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Widespread Evidence for Rapid Recent Changes in Global Range and Abundance of Threespine Stickleback (*Gasterosteus aculeatus*)

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ABSTRACT

The threespine stickleback, *Gasterosteus aculeatus*, has undergone dramatic increases in abundance in parts of its historical native range, and it is also undergoing a major range expansion. We review available information and discuss the vectors and sources of the species' range expansions, the genetic characteristics of recently founded populations and the ecological consequences of both stickleback introductions and increases in abundance. Dramatic range expansions occurred in the Caspian Sea drainage, large rivers in the Black Sea drainage, reservoirs of the Rhine basin, isolated lakes in North America and Japan and remote islands in the Arctic. Likely reasons for these range expansions include canal construction, accidental inclusion with stocking of commercially valuable fish, intentional release by aquarists and fishermen and climate change. In some cases, range expansions of stickleback were likely facilitated by genetic admixture of previously separated lineages, as well as by high-standing genetic variation that promotes rapid adaptation to new habitats. Accordingly, range expansions are often accompanied by striking increases in abundance, although these are two distinct processes. Notably, population growth within the species' native range, particularly in the White and Baltic Seas, has been observed alongside expansions into new areas. Where stickleback colonise new habitats or increase in abundance, extensive ecological impacts on ecosystems typically occur. Given these massive and widespread changes, the species has the potential to provide considerable insight into the evolutionary and ecological effects of human impacts on aquatic ecosystems.

1 | Introduction

The threespine stickleback, *Gasterosteus aculeatus* (henceforth simply "stickleback"), is known as a model species in evolutionary biology (Bell and Foster 1994; McKinnon and Rundle 2002; Östlund-Nilsson, Mayer, and Huntingford 2007; Hendry et al. 2013; Reid et al. 2021). A number of studies are also devoted to the ecology of this species, including those addressing the ecological effects of the stickleback on aquatic food webs (Candolin 2019; Eklöf et al. 2020; Lajus et al. 2020; Bretzel et al. 2021; Hudson et al. 2021). Moreover, stickleback appears to be particularly successful under certain disturbed conditions, such as those caused by fishing, pollution, habitat disruption or climate change (Iacarella et al. 2018; Olin et al. 2022). We might therefore expect stickleback to show rapid range expansions and abundance increases in our increasingly modified world.

Indeed, stickleback range expansions appear common through both natural and artificial means and routes. Stickleback has been introduced into (or recently become established in) dozens to hundreds of lakes as a result of diverse events such as earthquake-caused land upheaval (Lescak et al. 2015), tsunamis (Kume et al. 2018), canal construction (Marques et al. 2019), reservoir construction (Hendry et al. 2013), accidental introductions (Yoshida et al. 2016) or intentional introductions (Marques et al. 2018). Events such as these—alongside recent climate change—have led to the appearance of new stickleback populations in isolated lakes, new tributaries within drainages, new drainages, or even entirely new geographic regions. These expansions are expected to continue, and to accelerate, in the future—especially when sticklebacks colonise (typically through introductions) new drainages or regions and then spread on their own from the initial point of colonisation. The evolutionary and ecological consequences of this massive re-organisation of the species range are not known.

Many populations of stickleback—even in their native range—have shown dramatic recent increases in abundance. (Of course, the species also has decreased in abundance in some other locations; McPhail 1994; Haught and von Hippel 2011; Morozińska-Gogol 2015). Within the last two to three decades in the White Sea, stickleback populations have drastically increased, becoming the most abundant fish species in the sea (Ivanova et al. 2016; Lajus et al. 2020, 2021). Multifold increases in stickleback abundance also have occurred in recent decades in the Baltic Sea (Bergström et al. 2015; Olsson et al. 2019). Since 2012, in Lake Constance, an invasive population of stickleback rapidly increased in the pelagic zone, reaching abundances of up to several thousand individuals per ha (Roch et al. 2018; Eckmann and Engesser 2019). Sticklebacks are an important intermediate link between different trophic levels of the ecosystem (Bergström et al. 2015; Candolin 2019; Genelt-Yanovskaya et al. 2022). Therefore, changes in stickleback abundance have the potential to have important ecological effects that cascade to the ecosystem level given the species' key role in the food web.

This combination of range expansions, abundance increases and potential critical effects on communities and ecosystems suggests that stickleback could be a major player in global environmental change—either by moderating or exacerbating the effects of other disturbances. Further, the contemporary, or 'rapid' evolution of stickleback in new environments could have additional cascading effects on their range expansion and abundance changes. Our goal is to provide a context for these potential future effects by reviewing the global distribution of stickleback range expansions and also, instances of particularly dramatic abundance increase in native range.

