



Worldwide phylogeny of three-spined sticklebacks

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ARTICLE INFO

Keywords:

Coalescent
Gasterosteus
Phylogenomics
RAD-seq
SNP
Threespine stickleback

ABSTRACT

Stickleback fishes in the family *Gasterosteidae* have become model organisms in ecology and evolutionary biology. However, even in the case of the most widely studied species in this family – the three-spined stickleback (*Gasterosteus aculeatus*) – the worldwide phylogenetic relationships and colonization history of the different populations and lineages remain poorly resolved. Using a large collection of samples covering most parts of the species distribution range, we subjected thousands of single nucleotide polymorphisms to coalescent analyses in order to reconstruct a robust worldwide phylogeny of extant *G. aculeatus* populations, as well as their ancestral geographic distributions using Statistical-Dispersal Vicariance and Bayesian Binary MCMC analyses. The results suggest that contemporary populations originated from the Pacific Ocean in the Late Pleistocene, and the Atlantic was colonized through the Arctic Ocean by a lineage that diverged from Pacific sticklebacks ca 44.6 Kya. This lineage contains two branches: one that is distributed in the Mediterranean area, from the Iberian Peninsula to the Black Sea ('Southern European Clade'), and another that is comprised of populations from northern Europe and the east coast of North America ('Trans-Atlantic Clade'). Hence, the results suggest that the North American East Coast was colonized by trans-Atlantic migration. Coalescence-based divergence time estimates suggest that divergence among major clades is much more recent than previously estimated.

1. Introduction

During the past two decades, the three-spined stickleback (*Gasterosteus aculeatus*), a small teleost easily reared in laboratory conditions, has become one of the most important model species in ecology and evolutionary biology (Bell and Foster, 1994; Gibson, 2005; Hendry et al., 2013; Östlund-Nilsson et al., 2006). With a nearly circumpolar marine distribution in the Northern Hemisphere, this species has colonized freshwater habitats multiple times since the last glacial maximum, evolving dramatic morphological, physiological and behavioral adaptations in remarkably short periods of time (Barrett et al., 2011). In recent years, the development of restriction site-associated DNA (RAD) and whole-genome sequencing (WGS) has resulted in a plethora of studies exploring the genomic basis of these adaptations (Baird et al., 2008; Hohenlohe et al., 2010; Jones et al., 2012, etc.). As such, the combination of a broad geographic distribution, high degree of morphological, physiological and behavioral diversity, and the availability of extensive genomic resources has made the three-spined stickleback an ideal candidate species to test hypotheses in the fields of biogeography (Mäkinen et al., 2006; Orti et al., 1994), physiology (Barrett et al., 2011; Bell, 2001; Kitano et al., 2010), developmental biology (Shapiro et al.,

2004), population genetics (Cresko et al., 2004; Leinonen et al., 2006), comparative genomics (Guo et al., 2013), ethology (Huntingford and Ruiz-Gomez, 2009; Von Hippel, 2010), adaptive evolution and speciation (Gibson, 2005; Jones et al., 2012; McKinnon and Rundle, 2002).

A well-supported and highly resolved phylogeny is a prerequisite for understanding evolutionary processes and testing ecological and evolutionary hypotheses, and in particular, for untangling processes that have shaped genomic divergence, such as natural selection and demographic changes (Delsuc et al., 2005). Interestingly, despite its importance as a model species for ecological and evolutionary studies, the worldwide phylogenetic relationships and the colonization history of three-spined sticklebacks in different ocean basins has yet to be fully resolved. As a result, the dispersal routes and refugial origins of various lineages and populations have been disputed. There are a number of reasons for this.

