U.S. Fish & Wildlife Service

Threespine Stickleback (*Gasterosteus aculeatus*)

Ecological Risk Screening Summary

U.S. Fish & Wildlife Service, February 2011
Revised, January 2017, October 2017, December 2017
Web version, 8/16/2017

Photo: Ross D. Robertson. Licensed under Creative Commons BY-NC 3.0. Available: http://eol.org/data_objects/13237097. (October 31, 2017).

This species has both a freshwater/brackish and a marine form. This ERSS is only for the freshwater/brackish form.

1 Native Range and Status in the United States

Native Range

From Fuller et al. (2016):

"Range in North America extends from Cape Fear Estuary north to Hudson Bay and Baffin Island, and along the west coast from Alaska and British Columbia to southern California (Scott and Crossman 1973). This species also occurs in Europe, Iceland, Greenland, and along the Pacific coast of Asia. Freshwater populations are distributed along the coast of the Mediterranean and in inland waters across Eastern Europe to the Baltic Sea (Page and Burr 1991). *Gasterosteus aculeatus* is native to the Lake Ontario basin, below Niagara Falls (Stedman and Bowen 1985)."

From Froese and Pauly (2016):

"Circumarctic and temperate regions: Extending south to the Black Sea, southern Italy, Iberian Peninsula, North Africa; in Eastern Asia north of Japan (35°N), in North America north of 30-32°N; Greenland."

Status in the United States

Gasterosteus aculeatus is native to some areas of the United States (Fuller et al. 2016; see previous section).

From Fuller et al. (2016):

"The threespine stickleback was reported from Sitkalidak Island, Alaska, outside of its native distribution (Miller and Hubbs 1969). This species is also known from the Santa Maria River system, Gull and June Lakes in Mono County, Mojave River drainage, Big Bear Lake in San Bernardino County, and several other locations throughout the state of California (Miller and Hubbs 1969, Moyle 1976, Swift 1993); Indiana Dunes National Lakeshore, Indiana (Tilmant 1999); Lake Michigan, Illinois (Burr 1991, Johnston 1991, Page and Laird 1993); a park in Boston, Massachusetts (Hartel et al. 1996); Lake Michigan, Lake Superior, Lake St. Clair, and Lake Huron, Michigan (Bailey and Smith 1991, Cudmore-Vokey and Crossman 2000, Czypinski, pers. comm., Hirsch 1998, Johnston 1991, Mattes, pers. comm., Roth et al. 2011, Stedman and Bowen 1985); several areas of Lake Superior in Minnesota including Silver Bay, an unspecified tributary on the north shore near Grand Marais, southwest of the Knife River, offshore from the Duluth ship canal, at Hovland, the St. Louis estuary (S. Geving, Natural Resource Specialist, Minnesota Department of Environmental Resources, pers. comm., Hirsch 1998), Skunk Creek and the mouth of the Baptism River (Schmidt, pers. comm.); Maumee Bay, Lake Erie, Ohio (T. Cavender, Ohio State University, Museum of Biological Diversity, pers. comm.); established in Crane Prarie Reservoir, Oregon (Ridler 2004); and Lake Michigan and the St. Louis River estuary and the mouth of Barnes Creek, Kenosha County, Wisconsin (Czypinski 1999, 2001, Hirsch 1998, Johnston 1991, K. Scheidegger, Bureau of Fisheries Management, pers. comm.). Threespine stickleback has been collected in South Bay, Manitoulin Island, Lake Huron, Ontario (Gibson 1982)."

“Reported in Ohio and Wisconsin, established in California, Massachusetts, and Michigan. A single fish was collected from the stomach of a lake trout taken in 150 feet of water southwest of Knife River in May 1996 (S. Geving, Natural Resource Specialist, Minnesota Department of Environmental Resources, pers. comm.). Also in May, two were collected in a commercial pound net in the St. Louis estuary under the Blatnik Interstate Bridge (S. Geving, Natural Resource Specialist, Minnesota Department of Environmental Resources, pers. comm.).

Great Lakes
First recorded in Lake Huron in 1982, where it apparently gained access through the Nipissing Canal from the Ottawa River (Smith 1985). During recent years, this species is reported as spreading rapidly throughout the upper Great Lakes (Burr 1991, Smith 1985). In June 1994, this species was reported from Taconite Harbor, Lake Superior, Minnesota, where eight specimens were taken from cooling tower intakes (J. Gunderson, Sea Grant Extension Program, pers. comm., [Hirsch] 1998). It also has been reported from the Canadian side of Lake Superior (J. Gunderson, Sea Grant Extension Program, pers. comm.) It is now considered introduced and established in Lakes Erie, Michigan, Huron, and Superior (Roth et al. 2011).”

Means of Introductions in the United States

From Fuller et al. (2016):

“According to Miller and Hubbs (1969), the threespine stickleback was introduced into the Mohave River drainage of California between 1938 and 1940. The species was presumably introduced due to escape or release of baitfish brought in by anglers from southern California coastal area. In addition to the earlier releases, it was probably introduced into the Mohave River with trout from the Fillmore Hatchery in 1947 (Miller and Hubbs 1969). *Gasterosteus aculeatus* was believed to have been introduced into Gull and June lakes by anglers, probably from the Ventura River drainage, and it was introduced into the Santa Maria River system along with trout from the Santa Ynez River in 1940 (Miller and Hubbs 1969). A population in Holcomb Creek in the Mojave River drainage may have been introduced with trout in the late 1800s (Bell 1982, Sigler and Sigler 1987). According to Hartel et al. (1996), the population in Boston's Olmsted Park may have been introduced as part of a museum exhibit. The park contains a pool that Fredrick Law Olmsted had designated for a stickleback exhibit.

Great Lakes
The threespine stickleback was not known from above Niagara Falls before 1979. The first specimens collected from above the falls were taken in 1980 from South Bay in Lake Huron (Stedman and Bowman 1985). Smith (1985) stated that the threespine stickleback gained access to the Upper Great Lakes from the Ottawa River and Lake Ontario through the artificial Nipissing Canal. However, Stedman and Bowman (1985) presented the possibility that it was transported by bait dealers and subsequently released by anglers. Mandrak and Crossman (1992) recorded it from Thunder Bay, Lake Superior (Canada) and attributed its presence there to a ballast water introduction.”

Remarks

This species has both a freshwater/brackish and a marine form. This ERSS is only for the freshwater/brackish form.

From Fuller et al. (2016):

"The unarmored threespine stickleback *G. a. williamsoni* has been on the decline in California and has been listed as federally endangered since 1971. The population in Boston, Massachusetts is unique in several ways. It is the southernmost freshwater population, contains 3 distinct lateral-plate morphs, and it represents only the fourth record of low plate individuals. Its urban location is another factor in support of an introduction (Hartel et al. 1996). Hubbs (1919) advocated the stocking of *G. aculeatus* in natural and artificial water bodies in California as a biological control against mosquitoes."

"*Gasterosteus aculeatus* actually may represent a complex of two or more distinct species; subspecies have been proposed but their ranges are poorly defined (Miller and Hubbs 1969, Page and Burr 1991). Because the taxonomy of this group is so complex, it is probably irresolvable (Gilbert, personal communication). The potential for rapid evolution in *G. aculeatus* was exhibited following a 1982 chemical eradication program at Loberg Lake, Alaska, whereby the entire freshwater stickleback population was killed off with the intention of increasing lake resources for the trout and salmon populations. Following eradication, anadromous sticklebacks made their way back into the lake through the Cook Inlet. Within the next 12 years, the frequency of the armored (oceanic) form in this stickleback population dropped from 100% to 11%, replaced by an unarmored (freshwater) form which increased to a frequency of 75%, with some intermediate forms making up the remainder (Bell et al. 2004)."

From NatureServe (2014):

"Complex patterns of variation make taxonomic treatment difficult. This stickleback may be considered a species complex with many unique and reproductively isolated populations, subspecies or species.

Populations exist that are strictly marine, anadromous, and freshwater resident. The marine and anadromous forms have given rise to diverse resident phenotypes. Subspecies have been recognized in the past, but current scientific discussion of this species complex recognizes multiple distinct species within evolutionary radiations; current genetic research is underway to determine relationships between evolutionary groups and species before names can be assigned (Hatfield 2001a, 2001b). Lateral plate morphs of resident freshwater forms are recognized as lows (i.e., lateral plates on anterior parts of the fish only), partials (i.e., lateral plates on anterior and posterior ends of the fish with a gap between), and completes (i.e., lateral plates in a continuous row anterior to posterior). In a rare form, plates are entirely absent; *G. a. williamsoni* is an endangered plateless form exhibiting reduction in pelvic structure, and only occurs in drainages in southern California. Lows from the Pacific coast of North America have been called *G. a. microcephalus*, Pacific coast completes are *G. a. aculeatus*, and Penczak (1964, in Wootton 1976) designated lows from Iceland as *G. a. islandicus*. A plateless form occurring in Shay

Creek, San Bernardino County, California, has been identified as *G. a. santaeannae* (or s*anta-annae*) but is currently recognized as synonymous with *G. a. williamsoni* (Ross 1973, Moyle et al. 1989).