The following systematic review and discussion will emphasise freshwater, anadromous and occasionally estuarine populations—a focus that reflects existing research efforts. However, we also refer to apparent expansions of marine ranges, which are less represented in the current literature and can facilitate colonisation of new freshwater or estuarine habitats. We discuss major abundance increases in some well-studied aquatic environments—especially the Baltic and White Seas and Lake Constance. Although we emphasise the colonisation of new locations, we also address recolonizations of habitats where stickleback had been extirpated. All of these types of events can help to inform the nature of stickleback colonisation of new locations and abundance increases in old and new habitats.

2 | Materials and Methods

We conducted a literature search in the ISI Web of Science Core Collection (https://apps.webofknowledge.com, last visited 3.08.2024) and the Russian Scientific Electronic Library (https://elibrary.ru, last visited 15.06.2024). These searches used the following keywords: 'three-spined stickleback', 'threespine stickleback' and '*Gasterosteus aculeatus*'. We examined monographs and articles written or edited by researchers whose work was discovered via these database searches. In total, we examined 1384 publications in Web of Science and 643 articles in the Russian Scientific Electronic Library. Based on titles and abstracts, we selected and further examined publications that addressed changes in the distribution or abundance of stickleback.

We then conducted additional searches on Google Scholar using a variety of keywords in combination with the species name (*Gasterosteus aculeatus*): alien, coloni*, dispers*, expan*, geograph*, indigenous, introduc*, inva*, non native, rotenone, stock (and) uninhabited. For the searches including alien, inva* or non native, the first 30 results were checked by abstract and then, when deemed potentially relevant as a reference, by article content. For the searches including coloni*, expan* or introduc*, the first 20 results were checked. For the searches including dispers*, indigenous, rotenone, stock or uninhabited, the first 10 results were checked. These different cut-offs were chosen because they included the relevant literature in each case. A supplementary search for public sector information discovered one report from the U.S. Fish and Wildlife Service (2011) that included many relevant references, which were then examined.

We included information on museum specimens collected outside the species' native range by N.G. Poznyak and described in conference abstracts (Poznyak and Frolenko 1998; Poznyak 2005). In some cases, we could also examine archival sources; in particular, to define the time when stickleback first appeared in the Caspian Sea drainage. In that case, we studied documents from the archive of Karl Ernst von Baer, which contains information about samples collected during his expedition to the Caspian Sea from 1853 to 1857.[1]

Each observation of stickleback could fall into one of three categories: (i) its native range where the species has been found since the first faunal surveys; (ii) a range expansion where the species was not reported in reliable initial surveys but was reported in more recent surveys and (iii) a re-appearance where the species was initially reported, then not reported in reliable surveys for a period of time, and then reported again in recent surveys.

The native range of the stickleback was defined as follows: fresh and coastal marine waters along the European shoreline from the Barents Sea to the Black Sea, the eastern (Asian) shoreline of the Black Sea, Turkey and Syria, northern Africa, islands of the North Atlantic, the northeastern and northwestern shorelines of northern North America and the eastern Asia shoreline from the Bering Strait and adjacent islands to Japan. The stickleback is unknown in the marine waters open waters of the Mediterranean Sea, although they live in many freshwater systems of its basin and some brackish lagoons; they are found in the Black Sea (Băcescu and Mayer 1956; Ziuganov 1991; Bell and Foster 1994; Paepke 2002; von Hippel et al. 2016; Bolshakova and Bolshakov 2018; Moreira et al. 2022; Şen et al. 2024). The absence of information on stickleback being present at a particular time and place does not necessarily mean that the species was absent; yet their absence from comprehensive surveys does suggest they were, at the least, very rare. We also noted instances within their native range where stickleback naturally colonised (e.g., after a tsunami or glacial retreat) specific locations from which they were formerly absent, or when stickleback was introduced by humans into new (or restored) locations. These events still represent range expansions, just on a small scale.

Finally, although we focused on range expansions and established populations, we also aimed to understand how often the opposite phenomena, such as range contraction and population decline, occur. To do this, we used the same keywords, adding terms like reduc*, contract*, decreas* and declin* to our search in Scopus for the period 2014–2024 (https://www.elsevier.com/products/scopus, last visited 21.09.2024). From the titles, we selected papers that addressed changes in range or abundance and categorised them into three groups: those reporting increases, decreases or no changes in range or population numbers.