The first reason is restricted geographic sampling. Previous phylogeographic studies have mostly been based on limited geographic sampling, with focus on specific geographic regions (Cano et al., 2008; Lucek et al., 2010; DeFaveri et al., 2012; Deagle et al., 2013; Ravinet et al., 2014; Sanz et al., 2015; Vila et al., 2017; Table 1). Although there are a few comprehensive studies that encompass a broader geographic

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Table 1

A review of previous representative large-scale phylogenetic studies for *G. aculeatus*. The table contains the type of genetic marker used, the number of sampling localities across the regions listed, and brief synopsis of the main results of each study. The most comprehensive studies conducted so far have focused on few mitochondrial gene fragments and a handful of microsatellite loci, or based on limited geographic sampling.

Studies	Years	Genetic marker	Location number	Sampling range					
				Pacific		Iberian Mediterranean			
				Western Pacific basin	Eastern Pacific basin	Iberian peninsula	Mediterranean	Adriatic sea	Black sea
Haglund et al.	1992	Allozyme	16	✓	✓		✓		
Orti et al.	1994	mtDNA	25	✓	✓				
Colosimo et al.	2005	SNPs	25	✓	✓				
Mäkinen et al.	2006	Microsatellite	73			✓	✓	✓	✓
Mäkinen and Merilä	2008	mtDNA	49			✓	✓	✓	✓
Cano et al.	2008	mtDNA & Microsatellite	18					✓	
DeFaveri et al.	2012	mtDNA & Microsatellite	10*					✓	
Ravinet et al.	2014	mtDNA & Microsatellite	46*			✓	✓	✓	✓
Sanz et al.	2015	mtDNA	7*			✓	✓	✓	✓
Liu et al.	2016	SNPs	5*		✓				
Vila et al.	2017	mtDNA & Microsatellite	17 [†]			✓		✓	✓
This study	2018	Genome-wide SNPs	70	✓	✓	✓	✓	✓	✓

Studies	Sampling range								Main findings
	Europe								
	Western Atlantic	Atlantic	Norwegian Sea	North sea	Barents sea	White sea	Baltic sea	Mainland Europe	
Haglund et al.	✓			✓			✓		Interpopulation divergence between Pacific and Atlantic
Orti et al.	✓	✓					✓	✓	Two divergent mitochondrial clades: <i>Japanese</i> and <i>North American-Atlantic</i> clade; Colonization of Atlantic dates to 260–90 Kya.
Colosimo et al.	✓	✓	✓	✓					Two major lineages: <i>Atlantic</i> and <i>Pacific</i> lineage
Mäkinen et al.	✓	✓	✓	✓	✓	✓	✓	✓	Marine ancestors colonize freshwater during post-glaciation; Mediterranean region colonization dates back to the Pleistocene
Mäkinen and Merilä	✓	✓	✓	✓	✓	✓	✓	✓	Three major mtDNA lineages: <i>Trans-Atlantic</i> , <i>European</i> and <i>Black Sea</i> lineage; The divergence between major lineages occurred 170–130 Kya based on a molecular clock calibration
Cano et al.			✓	✓	✓	✓	✓	✓	Adriatic lineage may have a long independent evolutionary history.
DeFaveri et al.			✓	✓	✓		✓	✓	Two divergent lineages: <i>Adriatic</i> and <i>European</i> lineage; Adriatic lineage is most divergent and ancient
Ravinet et al.	✓	✓	✓	✓	✓	✓	✓	✓	Two major lineages: <i>European</i> and <i>Trans-Atlantic</i> lineage
Sanz et al.	✓	✓	✓	✓	✓	✓	✓	✓	Two independent lineages in the Mediterranean region are divergent from Atlantic (Portuguese) lineage; Divergence among Iberian Mediterranean populations precedes last glaciation
Liu et al.	✓			✓			✓		Four lineages: <i>Japanese</i> , <i>Euro-American</i> , <i>Transatlantic</i> and <i>Europe</i> lineage; Freshwater populations are founded by marine ancestors post-glacially
Vila et al.		✓	✓	✓	✓	✓	✓	✓	Iberian Peninsula has a history of multiple colonization
This study	✓	✓	✓	✓	✓	✓	✓	✓	See discussion

* Other published haplotype data from previous literature were also included in the analyses.

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