Studies of allozyme variation (Haglund et al. 1992) and mitochondrial DNA sequences (Orti et al. 1994) in Asian, North American, and European populations recognized two primary clades: (1) European, North American, and some Japanese samples, which could be divided into an (1a) Atlantic basin clade comprising the eastern North American and European populations, and a (1b) basal Pacific basin assemblage comprising western North American and some Japanese populations; and (2) a divergent group of Japanese populations. The divergent Japanese clade deserves further study and possible taxonomic recognition.

Sympatric species pairs bearing "limnetic" and "benthic" life histories and distinct morphologies have evolved in several British Columbian lake systems (Thompson et al 1997, Hatfield 2001, Hatfield and Ptolemy 2001). Some populations of these are endangered or already extinct (Wood 2003).

Several low-lying lakes and streams in the Cook Inlet area contain rare and evolutionarily divergent populations of *G. aculeatus* including three populations polymorphic for lateral plate morphs, several populations polymorphic for pelvic armor morphs, one lake containing 2 freshwater morphs of the species (a benthic and a limnetic feeder), and one lake containing both anadromous and resident freshwater forms of the species (von Hippel, pers. comm.). Bell and Orti (1994) viewed divergent populations in freshwater habitats around Cook Inlet as parts of an endemic radiation warranting special consideration for conservation as a unit."

From USFWS (2017):

"Unarmored Threespine stickleback (*Gasterosteus aculeatus williamsoni*) […]
Listing Status: Endangered
Where Listed: WHEREVER FOUND"

From NatureServe (2015):

"Populations from the Atlantic and Black Sea basins have not yet been compared in detail. Preliminary observations suggest that they are probably distinct species."

"There is a hybrid zone with *G. gymnurus* in the English Channel, southern North Sea, Baltic Sea and their basins."

2 Biology and Ecology

Taxonomic Hierarchy and Taxonomic Standing

According to Eschmeyer et al. (2017), *Gasterosteus aculeatus* Linnaeus 1758 is the valid name for this species. It is also the original name for this species.

From ITIS (2016):

"Kingdom Animalia
Subkingdom Bilateria
Infrakingdom Deuterostomia
Phylum Chordata
Subphylum Vertebrata
Infraphylum Gnathostomata
Superclass Osteichthyes
Class Actinopterygii
Subclass Neopterygii
Infraclass Teleostei
Superorder Acanthopterygii
Order Gasterosteiformes
Suborder Gasterosteoidei
Family Gasterosteidae
Genus *Gasterosteus*
Species *Gasterosteus aculeatus* Linneaus, 1758"

Size, Weight, and Age Range

From Fuller et al. (2016):

"Usually between 3 and 8 cm long, average length about 5 cm (Scott and Crosman 1973). Maximum reported length 11 cm (Muus and Nielsen 1999)."

"The average lifespan of this species is ranges is only about 1 to 3 years (Wootton 1976), with a maximum documented age of about 8 years in captivity (Bell et al. 1994)."

From Froese and Pauly (2016):

"Maturity: L_m 5.5 […]
Max length: 11.0 cm TL male/unsexed; [Muus and Nielsen 1999]; common length: 5.1 cm TL male/unsexed; [Scott and Crossman 1973]; max. reported age: 8 years [Reimchen 1992]"

"Maximum length in freshwater is 8 cm while in saltwater is 11 cm [Muus and Nielsen 1999]."

Environment

From Froese and Pauly (2016):

"Marine; freshwater; brackish; benthopelagic; anadromous [Riede 2004]; depth range 0 - 100 m [Fedorov et al. 2003]. […]; 4°C - 20°C [assumed to be recommended aquarium temperature] [Riehl and Baensch 1991]; […]"

This species has both a freshwater/brackish and a marine form. This ERSS is only for the freshwater/brackish form.

Climate/Range

From Froese and Pauly (2016):

"Temperate; […] ; 71°N - 26°N, 117°E - 60°E [McDowall 1988]"

Distribution Outside the United States

Native

See Section 1 for a description of the native range within the United States.

From Fuller et al. (2016):

"This species also occurs in Europe, Iceland, Greenland, and along the Pacific coast of Asia. Freshwater populations are distributed along the coast of the Mediterranean and in inland waters across Eastern Europe to the Baltic Sea (Page and Burr 1991)."

From Froese and Pauly (2016):

"Circumarctic and temperate regions: Extending south to the Black Sea, southern Italy, Iberian Peninsula, North Africa; in Eastern Asia north of Japan (35°N), in North America north of 30-32°N; Greenland."

Introduced

Froese and Pauly (2016) list *Gasterosteus aculeatus* as introduced and established in Slovakia, Italy, Belarus, Austria, and the Czech Republic. It is listed as introduced and probably established in Iran and Hungary, introduced and not established in Mitidja Oueds, and introduced but status unknown in Germany.

FAO (2016) lists *Gasterosteus aculeatus aculeatus* as introduced and established to Austria, and Czechoslovakia; as introduced and probably established in Hungary; as introduced and establishment unknown in Iran (Caspian Sea), Italy. *Gasterosteus aculeatus* is listed as introduced and established in Slovakia, and introduced but status unknown in Germany.

According to NOBANIS (2017), *Gasterosteus aculeatus* was introduced to Austria sometime before 1900, it was first reported in 1900. The species is established and in commonly encountered.

From Lenhardt et al. (2011):

"The first record of the three-spined stickleback in Serbia was in 1995 (Cakic et al. 2000), but there are unverified earlier data on the existence of this species. Specimens of the species were recorded in July close to the riverbank of the Danube River at rkm 927. Several authors have published records of this species in the Danube delta (Banarescu 1964), in the Danube near Budapest (Berinkey 1960) and near Bratislava (Balon 1967; Bastl 1976)."

From Amundsen et al. (2013):

"Three-spined stickleback *Gasterosteus aculeatus* were introduced to Takvatn [Lake in Norway] in 1950 from Sagelvvatn, another nearby lake located 13 km away in a different watershed (Jørgensen and Klemetsen 1995)."

Means of Introduction Outside the United States

From FAO (2016):

"Reasons of Introduction: 1) accidental"

"Reasons of Introduction: 1) diffused from other countries"

From Lusk et al. (2010):

"*G. aculeatus* is the only alien species that had originated in aquarium cultures and has established permanent populations in a few localities."

From NOBANIS (2017):

"Type of introduction: Intentional"

From Lenhardt et al. (2011):

"Balon (1967), Ahnelt et al. (1998) reported that aquarists were responsible for the introduction and spread of the three-spined stickleback."

From Amundsen et al. (2013):

"This was a deliberate introduction to improve forage for brown trout and arctic charr by adding a prey fish species [*G. aculeatus*]."

Short Description

From Fuller et al. (2016):

"Small, streamlined torpedo shaped fish. Its common name is derived from the presence of two to four, but usually three sharp spines on the back forward of the dorsal fin. Dorsal fin is broad and has 10-14 soft rays; caudal fin contains 10 rays. Freshwater populations vary in body shape depending on the type of habitat it occupies. Fish inhabiting surface waters (limnetic form) tend to exhibit slender bodies with narrow mouths, long snouts, and large eyes. Benthic fish are deep bodied with a small eye and a wide, terminal gape. Pelvic fin is reduced to a sharp spine and a small ray. Gill rakers are long and slender, with 17 to 25 on the first arch for freshwater forms. While the oceanic form of *G. aculeatus* has up to 30 or more lateral bony plates on each side of the body as well as a pelvic girdle and lateral line with microscopic pores, these features tend to be reduced in freshwater forms. This species can be differentiated from other species in the genus by a crenulated posterior edge of scutes and by a set of scutes forming a lateral keel on the

caudal peduncle. In populations that co-occur with predatory fishes, dorsal and pelvic fins tend to be longer, and other anti-predatory features such as dorsal spines, the lateral plate, and the pelvic girdle tend to be more prominent (Grand 2000, Marchinko 2008, Reimchen 2000). Coloration is generally cryptic, with mottled brown-green barring on the upper side of the body and a white, silvery, or yellow underside. Sides are pale and fins are often spotted with dark dots. Breeding males develop a vivid blue-green coloration with blue or green eyes and the breast region develops an intense red-orange coloration (Baker et. al 1995, Bell et al. 1994, Cresko et al. 2007, Day et al. 1994, Morrow 1980)."