3 | Results

Here, we present results organised geographically. The state ownership of water basins is given according to the current situation, although references to past geopolitical divisions are sometimes made.

An analysis of 1117 publications referenced by Scopus revealed 30 papers addressing changes in range or abundance. Of these, 24 (80%) reported range expansion and increased abundance, 2 (7%) found no changes and 4 (13%) reported stickleback disappearance or population decline. These declines were observed near the southern distribution border in California, Italy, Spain and Japan and will be cited in the relevant sections.

3.1 | North America

Stickleback occurs naturally along the eastern coast of North America from at least the Cape Fear estuary in North Carolina to Hudson Bay and Baffin Island. Along the western coast, they occur from northwestern Baja California, México, to northern Alaska (Scott and Crossman 1973). The species is native in the Lake Ontario basin below Niagara Falls (Stedman and Bowen 1985; Figure 1).

There are several examples of lakes and rivers recently colonised by stickleback in northern North America (Figure 1). In 1964, land upheaval caused by the Great Alaska Earthquake formed new lakes on Middleton Island, Alaska. These new habitats were occupied by populations of formerly marine sticklebacks, which then rapidly adapted to their new freshwater habitats (Lescak et al. 2015). In the late 1970s, a glacial retreat in Alaska's Stonefly Creek in Glacier Bay created new freshwater habitats that were rapidly colonised by stickleback (Milner et al. 2011). In addition to these natural events, other stickleback colonisation events resulted directly from human activities. In Canada, Gloria Lake and Long Lake in the Yukon Territory received stickleback through stocking associated with the introduction of salmonids in the 1980s (Crossman 1991). In Alaska, stickleback was extirpated from many lakes by invasive northern pike *Esox lucius* or by Rotenone treatment used to eliminate the invader (Bell, Aguirre, and Buck 2004; Bell et al. 2016). Some of these lakes have since been recolonized by stickleback either naturally (e.g., Loberg Lake: Bell, Aguirre, and Buck 2004) or by intentional releases. Examples of the latter situation include Cheney Lake and Scout Lake (Bell et al. 2016; Wund et al. 2016) and more than 10 lakes on the Kenai Peninsula (A. Hendry, unpublished). In some cases, new stickleback populations are found in isolated post-Rotenone lakes without any record of their release, suggesting undocumented releases by local people (Arc Lake, Kenai Peninsula, A. Hendry, unpublished).

In southwestern North America, range contractions have been observed (Ono, Williams, and Wagner 1983; Richmond et al. 2024), yet range expansions are also occurring. For instance, several introductions of stickleback have occurred in California, USA. One, in Holcomb Creek in the San Bernardino Mountains, originally was thought to result from continued uplift since deglaciation (Bell 1982); yet more recent work suggests an origin in the 1930s during trout stocking (Bell 1982; Sigler and Sigler 1987). Appearance of stickleback in the Mohave River from 1938 to 1940 was probably due to bait dumping by anglers; and their appearance in the Santa Maria River in 1940 was probably due to trout stocking (Miller and Hubbs 1969). Other introductions likely caused by bait dumping in California include Death Valley's Mono Lake in the 1950s; and also Big Bear, Gull and June lakes in the 1960s (Miller and Hubbs 1969; Moyle 1976). In the early 1970s, stickleback recolonized Summit Lake in Washington following Rotenone treatment (Hagen and Gilbertson 1972). In the Upper Deschutes River basin in Oregon, stickleback was introduced as bait in the 1990s (Koketsu 2004).

In eastern North America, several natural range expansions and introductions have occurred. In the 1950s, an introduction occurred in Olmsted Park in Boston, Massachusetts, due to the escape of stickleback from a museum exhibit pond (Hartel, Halliwell, and Launer 1996). In 1988, stickleback appeared at the Drakes Island Marsh (Webhannet River basin) in Maine after it had been restored (Dionne, Short, and Burdick 1999). In Canada, two lakes of the Avalon Peninsula, Newfoundland, received intentional introductions of stickleback as forage fish before the mid-1970s (Van Zyll de Jong, Gibson, and Cowx 2004). The northmost report of stickleback in the region appears in the U.S. Fish & Wildlife Service report (2011) as Prince of Wales Island in Arctic Canada (Figure 1), but no

