (2008) Parc national du Lac-Témiscouata: Plan directeur provisoire. Bibliothèque et Archives nationales du Québec, Québec, QC
- Moodie GE, Reimchen TE (1973) Endemism and conservation of sticklebacks in the Queen Charlotte Islands. *Can Field-Nat* 87:173–175
- Moodie GEE, Reimchen TE (1976) Phenetic variation and habitat differences in *Gasterosteus* populations of the Queen Charlotte Islands. *Syst Zool* 25:49–61. <https://doi.org/10.2307/2412778>
- Morissette O (2021) Threespine Stickleback (*Gasterosteus aculeatus*). iNaturalist Canada. <https://www.inaturalist.org/observations/100646323>
- Muir AM, Hansen MJ, Bronte CR, Krueger CC (2016) If Arctic charr *Salvelinus alpinus* is 'the most diverse vertebrate', what is the lake charr *Salvelinus namaycush*? *Fish Fish* 17:1194–1207. <https://doi.org/10.1111/faf.12114>
- Near TJ et al (2012) Resolution of ray-finned fish phylogeny and timing of diversification. *PNAS* 109:13698–13703. <https://doi.org/10.1073/pnas.1206625109>
- NHESP Threespine stickleback fact sheet. In: Wildlife MDOF (ed). Natural Heritage & Endangered Species Program. <https://www.mass.gov/files/documents/2016/08/ni/gasterosteus-aculeatus.pdf>
- Oliver DR (1964) A limnological investigation of a large Arctic lake, Nettilling Lake, Baffin Island. *Arctic* 17:69–83
- Patankar R, von Hippel FA, Bell MA (2006) Extinction of a weakly armoured threespine stickleback (*Gasterosteus aculeatus*) population in Prator Lake, Alaska. *Ecol Freshwat Fish* 15:482–487. <https://doi.org/10.1111/j.1600-0633.2006.00186.x>
- Poulin R, Blamar CA, Thielges DW, Marcogliese DJ (2011) The biogeography of parasitism in sticklebacks: distance, habitat differences and the similarity in parasite occurrence and abundance. *Ecography* 34:540–551. <https://doi.org/10.1111/j.1600-0587.2010.06826.x>
- Reimchen TE (1984) Status of unarmoured and spine-deficient populations (Charlotte unarmoured stickleback) of threespine stickleback, *Gasterosteus* sp., on the Queen Charlotte Islands. *British Columbia Can Field-Nat* 98:120–126
- Reimchen TE (1991) Trout foraging failures and the evolution of body size in stickleback. *Copeia* 1991:1098–1104. <https://doi.org/10.2307/1446106>
- Reimchen TE (1992) Extended longevity in a large-bodied stickleback, *Gasterosteus*, population. *Can Field-Nat* 106:122–125
- Reimchen TE, Bergstrom C, Nosil P (2013) Natural selection and the adaptive radiation of Haida Gwaii stickleback. *Evol Ecol Res* 15:241–269
- Roberts Kingman GA et al (2021) Predicting future from past: The genomic basis of recurrent and rapid stickleback evolution. *Sci Adv* 7:eabg5285. <https://doi.org/10.1126/sciadv.abg5285>
- Roseman EF, Riley SC (2009) Biomass of deepwater demersal forage fishes in Lake Huron, 1994–2007: Implications for offshore predators. *Aquat Ecosyst Health Manage* 12:29–36. <https://doi.org/10.1080/14634980802711786>
- Rubec PJ (1975) Fish distribution in Gatineau Park, Quebec, in relation to postglacial dispersal, man's influence, and eutrophication. *Can Field-Nat* 89:389–399
- Samuk K, Iritani D, Schluter D (2014) Reversed brain size sexual dimorphism accompanies loss of parental care in

- white sticklebacks. *Ecol Evol* 4:3236–3243. <https://doi.org/10.1002/ece3.1175>
- Samuk KM (2016) The evolutionary genomics of adaptation and speciation in the threespine stickleback. PhD Thesis, The University of British Columbia
- Schluter D, Conte GL (2009) Genetics and ecological speciation. *PNAS* 106:9955–9962. <https://doi.org/10.1073/pnas.0901264106>