From Froese and Pauly (2016):

"Dorsal spines (total): 2 - 4; Dorsal soft rays (total): 10-14; Anal spines: 1; Anal soft rays: 8 - 10; Vertebrae: 29 - 33. Distinguished uniquely from its congeners in Europe by having trunk and caudal peduncle covered by a complete series of 29-35 bony scutes. Other characters important to separate this species from other species of the genus include posterior edge of scutes crenulated and scutes forming a lateral keel on caudal peduncle. Scutes may be missing on posterior part of trunk in hybrid zone with *Gasterosteus gymnurus* and in some isolated freshwater populations of northeastern Europe [Kottelat and Freyhof 2007]. Identified by the 3 to 4 sharp, free spines before the dorsal fin, the pelvic fin reduced to a sharp spine and a small ray, and the series of plates along the sides of the body [Morrow 1980]. Gill rakers long and slender, 17 to 25 on the first arch or strictly freshwater forms, 1 or 2 more in anadromous forms; lateral line with microscopic pores [Morrow 1980]. The anadromous form is fully plated, with up to 37 plates on the sides and a rather pronounced keel on each side of the caudal peduncle [Morrow 1980]. Dorsal spines separated from each other and from the soft-rayed fins, each spine having a reduced membrane attached to its posterior side; anal spine free from rest of the fin; posterior margin of pectorals nearly truncate; caudal truncate to slightly indented [Morrow 1980]. Freshwater forms usually mottled brown or greenish; anadromous forms silvery green to bluish black [Morrow 1980]. A few isolated populations are black [Morrow 1980]. Sides usually pale; belly yellow, white or silvery [Morrow 1980]. Fins pale; pectoral rays often have dark dots [Morrow 1980]. Breeding males (except for black forms) become brilliant bluish or green with blue or green eyes, and the forward part of the body, especially the breast region, turns bright red or orange [Morrow 1980]. Caudal fin with 12 rays [Spillman 1961]."

Biology

From Fuller et al. (2016):

"An enormous range of morphological variation is present within the threespine stickleback. There are two distinct varieties of the species, with one form having an anadromous existence and another form inhabiting strictly freshwater. The anadromous form spends most of its adult life in the ocean feeding on plankton and returns to freshwater to breed. The freshwater form inhabits a wide variety of lakes and streams, ranging from small, ephemeral streams, to large, permanently flowing water bodies, however it cannot exist in high gradient streams and is rarely found more than a few hundred meters above sea level. These freshwater populations are thought to have evolved from anadromous forms that were trapped in freshwater lakes during the last glacial melt (Bell et al. 1994). Within the freshwater variety, two morphological variations occur. One of these variations is known as the limnetic type, which is adapted to live in the water

column of oligotrophic lakes and feed on surface plankton, and the other form is the benthic type, which inhabits the bottom of shallow eutrophic lakes or the littoral zone of deeper lakes and feeds from the lakebed (Bell et al. 1994, Mattern et al. 2007, Shaw et al. 2007).

Breeding occurs annually from late April to July in ponds, rivers, lakes, drainage canals, marshes, sloughs, tidal creeks, and sublittoral zones of the sea (Bell et al. 1994, Mattern et al. 2007). Males are polygamous and attract several females into the nesting territory with zig-zag courtship dances over a 1- to 4-day period. The male will then fertilize all of the deposited eggs at one time and remain to guard them from predators and to ensure an ample oxygen supply (by fanning; Bell et al. 1994, Mattern et al. 2007). The eggs hatch 5 to 10 days after fertilization, and males stay with the newly hatched individuals for up to 2 weeks (Bell et al. 1994, Huntingford and Wright 1993). Individuals reach sexual maturity between 1 and 2 years of age. […]

Gasterosteus aculeatus is a generalist carnivore, feeding on benthic invertebrates, including crustaceans and larval insects (benthic form), and zooplankton (limnetic form). It exhibits a predation cycle that consists of search, pursuit, attack, and capture. As the threespine stickleback is small, abundant, and a slow swimmer, it serves as a suitable prey for a wide variety of species. Natural predators include fish in the families Percidae, Esocidae, and Salmonidae, as well as avian piscivores such as loons, herons, and kingfishers. Macroinvertebrates, such as dragonfly naiads and beetles feed on eggs, fry, and juvenile individuals, and leeches are known to feed on eggs and adult individuals that are stuck in traps (Bell et al. 1994, Messler et al. 2007). To counteract predation, the stickleback exhibits shoaling behavior and relies heavily on chemical and olfactory pathways to detect predators and control shoal size and foraging activity (Mattern et al. 2007, Peuhkuri 1998)."

From Froese and Pauly (2016):

"Form schools. Young associated with drifting seaweed [Safran 1990, Safran and Omori 1990]. Juveniles move to the sea (anadromous populations) or to deeper, larger water bodies (freshwater populations) in July-August, forming large feeding schools [Kottelat and Freyhof 2007]. Feed on worms, crustaceans, larvae and adult aquatic insects, drowned aerial insects, and small fishes; has also been reported to feed on their own fry and eggs [Scott and Crossman 1973]. Eggs are found in nests constructed from plant material [Pinder 2001]. Males build, guard and aerate the nest where the eggs are deposited [Breder and Rosen 1966]."

"Spawning behavior is similar for both freshwater and anadromous forms [McPhail 1969]. Just before breeding, males become very territorial. The male builds a nest of plant-material glued together with spiggin, a protein produced in the kidney [Jakobsson et al. 1999]. Once a nest is built, the male entices the female into the nest by performing a courtship dance which is a series of zigzag movements [Scott and Crossman 1973]. A receptive female follows the male who points the opening of the nest by posing above it with his head down. The female enters the nest, deposits up to a few hundred eggs, and is driven out by the male after eggs have been deposited. The male then enters the nest to fertilize the eggs. The male can choose to court another female to enter the nest and lay eggs before entering himself to fertilise the deposited eggs. Females may lay eggs in several nests over a period of several days or may be courted by the same male [Morrow 1980]. The male guards and ventilates the eggs and young [Scott and Crossman 1973].

During spawning season, males develop a bright orange to red belly and blue-green flank and eyes. Eggs hatch in 7-8 days. Anadromous forms usually die of exhaustion after spawning cycle. Freshwater individuals are able to complete several cycles within one year or sometimes over several years [Kottelat and Freyhof 2007]."

"Adults occur in fresh waters, estuaries and coastal seas [Banister 1986]. Anadromous, with numerous non-anadromous populations in brackish or pure freshwater, rarely in marine waters. In the sea, confined to coastal waters. In freshwater, adults prefer to live in small stream but may occur in a variety of habitats including lakes and large rivers [Kottelat and Freyhof 2007]. Inhabit shallow vegetated areas, usually over mud or sand [Page and Burr 1991]."

Human Uses

From Froese and Pauly (2016):

"Occasionally taken commercially in Scandinavia and processed into fishmeal and oil [Bigelow and Welsh 1925, Nikolskii 1961]. Commonly used as a laboratory animal [Scott and Crossman 1973]."

From NatureServe (2014):

"Has been used in carcinogenesis testing (Metcalfe 1989)."

Diseases

No records of OIE reportable diseases were found.

From Rolbiecki (2004):

"As shown by the present study, both smelt and stickleback [*Gasterosteus aculeatus*] from the Gulf of Gdañsk and the Vistula Lagoon can be paratenic hosts for *Anguillicola crassus*."

From Bailly (2013):

"*Argulus canadensis* Wilson C.B., 1916 (parasitic: ectoparasitic)
Argulus foliaceus (Linnaeus, 1758) (parasitic: ectoparasitic)
Bomolochus cuneatus Fraser, 1920 (parasitic: ectoparasitic)
Bothriocephalus scorpii (Müller, 1776) (parasite)
*Caligus clemens*i Parker & Margolis, 1964 (parasitic: ectoparasitic)
Caligus lacustris Steenstrup & Lütken, 1861 (parasitic: ectoparasitic)
Diphyllobothrium dendriticum (Nitzsch, 1824) (parasite)
Diphyllobothrium ditremum (Creplin, 1825) (parasite)
Ergasilus auritus Markevich, 1940 (parasitic: ectoparasitic)
Ergasilus biuncinatus Gadd, 1901 (parasitic: ectoparasitic)
Ergasilus funduli Krøyer, 1863 (parasitic: ectoparasitic)
Ergasilus manicatus Wilson C.B., 1911 (parasitic: ectoparasitic)
Ergasilus nerkae Roberts, 1963 (parasitic: ectoparasitic)
Ergasilus sieboldi Nordmann, 1832 (parasitic: ectoparasitic)

Ergasilus turgidus Fraser, 1920 (parasitic: ectoparasitic)
Eubothrium crassum (Bloch, 1779) (parasite)
Glugea anomala (Moniez, 1887) Gurley, 1893 (parasite)
Glugea gasterostei Voronin, 1974 (parasite)
Lernaea cyprinacea Linnaeus, 1758 (parasitic: ectoparasitic)
Lernaeocera gasterostei Bruhl, 1860 (parasitic: ectoparasitic)
Myxobilatus gasterostei (Parisi, 1912) (parasite)
Proteocephalus filicollis (Rudolphi, 1810) (parasite)
Proteocephalus longicollis (Zeder, 1800) (parasite)
Proteocephalus percae (Müller, 1780) (parasite)
Schistocephalus solidus (Müller, 1776) (parasite)
Sphaerospora elegans Thélohan, 1892 (parasite)
Thersitina gasterostei (Pagenstecher, 1861) (parasitic: ectoparasitic)
Triaenophorus crassus Forel, 1868 (parasite)
Trichodina domerguei (Wallengren, 1897) (parasite)
Trichodina tenuidens Fauré-Fremiet, 1943 (parasite)
Tylodelphys clavata (von Nordmann, 1832) (parasitic: endoparasitic)"

From Amundsen et al. (2013):

"Similarly, the introduction of three-spined stickleback resulted in the arrival of another two parasite species [*Schistocephalus solidus* (PA6) and *Gyrodactylus arcuatus* (PA10)] […]."