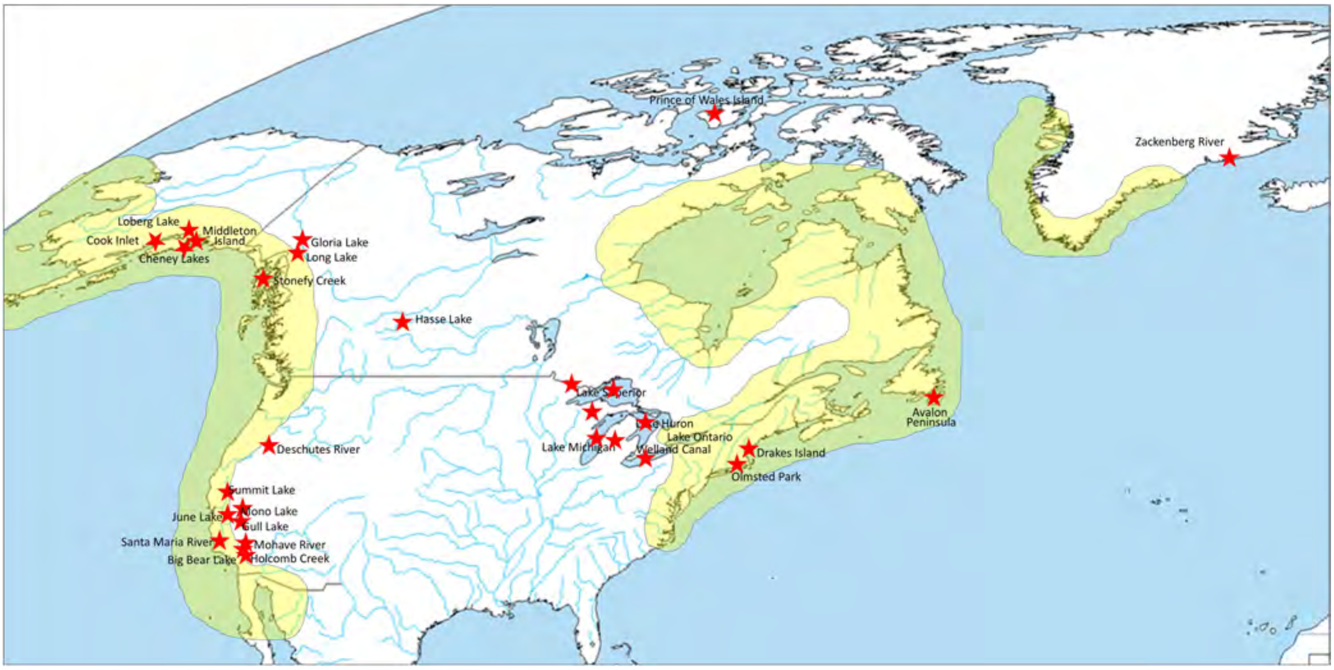

FIGURE 1 | Native range (yellow filling) and new records (red asterisks) of threespine stickleback in North America (based on U.S. Fish and Wildlife Service 2011). Note that here and in other maps, in some cases new records are inside the native range as not all waterbodies there were originally inhabited by stickleback.

contextual information was provided. As this location is well beyond the known native range, we considered it either to be an error or a sample of non-breeding marine fish, or an introduction—but we have no further information on this report.

Most of the above-range expansions are rather small-scale; yet some small-scale events may eventually cause broader expansions. For instance, probably the greatest range expansion of stickleback in North America thus far has been in the Laurentian Great Lakes. Before 1980, the species was reported only downstream of Niagara Falls in Lake Ontario (Stedman and Bowen 1985; Nelson and Paetz 1992). After 1980, however, the species was documented upstream of Niagara Falls, and it is now in Lakes Erie, Huron, Michigan and Superior basins (Roth et al. 2013). This range expansion has been attributed to either the artificial Welland Canal (Smith 1985), to bait dealers (Stedman and Bowen 1985) or to ballast waters (Wonham et al. 2000). Several other small-scale colonisation events could have important implications. In the 1980s, sticklebacks were discovered in Hasse Lake, Alberta, where they were previously absent (Nelson and Harris 1987; Nelson and Paetz 1992). Sticklebacks have appeared in several lakes in the Yukon Territory (N. Millar, pers. comm.). Both of these events have the potential to drive massive future range expansions because they occurred in the upper reaches of the Saskatchewan/Nelson River drainage (Hasse Lake) and the Yukon River drainage (Gloria & Long), which respectively offer > 1,000,000 and > 800,000 km^2 of drainage currently devoid of native stickleback.

In Greenland, which is part of North America but also neighbours the Eurasian Arctic, sticklebacks have expanded their range northwards in the eastern part of the island. They were detected from 1998 to 2010 in the Zackenberg River and several adjacent lakes, about 2.5° north of their previously known northern range limit (Nielsen, Hamerlik, and Christoffersen 2012; Jeppesen et al. 2017). Sticklebacks have also been released into several lakes in Greenland for research purposes (B. Matthews, pers. comm.).