- Schluter D, McPhail JD (1992) Ecological character displacement and speciation in sticklebacks. *Am Nat* 140:85–108. <https://doi.org/10.1086/285404>
- Schmid DW, McGee MD, Best RJ, Seehausen O, Matthews B (2019) Rapid divergence of predator functional traits affects prey composition in aquatic communities. *Am Nat* 193:331–345. <https://doi.org/10.1086/701784>
- Schroeder BS (2012) Using morphological and microsatellite analysis to investigate postglacial diversity in an isolated population of threespine stickleback (*Gasterosteus aculeatus*) in Nueltin Lake, Manitoba. MSc Thesis, University of Manitoba
- Scott WB, Crossman EJ (1973) Freshwater fishes of Canada. Fisheries Research Board of Canada, Ottawa
- Scott RJ, Haines GE, Biedak NR, Baker JA (2022a) Variation in morphology among populations of threespine stickleback (*Gasterosteus aculeatus*) from western Newfoundland, Canada. *BioRxiv*. <https://doi.org/10.1101/2022.09.08.507156>
- Scott RJ, Haines GE, Trask CA (2022b) Armor reduction and pelvic girdle loss in a population of threespine stickleback (*Gasterosteus aculeatus*) from western Newfoundland, Canada. *BioRxiv*. <https://doi.org/10.1101/2022.09.20.508658>
- Scudder SH (1893) Report of the Board of Directors of the Natural History Gardens and Aquaria. *Proceedings of the Boston Society of Natural History* 26:137–139
- Sleezer LJ, Angermeier PL, Frimpong EA, Brown BL (2021) A new composite abundance metric detects stream fish declines and community homogenization during six decades of invasions. *Divers Distrib* 27:2136–2156. <https://doi.org/10.1111/ddi.13393>
- Spoljaric MA, Reimchen TE (2007) 10 000 years later: evolution of body shape in Haida Gwaii three-spined stickleback. *J Fish Biol* 70:1484–1503. <https://doi.org/10.1111/j.1095-8649.2007.01425.x>
- Stedman RM, Bowen CA II (1985) Introduction and spread of the threespine stickleback (*Gasterosteus aculeatus*) in Lakes Huron and Michigan. *J Great Lakes Res* 11:508–511. [https://doi.org/10.1016/S0380-1330\(85\)71794-7](https://doi.org/10.1016/S0380-1330(85)71794-7)
- Taylor EB, Boughman JW, Groenenboom M, Sniatynski M, Schluter D, Gow JL (2006) Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. *Mol Ecol* 15:343–355. <https://doi.org/10.1111/j.1365-294X.2005.02794.x>
- Tessier I (2008) États des Connaissances: Parc national du Lac-Témiscouata. In: MDDEP (ed).
- U.S. Geological Survey (2021) *Gasterosteus aculeatus*: U.S. Geological Survey, Nonindigenous Aquatic Species Database. Gainesville, FL. nas.er.usgs.gov
- Vachon J, Lavallée BF, Chapleau F (2005) Caractéristiques d'une population introduit du Grand brochet, *Esox lucius*, dans le lac Ramsay, Parc de la Gatineau, Québec, et impact sur l'ichtyofaune. *Can Field-Nat* 119:359–366. <https://doi.org/10.22621/cfn.v119i3.146>
- Walsh T (2021) Threespine stickleback (*Gasterosteus aculeatus*). iNaturalist Canada. <https://www.inaturalist.org/observations/90757153>
- Wootton RJ (2010) Dynamics of extinction of a small population of the three-spined stickleback (*Gasterosteus aculeatus* L) caused by habitat modification. *Aquat Conserv: Mar Freshwat Ecosyst* 20:365–370. <https://doi.org/10.1002/aqc.1109>
- Xie KT et al (2019) DNA fragility in the parallel evolution of pelvic reduction in stickleback fish. *Science* 363:81–84. <https://doi.org/10.1126/science.aan1425>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.