Threat to Humans

From Froese and Pauly (2016):

"Harmless"

3 Impacts of Introductions

From Lusk et al. (2010):

"*G. aculeatus* has established permanent population in a few localities only, without any marked impact on either ecosystems or biodiversity."

From Lenhardt et al. (2011):

"Its negative effects on native fish species have not been investigated [in Serbia]."

From Fuller et al. (2016):

"Miller and Hubbs (1969) reported the stockings of armoured threespine stickleback *G. a. microcephalus* into the native range of the unarmoured threespine stickleback *G. a. williamsoni* in certain California drainages. One consequence has been extensive hybridization between the two subspecies (Miller and Hubbs 1969; Moyle 1976b). The three-spined stickleback is known to prey on eggs of other species (Page and Laird 1993)."

From Wisconsin SeaGrant (2016):

“This invasive stickleback eats the eggs and larvae of native fish. It also competes with them for food and habitat. Additionally, the threespine stickleback may hybridize with native sticklebacks.”

From Amundsen et al. (2013):

“Similarly, the introduction of three-spined stickleback resulted in the arrival of another two parasite species [*Schistocephalus solidus* (PA6) and *Gyrodactylus arcuatus* (PA10)] that both have the stickleback as an obligate host in their life cycle. Several of these parasite species also infect many native species in the web during the completion of their life cycles.”

“At the third consumer level, the introduced three-spined stickleback became the principal consumer of zooplankton (Fig. 1 [in source material]).”

“The introduction of arctic charr and three-spined stickleback altered the Takvatn pelagic food web, increasing species richness beyond the mere addition of the two introduced species by facilitating the establishment of several hitchhiking or independently arriving parasite species and constituting essential food resources for new avian predators. Hence, the introductions of the 2 fish species facilitated the addition of another 9 species to the pelagic community, increasing richness from 39 to 50 species. These species additions also resulted in a large increase in the number of trophic links, and the topology of the food web changed dramatically.”

“Intensified piscivory by birds related to the presence of three-spined stickleback and arctic charr has furthermore increased the transmission rates of several bird parasites that use fish as intermediate hosts (Knudsen et al. 1996).”

4 Global Distribution

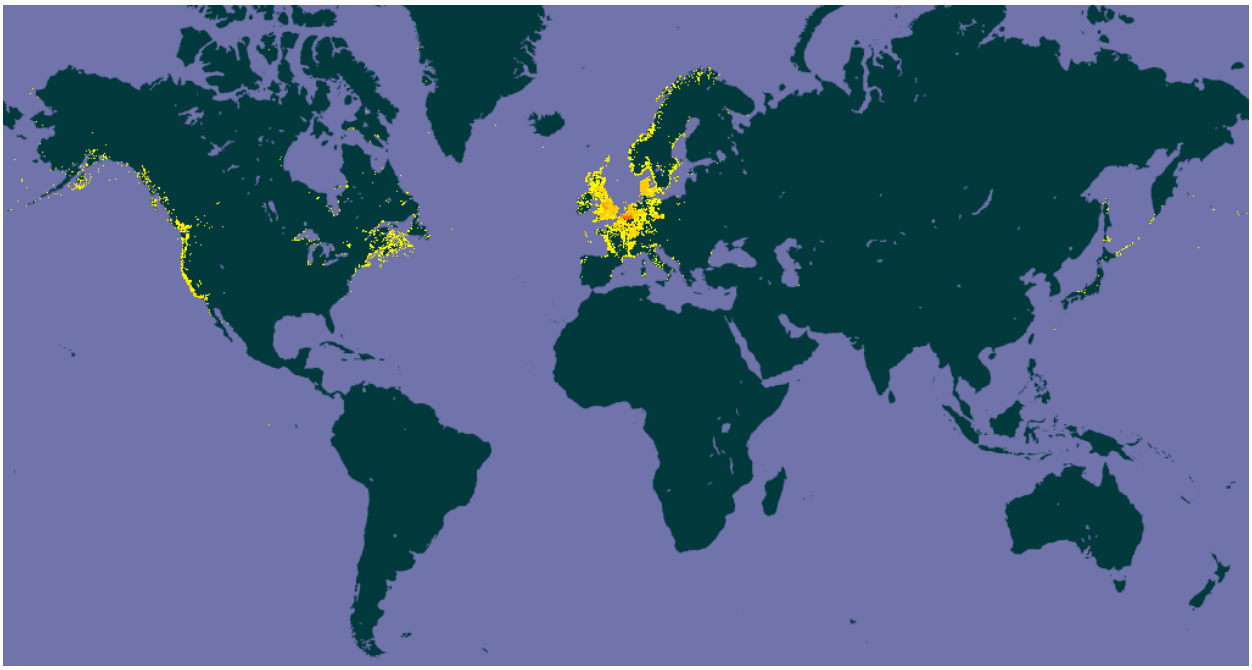

Figure 1. Known global distribution of *Gasterosteus aculeatus*. Map from GBIF Secretariat (2016).

This ERSS is only for the freshwater/brackish form of the species. No marine observations were used as source points in the climate match.

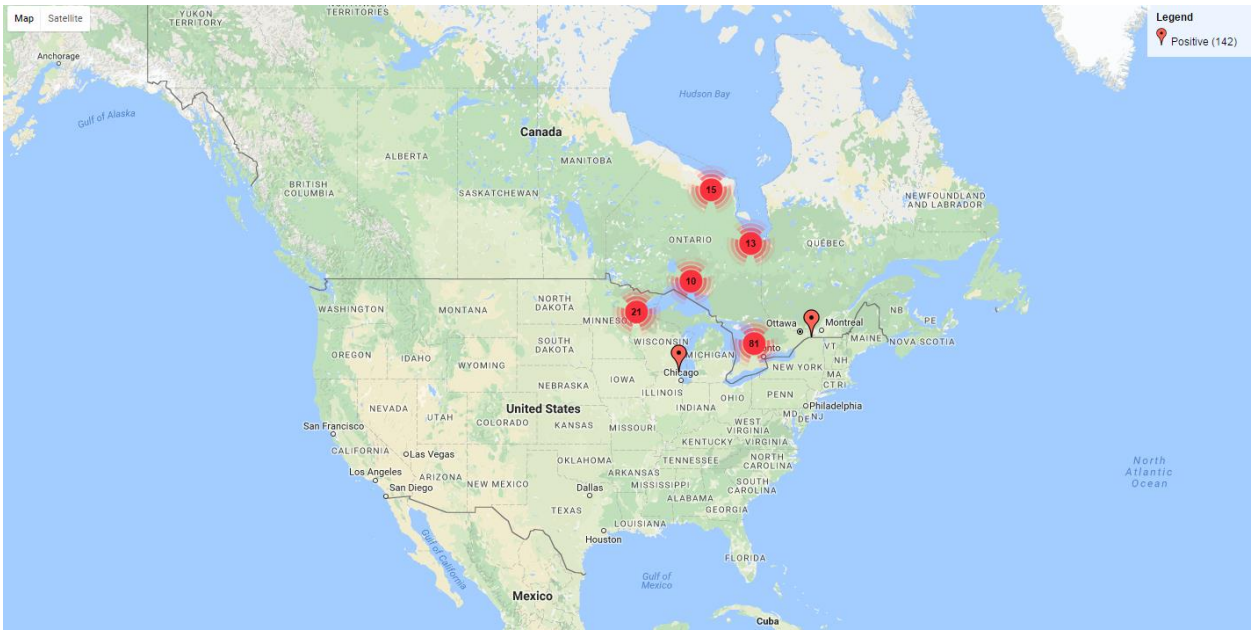

Figure 2. North American distribution of *Gasterosteus aculeatus*. Locations are in Canada and the United States. Map from EDDMapS (2017).