3.2 | Eurasian Arctic

According to historical literature, the eastern border of the stickleback's native range in the Eurasian Arctic was the southeast coast of the Barents Sea, to the Khaipudyrskaya inlet east of Pechora Inlet (Figure 2). Sticklebacks were known to also spawn in some rivers and lakes in the southern part of the Novaya Zemlya Archipelago (Knipowitsch 1897). However, we found no reports in the 19th and 20th centuries of stickleback in freshwater habitats of other Barents Sea islands. Further, stickleback were historically—and probably now as well—absent along the entire Siberian coast up to the Bering Strait (Chereshnev 2008; Dolgov et al. 2018). In the west, sticklebacks were historically present in many lakes and rivers of Iceland (Berg 1949).

Recent studies show evidence of range expansion by stickleback to the north and northeast of the above historical records. In 2001 and 2006, four stickleback individuals were found in Straumsjøen and Linne Lakes of the Svalbard Archipelago, which could be related to warming conditions (Svenning, Aas, and Borgstrøm 2015). Recently, stickleback was noted in Abrosimov Inlet on the eastern coast of the Novaya Zemlya Archipelago (Bolshakova and Bolshakov 2018) and in Baidaratskaya Bay (Dolgov et al. 2018), suggesting the species' northeastwards range extension. Further east, in the Ob Inlet of the Kara Sea, local people reported regular occurrence of

FIGURE 2 | Native range (yellow filling) and new records (red asterisks) of threespine stickleback in the Eurasian Arctic.

stickleback in recent years during summer periods, and the species was also observed in a small lake near Antipaiuta village (V. Alekseev, pers. comm., 2018).

The northernmost report in the region was of two dead sticklebacks on Oktiabrskoy Revoliutsii (October Revolution) Island in the Severnaya Zemlya archipelago (Chernova et al. 2021). This archipelago is some 1000 km north of Ob Inlet and about 200 km north of the nearest mainland, the Taimyr Peninsula. The report is based on two full-plated individuals dropped by a Kittiwake *Rissa tridactyla* in 1985. It is most likely that the two fish originated from marine waters near the island.

Several small-scale introductions have also taken place. In Iceland, sticklebacks were introduced into man-made ponds near Nedri As farm in 2003 (Kristjánsson 2005). Also in Iceland, formerly anadromous (or marine) stickleback became land-locked due to the damming of a fjord in Snæfellsnes Peninsular for salmon ranching in 1987 (Kristjánsson, Skúlason, and Noakes 2002). Around the White Sea, sticklebacks were introduced into several freshwater ponds for research purposes (Ziuganov 1991; Terekhanova et al. 2014; Yurtseva et al. 2019).

In the White Sea, where marine sticklebacks prevail, they have shown a drastic increase in abundance over the last two to three decades. The density of stickleback on spawning grounds now often exceeds 100 individuals per square meter, and sometimes even doubles these values, representing what is likely the highest densities in spawning grounds for this species. Their numbers have increased by two to three orders of magnitude compared to the 1970s and 1980s. Historical analyses indicate that similar numbers occurred in the 1920s to 1940s, during a warm period in the Arctic (Lajus et al. 2021).

3.3 | North Sea

Sticklebacks are found throughout the North Sea, as well as in fresh waters of adjacent parts of the mainland and islands. Anadromous stickleback migrates upstream into several European rivers for spawning (Berg 1949; Wootton 1976; Ziuganov 1991; Figure 3)—yet it is the spread of freshwater populations in these larger river systems that are the most obvious instances of range expansion within the region.

Prior to the 1870s, stickleback occurred in the Rhine River only in its downstream sections. Since that time, the species has expanded into the upper parts of the river in Switzerland, which—as the result of various canals and water diversions—now links the North, Mediterranean and Black seas (Figure 3). Initial colonisation of the area appears to have resulted from introductions by aquarists (Lucek et al. 2010; Marques et al. 2019). In 1951, sticklebacks were first recorded in the littoral areas of Lake Constance (Muckle 1972) and then, in about 2012, they showed a massive expansion into the pelagic area of the lake (Roch et al. 2018; Hudson et al. 2021). This expansion is suggested to have been facilitated by genetic variation brought by secondary contact and admixture between two old lineages that mixed in the drainage (Marques et al. 2019). The rapid increase in stickleback in the pelagic zone of Lake Constance negatively influenced the growth and survival of native whitefish *Coregonus wartmanni*—and the authors concluded that it led to their dramatic population decline (Roch et al. 2018).