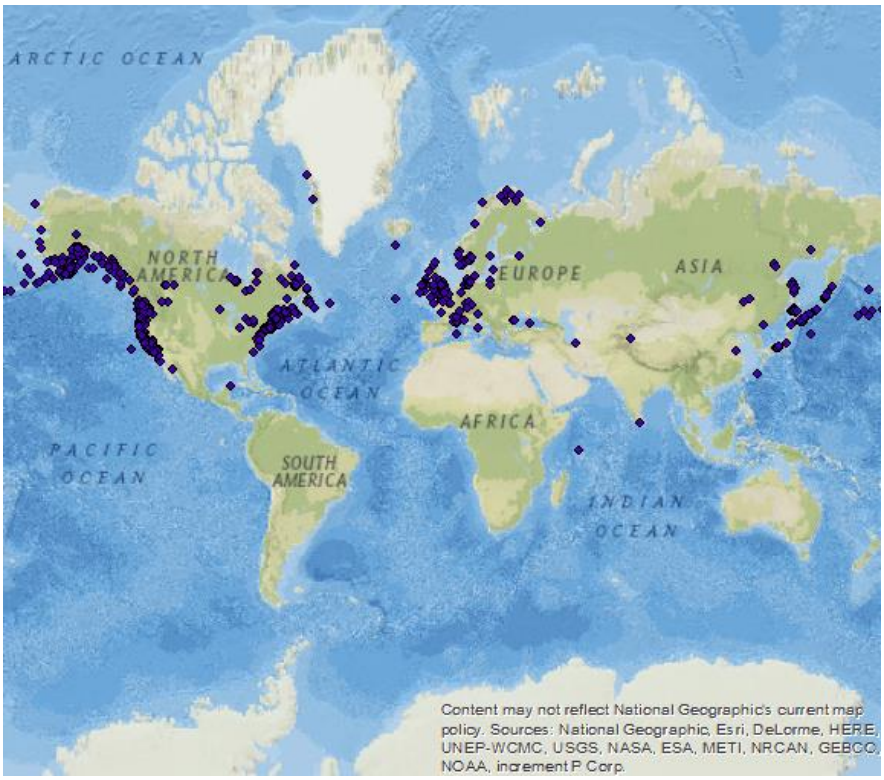

Figure 3. Global distribution of *Gasterosteus aculeatus*. Map from VertNet (2017).

The observations in the Indian Ocean and off the east coast of Africa were not used as a source point for the climate match, the record details show this observation is for *Rhinecanthus aculeatus* not *Gasterosteus aculeatus* (VertNet 2017).

The observation in far western China was not used as a source point as its record indicates the specimen was collected in Maryland, USA not China (VertNet 2017).

The observation off of Mexico in the Gulf of Mexico was also not used as a source point for the climate match. Its record indicated a discrepancy between the coordinates and where the specimen was collected (VertNet 2017).

This ERSS is only for the freshwater/brackish form of the species. No marine observations were used as source points in the climate match.

5 Distribution Within the United States

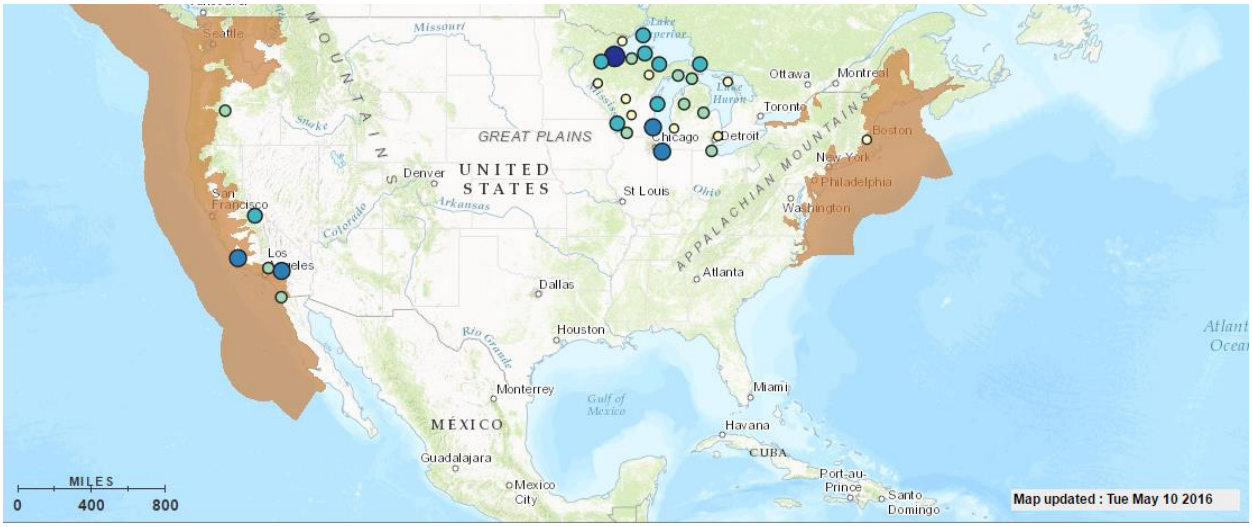

Figure 4. Known distribution of *Gasterosteus aculeatus* in the United States. The brown area indicates the native range of the species, including the range of the marine form in coastal United States waters. No marine observations were used as soruce points for the climate match. Map from Fuller et al. (2016).

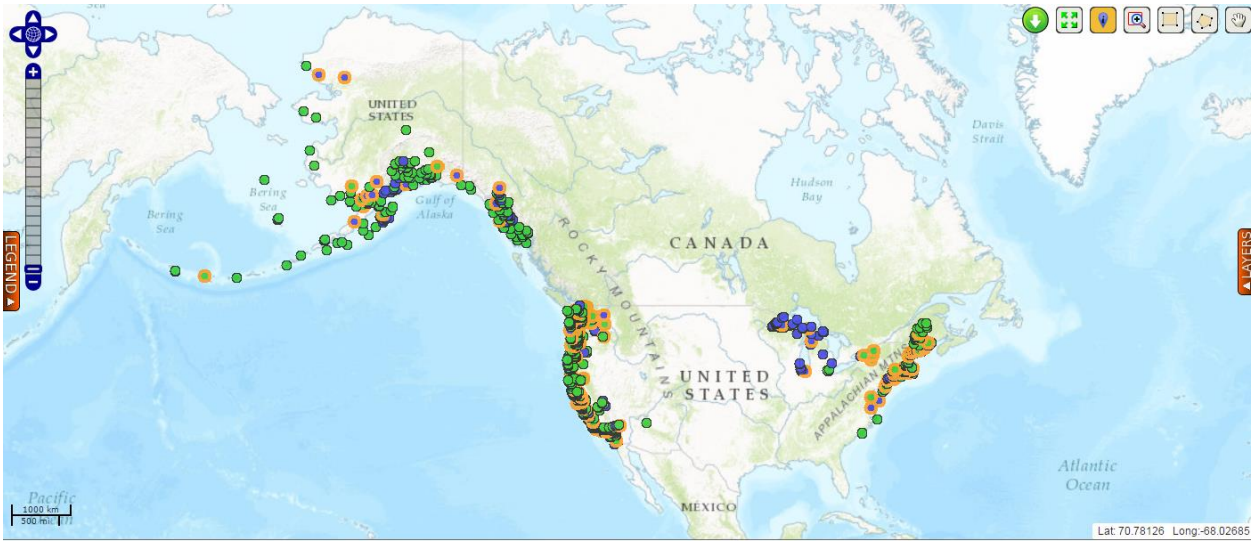

Figure 5. Known distribution of *Gasterosteus aculeatus* in the United States. No marine observations were used as source points for the climate match. Map from BISON (2017).

6 Climate Matching

Summary of Climate Matching Analysis

The climate match for *Gasterosteus aculeatus* was high for most of the country. There were small areas of low match in extreme southern Florida and in pockets of the southern states. The Climate 6 score (Sanders et al. 2014; 16 climate variables; Euclidean distance) for the contiguous United States was 0.862, high, and individually high in Arkansas, Arizona, Colorado, Florida, Idaho, Indiana, Kentucky, Michigan, Minnesota, Missouri, Montana, Nebraska, Nevada, New Mexico, North Carolina, North Dakota, Ohio, Oklahoma, South Carolina, South Dakota, Tennessee, Utah, Vermont, Washington D.C., West Virginia, Wisconsin, and Wyoming. The climate match was also individually high for states in the native range of *Gasterosteus aculeatus*: California, Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Oregon, Pennsylvania, Rhode Island, Virginia, and Washington. All source points were from freshwater/brackish observations.

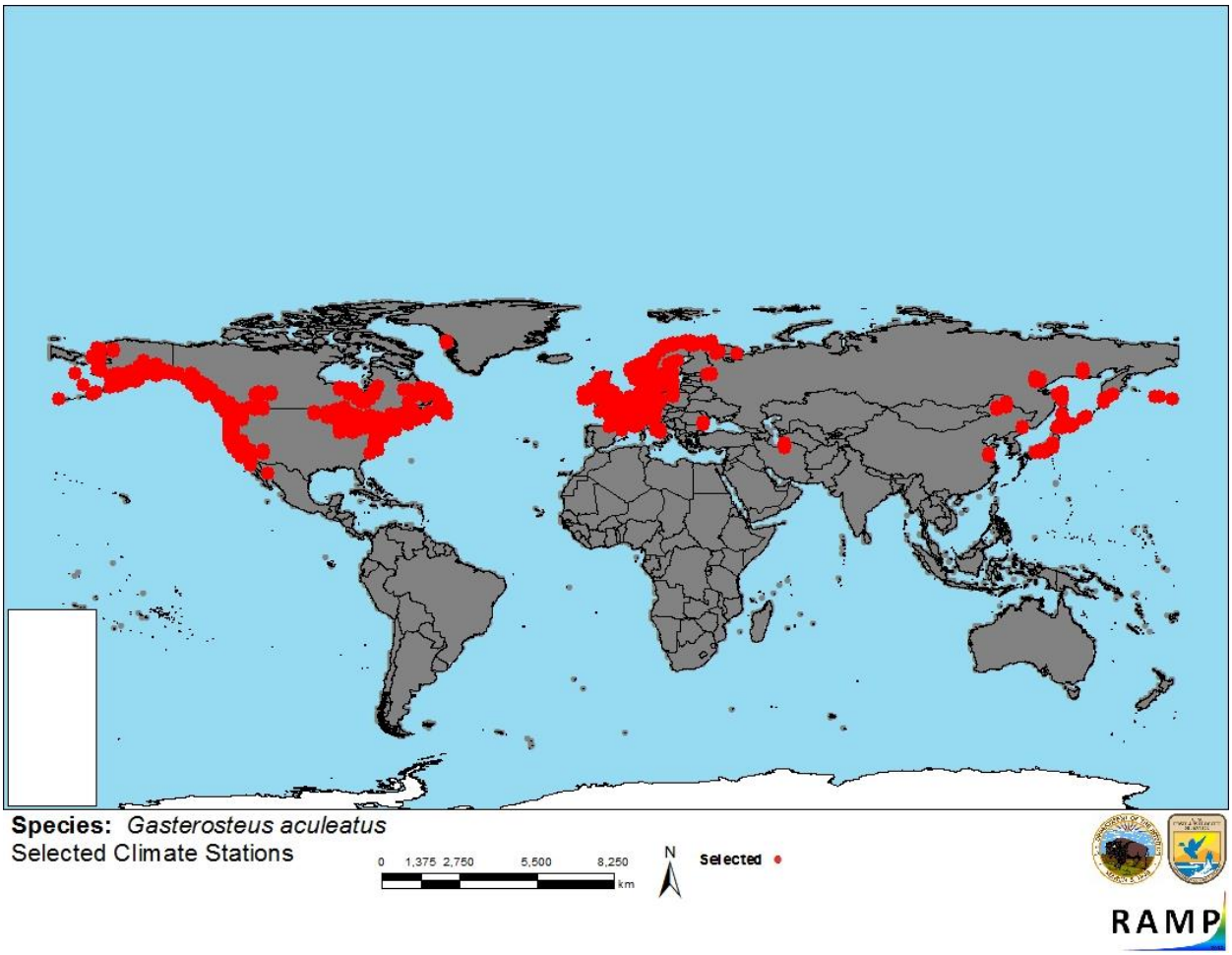

Figure 6. RAMP (Sanders et al. 2014) source map showing weather stations across the world selected as source locations (red) and non-source locations (gray) for *Gasterosteus aculeatus* climate matching. Source locations from GBIF Secretariat (2016), Fuller et al. (2016), BISON (2017), EDDMapS (2017), and VertNet (2017).

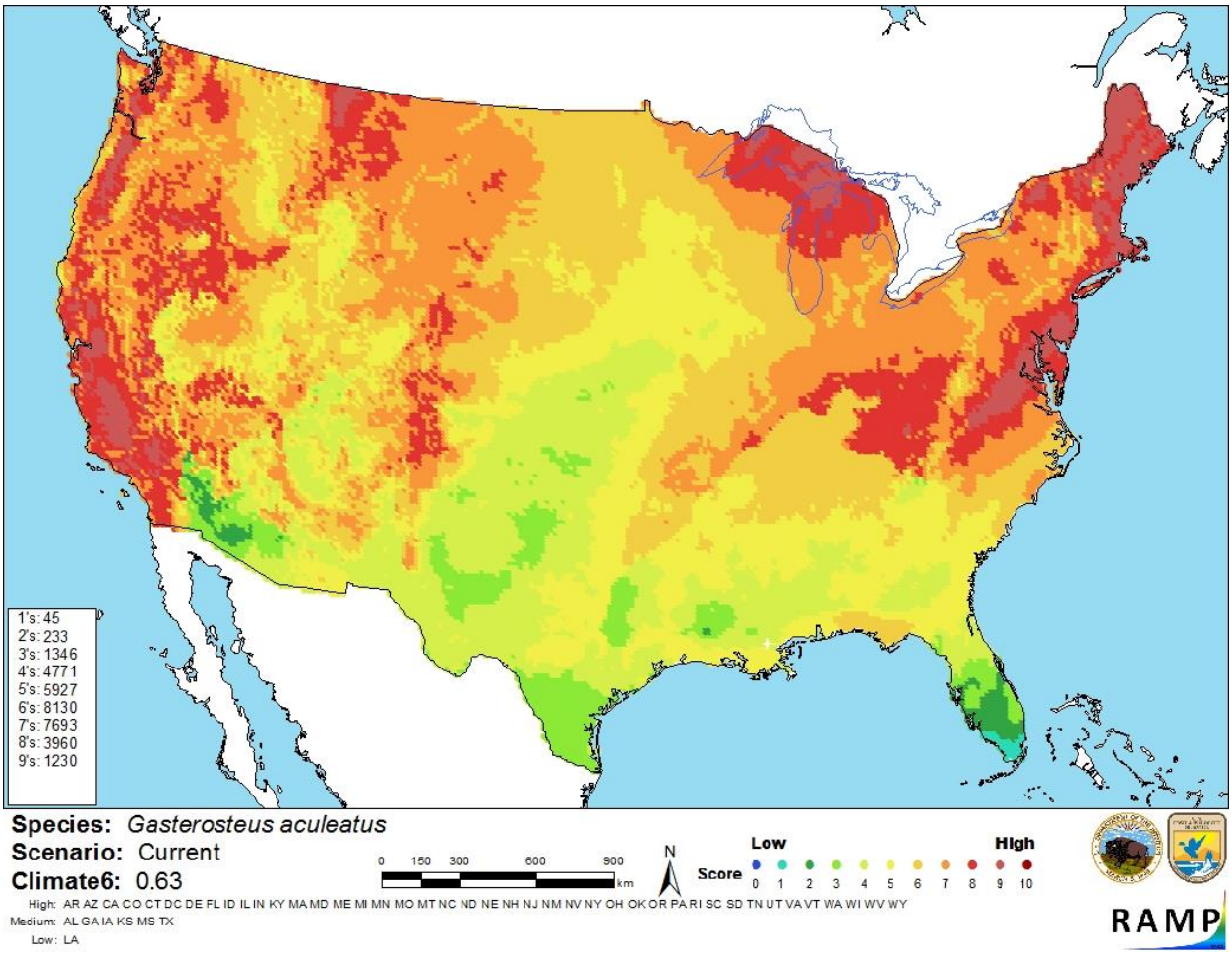

Figure 7. Map of RAMP (Sanders et al. 2014) climate matches for *Gasterosteus aculeatus* in the contiguous United States based on source locations reported by GBIF Secretariat (2016), Fuller et al. (2016), BISON (2017), EDDMapS (2017), and VertNet (2017). 0 = Lowest match, 10 = Highest match. Counts of climate match scores are tabulated on the left.

The High, Medium, and Low Climate match Categories are based on the following table:

Climate 6: Proportion of (Sum of Climate Scores 6-10) / (Sum of total Climate Scores)	Climate Match Category
0.000≤X≤0.005	Low
0.005<X<0.103	Medium
≧0.103	High

7 Certainty of Assessment

The certainty of assessment is high. There was more than adequate quality information available about *Gasterosteus aculeatus*. Records of introduction and establishment were found. Information on impacts of the introductions was not plentiful but clearly indicates ecologically detrimental impacts.

8 Risk Assessment

Summary of Risk to the Contiguous United States

The Threespine Stickleback (*Gasterosteus aculeatus*) is native to most inland coastal waters above 30°N. It is used as a research model and is occasionally commercially fished. The species has a marine and a freshwater/brackish form. This ERSS is only for the freshwater/brackish form. The history of invasiveness for *Gasterosteus aculeatus* is high. Records of introductions and establishment were found and records of detrimental impacts were available. The main impacts result from the fish's aggressive nature in its foraging for food, its ability to hybridize with both native sticklebacks and local, genetically distinct subspecies, and introductions of new parasites in conjunction with the introductions of *G. aculeatus*. The climate match was high. The native range of this species is in the United States and the highest match centers around the native range but indicates that there are many areas outside the native range that could have suitable climate to support this species. The certainty of assessment is high. The overall risk assessment category is high.

Assessment Elements

- **History of Invasiveness (Sec. 3): High**
- **Climate Match (Sec. 6): High**
- **Certainty of Assessment (Sec. 7): High**
- **Remarks/Important additional information** Native to northern coastal areas of the United States. Hybridizes easily with other sticklebacks.
- **Overall Risk Assessment Category: High**

9 References

Note: The following references were accessed for this ERSS. References cited within quoted text but not accessed are included below in Section 10.