In the upper Odra River basin in the Czech Republic, sticklebacks were introduced by aquarists (Hanel 2003, as cited by Lojkásek and Lusk 2018), but now appear absent from that area (Lojkásek and Lusk 2018). Further, a number of small-scale introductions have taken place in the North Sea basin, including a pond in the city of Bergen (Norway) in 1987 (Le Rouzic et al. 2011; Raeymaekers 2011), and the drained area Wieringerwaard in the nature reserve Het Zwanenwater in The Netherlands. Colonisation in the latter case occurred after the polders were connected to the sea by a new fish ladder in 1988–1989 (Kemper 1995). Other undocumented introductions and expansions have surely occurred into various streams, lakes and ponds within the region.

3.4 | Mediterranean Sea

Anadromous and marine forms of stickleback were not recorded in the open waters of the Mediterranean Sea until the very recent discovery of this species in the marine waters of the Marmara Sea (Şen et al. 2024). However, they do still occur in various lagoons and estuaries. Further, freshwater resident forms inhabit some mountain rivers and lakes of the northern part of its basin, as well as on some islands (Figure 3). It was previously believed that the stickleback penetrated the Mediterranean Sea and settled in its basin during the glacial period (Lucek and

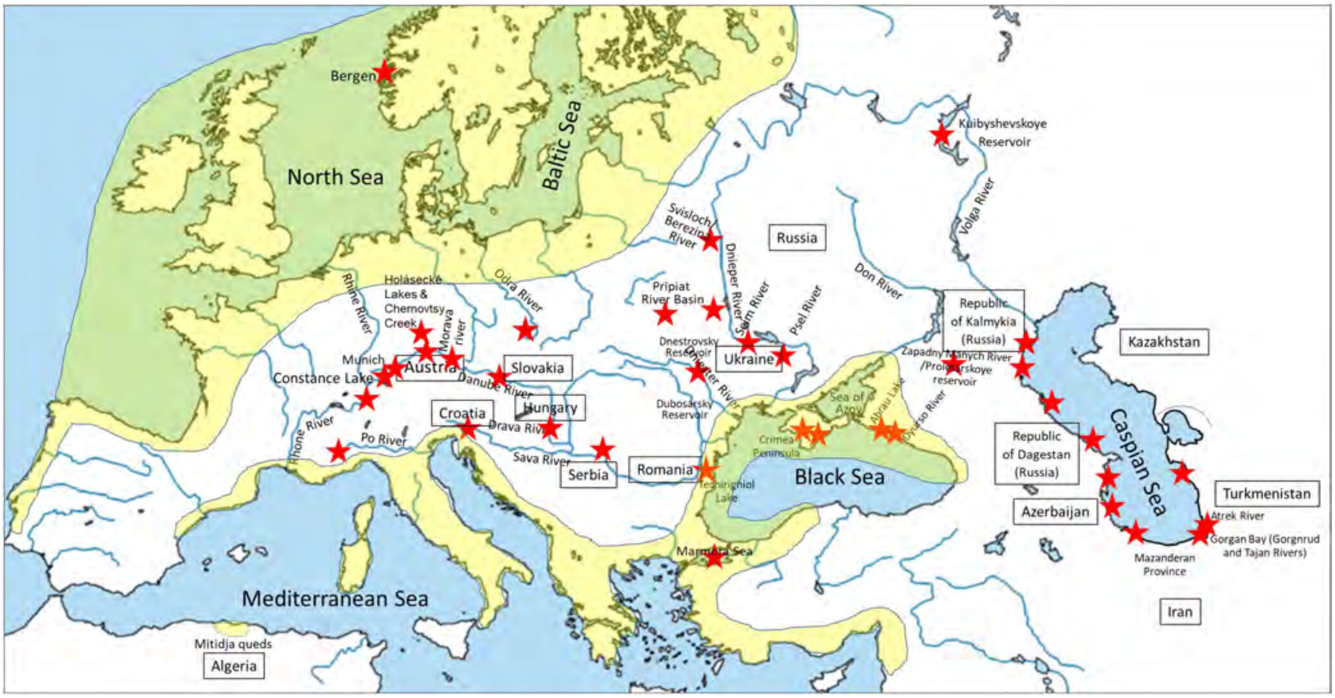

FIGURE 3 | Native range (yellow filling) and new records (red asterisks) of threespine stickleback in Europe, Africa and West Asia. Names of countries or republics are in boxes. Only rivers referred to in the text are named (based on Berg 1949; Wootton 1976; Ziuganov 1991; Vila et al. 2017).