Amundsen, P.-A., K. D. Lafferty, R. Knudsen, R. Primicerio, R. Kristoffersen, A. Klemetsen, A. M. Kuris. 2013. New parasites and predators follow the introduction of two fish species to a subarctic lake: implications for food-web structure and functioning. Oecologia 171:993–1002.

Bailly, N. 2013. *Gasterosteus aculeatus* Linnaeus, 1758. *In* World Register of Marine Species. Available: http://www.marinespecies.org/aphia.php?p=taxdetails&id=126505. (January 2017).

BISON. 2017. Biodiversity Information Serving Our Nation (BISON). U.S. Geological Survey. Available: https://bison.usgs.gov. (October 2017).

EDDMapS. 2017. Early Detection & Distribution Mapping System. University of Georgia, Center for Invasive Species and Ecosystem Health, Tifton, Geogria. Available: https://www.eddmaps.org/distribution/viewmap.cfm?sub=61345. (January 2017).

Eschmeyer, W. N., R. Fricke, and R. van der Laan, editors. 2017. Catalog of fishes: genera, species, references. Available: http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp. (October 2017).

FAO (Fisheries and Agriculture Organization of the United Nations). 2016. Database on introductions of aquatic species. FAO, Rome. Available: http://www.fao.org/fishery/introsp/search/en. (May 2016).

Froese, R., and D. Pauly, editors. 2016. *Gasterosteus aculeatus* Linnaeus, 1758. FishBase. Available: http://www.fishbase.se/summary/Gasterosteus-aculeatus.html. (May 2016).

Fuller, P., K. Dettloff, and R. Sturtevant. 2016. *Gasterosteus aculeatus*. U.S. Geological Survey, Nonindigenous Aquatic Species Database, Gainesville, Florida. Available: http://nas.er.usgs.gov/queries/FactSheet.aspx?SpeciesID=702. (May 2016).

GBIF Secretariat. 2016. GBIF backbone taxonomy: *Gasterosteus aculeatus* Linnaeus, 1758. Global Biodiversity Information Facility, Copenhagen. Available: http://www.gbif.org/species/4286327. (May 2016).

ITIS (Integrated Taxonomic Information System). 2016. *Gasterosteus aculeatus* Linnaeus, 1758. Integrated Taxonomic Information System, Reston, Virginia. Available: http://www.itis.gov/servlet/SingleRpt/SingleRpt?search_topic=TSN&search_value=166365. (May 2016).

Lenhardt, M., G. Markovic, A. Hegedis, S. Maletin, M. Cirkovic, Z. Markovic. 2011. Non-native and translocated fish species in Serbia and their impact on the native ichthyofauna. Reviews in Fish Biology Fisheries. Reviews is Fish Biology and Fisheries 21(3):407–421.

Lusk, S., V. Lusková, and L. Hanel. 2010. Alien fish species in the Czech Republic and their impact on the native fish fauna. Folia Zoologia 59(1):57–72.

NatureServe. 2014. NatureServe Explorer: an online encyclopedia of life, version 7.1. NatureServe, Arlington, Virginia. Available: http://explorer.natureserve.org. (June 2014).

NatureServe. 2015. *Gasterosteus aculeatus*. The IUCN Red List of Threatened Species 2015. Available: http://www.iucnredlist.org/details/full/8951/0. (January 2017).

NOBANIS. 2017. *Gasterosteus aculeatus.* Available: https://www.nobanis.org/species-info/?taxaId=12211. (January 2017).

Rolbiecki, L. 2004. Larvae of *Anguillicola crassus* (Nematoda, Dracunculoidea) in stickleback (*Gasterosteus aculeatus*) and smelt (*Osmerus eperlanus*) from the Gulf of Gdańsk and the Vistula Lagoon. Zoologica Poloniae 49(1–4):29–35.

Sanders, S., C. Castiglione, and M. Hoff. 2014. Risk assessment mapping program: RAMP. U.S. Fish and Wildlife Service.

USFWS (U.S. Fish and Wildlife Service). 2017. Species profile for unarmored Threespine stickleback (*Gasterosteus aculeatus williamsoni*). ECOS – Environmental Conservation Online System. Available: http://ecos.fws.gov/ecp0/profile/speciesProfile?spcode=E00X. (January 2017).

VertNet. 2017. VertNet. Available: h http://portal.vertnet.org/search?q=Gasterosteus+aculeatus. (October 2017)

Wisconsin SeaGrant. 2016. Threespine stickleback (*Gasterosteus aculeatus*). University of Wisconsin Sea Grant Institute, Madison. Available: http://seagrant.wisc.edu/Home/Topics/InvasiveSpecies/InvasiveSpeciesFactSheets/Details.aspx?PostID=2003. (May 2016).

10 References Quoted But Not Accessed

Note: The following references are cited within quoted text within this ERSS, but were not accessed for its preparation. They are included here to provide the reader with more information.

Ahnelt, H., H. Pohl, H. Hilgers, and H. Splechtna. 1998. The Threespine stickleback in Austria (*Gasterosteus aculeatus* L., Pisces: Gasterosteidae)–Morphological variations. Annalen des Naturhistorischen Museums in Wien 100B:395–404

Bailey, R. M., and G. R. Smith. 1991. Names of Michigan fishes. Unpublished mimeograph.

Baker, J., S. Foster, and M. Bell. 1995. Armor morphology and reproductive output in threespine stickleback, *Gasterosteus aculeatus*. Environmental Biology of Fishes 44:225–233.

Balon, E. K. 1967. Three-spined stickleback–*Gasterousteus aculeatus* Linnaeus, 1758 in the Danube near Bratislava. Ac Rer Nat Mus Nat Slov 13:127–134

Banarescu, B. 1964. Fauna Republicii populare romine (Pisces– Osteichthyes). Academiei Republicii Romine, Bucuresti, Romania. (In Romanian.)

Banister, K. 1986. Gasterosteidae. Pages 640–643 *in* P. J. P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen, and E. Tortonese, editors. Fishes of the north-eastern Atlantic and the Mediterranean, volume 2. UNESCO, Paris.

Bastl, I. 1976. Another evidence of occurrence of threespined stickleback (*Gasterosteus aculeatus* Linnaeus, 1758) in the Danube river floodplain on Czechoslovak territory. Biology 31:885–886

Bell, M. A. 1982. Melanism in a high elevation population of *Gasterosteus aculeatus*. Copeia 1982:829–835.

Bell, M. A., W. E. Aquirre, and N. J. Buck. 2004. Twelve years of contemporary armor evolution in a threespine stickleback population. Evolution 58(4):814–824.

Bell, et al. 1994. [Source material did not give full citation for this reference.]

Bell, M. A., and G. Orti. 1994. Pelvic reduction in threespine stickleback from Cook Inlet Lakes: geographical distribution and intrapopulation variation. Copeia 1994:314–325.

Berinkey, L. 1960. The stickleback (*Gasterosteus aculeatus*), a new fish species from Hungary. Vertebr Hung, Mus Hist Nat Hung 2:1–10

Bigelow, H. B., and W. W. Welsh. 1925. Fishes of the Gulf of Maine. Bulletin of the United States Bureau of Fisheries 40:1–567.

Breder, C. M., and D. E. Rosen. 1966. Modes of reproduction in fishes. T.F.H. Publications, Neptune City, New Jersey.

Burr, B. M. 1991. The fishes of Illinois: an overview of a dynamic fauna. Proceedings of our living heritage symposium. Illinois Natural History Survey Bulletin 34(4):417–427.

Cakic, P., M. Lenhardt, and Z. Petrovic. 2000. The first record of *Gasterosteus aculeatus* L. 1758 (Pisces: Gasterosteidae) in the Yugoslav section of the Danube. Ichthyology 32:79–82

Cresko, W., K. McGuigan, P. Phillips, and J. Postlethwait. 2007. Studies of threespine stickleback developmental evolution: progress and promise. Genetica 129:105–126.

Cudmore-Vokey, B., and E. J. Crossman. 2000. Checklists of the fish fauna of the Laurentian Great Lakes and their connecting channels. Canadian Manuscript Report of Fisheries and Aquatic Science 2500.

Czypinski, G. D., A. K. Hintz, M. T. Weimer, and A. Dextrase. 1999. Surveillance for Ruffe in the Great Lakes, 1999. U.S. Fish and Wildlife Service, Ashland, Wisconsin.

Czypinski, G. D., A. K. Bowen, M. T. Weimer, and A. Dextrase. 2001. Surveillance for Ruffe in the Great Lakes, 2001. U.S. Fish and Wildlife Service, Ashland, Wisconsin.

Day, T., J. Pritchard, and D. Schluter. 1994. A comparison of two sticklebacks. Evolution 48(5):1723–1734.