Seehausen 2015), but genetic data indicate that the freshwater populations in this basin are relatively old compared to other European populations (e.g., Artamonova et al. 2022; Dahms et al. 2022). Yet, sticklebacks were also historically absent from larger areas, including all but the downstream areas of the Rhone and Po basins (Berg 1949). After the 1870s, stickleback colonised the upstream parts of both rivers, probably due to releases by aquarists (Lucek et al. 2010; Figure 3). A few reintroductions with very limited success (not indicated in Figure 3) took place in the 2000s and 2010s along the southern part of the Iberian Peninsula after the extinction of native populations in the 1980s and 1990s (Vila et al. 2017). Another example of stickleback extinction is in Lake Bracciano near Rome (Sharda and Argenti 2018).

Further, Cauvet (1930, as cited by Kara 2012) reported finding stickleback in Mitidja Oueds in the central part of the Algerian coast, and assumed they originated from Europe during the first wave of fish introductions in Algeria in 1858–1931. Boulenger (1916) also provides several references on stickleback in North Algeria in 1869–1874.

3.5 | Black Sea and the Sea of Azov

Before the mid-20th century, stickleback occurred in the Black Sea and the Sea of Azov, and in only the downstream sections of the large rivers entering those seas, including the Danube, Dnieper, Dniester and Don (Berg 1949; Figure 3). The situation has changed considerably in the last hundred years.

In the Danube River, sticklebacks were historically only in the downstream part, not more than 100 km from the mouth (Băcescu and Mayer 1956). In the 19th century, they expanded about 2000 km upstream to modern-day Austria (Ahnelt 1986; Figure 3). This spread is thought to have been driven by aquarists releasing fish into the wild (Ahnelt et al. 1998, as cited by Piria et al. 2018). Eventually, stickleback spread both upstream and downstream from the release locations. By the early 20th century, sticklebacks were found near the City of Munich, approximately 2500 km from the mouth (Grote, Vogt, and Hofer 1909). By 1915, they occurred downstream from Austria in the Czech Republic (Morava River), in the Holásecké Lakes (10 small lakes) and in Černovický Creek (Lojkásek and Lusk 2018). The species subsequently spread to the Drava River some 1400 km from the Danube mouth (Povž et al. 2015, as cited by Piria et al. 2018), and then downstream to Hungary in 1956 (Berinkey 1960), Slovakia in 1966 (Balon 1967), Serbia in 1995 (Cakić, Lenhardt, and Petrović 2000; Lenhardt et al. 2011; Zorić et al. 2014), and Croatia in 2014 (Lisjak et al. 2015).

In the Dniester River, stickleback were historically mostly in the lower reaches (i.e., downstream of the Dubosarsky Reservoir) and only rarely in the middle reaches of the river, but recently, however, they dramatically increased in abundance in the middle reaches of the river (Goncharenko and Shevtsova 2007), and they are rapidly spreading in the upstream parts of the river above the Dnestrovsky Reservoir (Hoch 2008).

In the Dnieper River drainage in 1848 and 1849, stickleback occurred in the middle and downstream areas, specifically in the Seim and Psel rivers (Chernay 1852); and then, in 1915, they were found in a small lake in the upstream part of the Pripyat River basin (Grochmalicki 1920). However, detailed surveys in the early and middle of the 20th century reported stickleback only in the very mouth of the Dnieper River (Beling 1935; Ambroz 1956). Then, in 1966, they were reported in the Svisloch River, a tributary of Berezina

River, which is a first-order tributary in the upper part of the Dnieper basin; and, in 1981–1982, they were found in the Pripiat River in quite high numbers (Zhukov, Kunitsky, and Rizevsky 1986). Currently, stickleback are reported in most parts of the Dnieper River basin, including areas where they were not previously reported—for instance in Ukraine (Novitsky et al. 2005; Kutsokon 2010; Movchan 2012; Kvach and Kutsokon 2017).

In the Don River basin, sticklebacks were first reported in the 1980s in the Proletarsky Reservoir located on the Zapadny Manych River, where the species eventually reached—and still maintains—high abundance (Poznyak and Frolenko 1998; Stepanyan and Startsev 2014). The reservoir was created between 1933 and 1954, and a fish survey conducted in 1953 reported no stickleback (Syrovatskaya 1954), suggesting colonisation occurred sometime between then and the 1980s. It appears that the stickleback entered this reservoir through canals from the Kuban River basin.