Fedorov, V. V., I. A. Chereshnev, M. V. Nazarkin, A. V. Shestakov, and V. V. Volobuev. 2003. Catalog of marine and freshwater fishes of the northern part of the Sea of Okhotsk. Dalnauka, Vladivostok, Russia.

Gibson, D. W. 1982. Range extension of the threespine stickleback, *Gasterosteus aculeatus*, to Manitoulin Island, Ontario. Canadian Field-Naturalist 96(1):86.

Grand. 2000. [Source material did not give full citation for this reference.]

Haglund, T. R., D. G. Buth, and R. Lawson. 1992. Allozyme variation and phylogenetic relationships in Asian, North American, and European populations of the threespine stickleback, *Gasteosteus aculeatus*. Copeia 1992(2):432–443.

Hartel, K. E., D. B. Halliwell, and A. E. Launer. 1996. An annotated working list of the inland fishes of Massachusetts. Available: http://www.mcz.harvard.edu/fish/ma_fam.htm. (June 2011).

Hatfield, T. 2001a. Status of the stickleback species pair, *Gasterosteus* spp., in Hadley Lake, Lasqueti Island, British Columbia. Canadian Field-Naturalist 115(4):579–583.

Hatfield, T. 2001b. Status of the stickleback species pair, *Gasterosteus* spp., in the Vananda Creek watershed of Texada Island, British Columbia. Canadian Field-Naturalist 115(4):584–590.

Hatfield, T., and J. Ptolemy. 2001. Status of the stickleback species pair, *Gasterosteus* spp. in Paxton Lake, Texada Island, British Columbia. Canadian Field-Naturalist 115(4):591–596.

Hirsch, J. 1998. Nonindigenous fish in inland waters: response plan to new introductions. Minnesota DNR Special Publication 152.

Hubbs. 1919. [Source material did not give full citation for this reference.]

Huntingford, F., and P. Wright. 1993. Behavioral ecology of fishes. Harwood Academic Press, Switzerland.

Jakobsson, S., B. Borg, C. Haux, and S. J. Hyllner, 1999. An 11-ketotestosterone induced kidney-secreted protein: the nest building glue from male three-spined stickleback, *Gasterosteus aculeatus*. Fish Physiology and Biochemistry 20:79–85.

Johnston, C. E. 1991. Discovery of the threespine stickleback (*Gasterosteus aculeatus*) (Pisces: Gasterosteidae) in the Lake Michigan drainage, Illinois. Transactions of the Illinois State Academy of Science 84(3&4):173–174.

Knudsen, R., A. Klemetsen, and F. J. Staldvik. 1996. Parasites as indicators of individual feeding specialization in Arctic charr during winter in northern Norway. Journal of Fish Biology 48:1256–1265.

Kottelat, M., and J. Freyhof. 2007. Handbook of European freshwater fishes. Publications Kottelat, Cornol, Switzerland, and Freyhof, Berlin.

Mandrak, N. E., and E. J. Crossman. 1992. Postglacial dispersal of freshwater fishes in Ontario. Canadian Journal of Zoology 70:2247–2259.

Marchinko. 2008. [Source material did not give full citation for this reference.]

Mattern, M., D. Kingsley, C. Peichel, J. Boughman, F. Huntingford, S. Coyle, S. Ostlund-Nilsson, D. McLennan, B. Borg, I. Mayer, M. Pall, I. Barber, and I. Katsiadaki. 2007. Biology of the three-spined stickleback. CRC Press, Boca Raton, Florida.

McDowall, R. M. 1988. Diadromy in fishes: migrations between freshwater and marine environments. Croom Helm, London.

McPhail, J. D. 1969. Predation and the evolution of a stickleback (*Gasterosteus*). Journal of Fisheries Research Board Canada 26(12):3183–3028.

Messler, A., M. Wund, B. John, and S. Foster. 2007. The effects of relaxed and reversed selection by predators on the antipredator behavior of the threespine stickleback, *Gasterosteus aculeatus*. Ethology 113: 853–863.

Metcalfe. 1989. [Source material did not give full citation for this reference.]

Miller R. R., and C. L. Hubbs. 1969. Systematics of *Gasterosteus aculeatus* with particular reference to intergradation and introgression along the Pacific Coast of North America: a commentary on a recent contribution. Copeia 1969(1):52–69.

Morrow, J. E. 1980. The freshwater fishes of Alaska. University of British Columbia Animal Resources Ecology Library.

Moyle, P. B. 1976a. Inland fishes of California. University of California Press Berkeley.

Moyle, P. B. 1976b. Fish introduction in California: history and impact on native fishes. Biological Conservation 9:101–118.

Moyle, P. B., J. E. Williams, and E. D. Wikramanayake. 1989. Fish species of special concern of California. Final Report. California Department of Fish and Game, Inland Fisheries Division, Rancho Cordova.

Muus, B. J., and J. G. Nielsen. 1999. Sea fish. Scandinavian Fishing Year Book, Hedehusene, Denmark.

Nikolskii, G. V. 1961. Special ichthyology. Israel Program for Scientific Translations.

Orti, G., M. A. Bell, T. E. Reimchen, and A. Meyer. 1994. Global survey of mitochondrial DNA sequences in the threespine stickleback: evidence for recent migrations. Evolution 48:608–622.

Page, L. M., and B. M. Burr. 1991. A field guide to freshwater fishes of North America north of Mexico. The Peterson Field Guide Series, volume 42. Houghton Mifflin, Boston.

Page, L. M., and C. A. Laird. 1993. The identification of the nonnative fishes inhabiting Illinois waters. Center for Biodiversity, Illinois Natural History Survey, Technical Report 1993(4). Illinois Department of Conservation, Springfield.

Peuhkuri, N. 1998. Shoal composition, body size and foraging in sticklebacks. Behavioral Ecology and Sociobiology 43:333–337.

Pinder, A. C. 2001. Keys to larval and juvenile stages of coarse fishes from fresh waters in the British Isles. Freshwater Biological Association, Scientific Publication 60. The Ferry House, Far Sawrey, Ambleside, Cumbria, UK.

Reimchen, T. E. 1992. Extended longevity in a large-bodied stickleback, *Gasterosteus*, population. Canadian Field Naturalist 106:129–131.

Reimchen. 2000. [Source material did not give full citation for this reference.]

Ridler, K. 2004. Foreign fish invading reservoir. Available: statesmanjournal.com. (April 2004).

Riede, K. 2004. Global register of migratory species - from global to regional scales. Final Report of the R&D-Projekt 808 05 081. Federal Agency for Nature Conservation, Bonn.

Riehl, R., and H. A. Baensch. 1991. Aquarien atlas. Band. 1. Melle: Mergus, Verlag für Natur- und Heimtierkunde, Germany.

Ross, S. T. 1973. The systematics of *Gasterosteus aculeatus* (Pisces: Gasterosteidae) in central and southern California. Contributions in Science 243, Los Angeles Natural History Museum, Los Angeles.

Roth, et al. 2011. [Source material did not give full citation for this reference.]

Safran, P. 1990. Drifting seaweed and associated ichthyofauna: floating nursery in Tohoku waters. La mer 28(4):225–239.

Safran, P., and M. Omori. 1990. Some ecological observations on fishes associated with drifting seaweed off Tohoku coast. Japanese Marine Biology 105:395–402.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin of Fisheries Research Board of Canada 184:1–966.

Shaw, K., M. Scotti, and S. Foster. 2007. Ancestral plasticity and the evolutionary diversification of courtship behavior in threespine sticklebacks. Animal Behaviour 73:415–422.

Sigler, W. F., and J. W. Sigler. 1987. Fishes of the Great Basin: a natural history. University of Nevada Press, Reno.

Smith, C. L. 1985. The inland fishes of New York State. New York State Department of Environmental Conservation, Albany.

Spillman, C.-J. 1961. Faune de France: Poissons d'eau douce. Fédération Française des Sociétés Naturelles, Tome 65. Paris.

Stedman, R. M., and C. A. Bowen. 1985. Introduction and spread of the threespine stickleback (*Gasterosteus aculeatus*) in Lakes Huron and Michigan. Journal of the Great Lakes Research 11:508–511.

Stedman and Bowman. 1985. [Source material did not give full citation for this reference].

Swift. 1993. [Source material did not give full citation for this reference].

Swift, C. C., T. R. Haglund, M. Ruiz, and R. N. Fisher. 1993. The status and distribution of the freshwater fishes of southern California. Bulletin of the Southern California Academy of Sciences 92(3):101–167.

Thompson, C. E., E. B. Taylor, and J. D. McPhail. 1997. Parallel evolution of lake-stream pairs of threespine sticklebacks (*Gasterosteus aculeatus*) inferred from mitochondrial DNA variation. Evolution 51:1955–1965.

Tilmant, J. T. 1999. Management of nonindigenous aquatic fish in the U.S. National Park System. National Park Service.

Wood, P. M. 2003. Will Canadian policies protect British Columbia's endangered pairs of sympatric sticklebacks? Fisheries 28(5):19–26.

Wootton, R. J. 1976. The biology of the sticklebacks. Academic Press, New York.