Stickleback also has recently colonised several other smaller rivers and lakes of the Black Sea basin. In the Dyurso River in the northeast part of the sea, no stickleback was reported during a survey in 1935–1936 (Kryzhanovsky and Troitsky 1954); but, in 1995–2000, they were reported in the downstream areas (Luzhnyak 2003). In 2007, sticklebacks were found in the middle reaches of the Dyurso River (Reshetnikov, Pashkov, and Makhrov 2015); and, in 2013, they were detected in the upper reaches of the river (Artamonova et al. 2014). In the small Lake Abrau ($S \approx 3\,km^2$), not far from the Dyurso River, sticklebacks were observed from 1995 to 2000 (Luzhnyak 2003), but were again absent in 2012 (Karnaukhov et al. 2013). In 2003–2004, sticklebacks were found for the first time in some rivers and lakes of the Crimea Peninsula (Karpova 2016). Further, in the second half of the 20th century, stickleback penetrated from the sea to the brackish Lake Techirghiol in Romania, which was separated from the sea by a narrow isthmus (Bănărescu 1994).

3.6 | Caspian Sea

Sticklebacks were reported in the Caspian Sea in several surveys in the 18th and 19th centuries by J.G. Georgi, K.E. von Eichwald and A. Peltsam (as reviewed by Kessler 1877). Collections in the Zoological Institute of the Russian Academy of Science contain seven specimens (No. 30.162) marked ‘Baku. Baer. 1877’. The famous Russian biologist Karl Ernst von Baer visited Baku in 1855 (Gadzhieva 2011), and we assume that his specimens were stored in the Zoological Museum unsorted until his death in 1876, and then sorted in 1877. Therefore, these samples confirm the presence of stickleback in the Caspian Sea in the mid-19th century. However, after that, no stickleback was reported until the late 20th century despite numerous expeditions (Kazancheev 1981).

In 1981, stickleback was reported in Turkmenbashi Bay (formerly Krasnovodsky Bay) on the eastern coast of the Caspian Sea in Turkmenistan (Berdyev 1987; Figure 3). In 1982, the species was found along the western coast of Azerbaijan, where it now attains very high abundance (Zarbaliyeva et al. 2016). In 1988, stickleback was found in the Atrek River on the southern coast of the sea on the border between Turkmenistan and Iran (Berdyev 1987; Salnikov 1998). In 1992, one individual was found in Iran in the province of Mazanderan on the Caspian Sea coast (Coad and Abdoli 1993). By 1995, the species was observed in the southeastern part of the Caspian Sea and in the Gorganrud and Tajan rivers flowing into Gorgan Bay (Kiabi, Abdoli, and Naderi 1999). Since 2004, sticklebacks also have been reported in fresh and marine waters of the northwestern coast of the Caspian Sea in the Russia Republics of Kalmykia and Dagestan (Poznyak 2005; Shikhshabekov, Barkhalov, and Rabazanov 2007). Therefore, sticklebacks are now confirmed to inhabit the entire Caspian Sea coast with the exception of Kazakhstan (Doukravets 2015).

Moreover, sticklebacks were found in 2010 in the Volga River's Kuibyshevskoye Reservoir, more than 1000 km upstream of the river mouth (Semenov 2012; Shakirova, Severov, and Latypova 2015), but no data are available about the presence of stickleback in the Volga River downstream of the Kuibyshev reservoir.

Finally, between 2010 and 2020, stickleback penetrated the Caspian basin once again—they were found in the Chograiskoye Reservoir located on the East Manych River in the western part of the Caspian basin (Karnaukhov et al. 2021).

3.7 | Japan

The genus *Gasterosteus* is distributed in Japan north to 35° N latitude (Ikeda 1933, as cited by Higuchi and Goto 1996). It is represented here by two closely related species: *G. aculeatus* and *Gasterosteus nipponicus*, the latter having been described relatively recently (Higuchi and Goto 1996; Higuchi, Sakai, and Goto 2014; Figure 4). Consequently, in some publications, *G. nipponicus* may not be separated from *G. aculeatus*. In Japan, *G. nipponicus* has a larger range than *G. aculeatus*, the former covering almost the entire country except the very southern part facing the Pacific Ocean. *G. nipponicus* is anadromous and does not appear to have established any resident freshwater populations. *G. aculeatus* inhabits mostly the northern part of Japan and is represented by both anadromous and resident freshwater populations (Higuchi, Sakai, and Goto 2014).

In Japan, the stickleback is considered an endangered species due to the extinction of several populations and the risk of extinction for others (Kitano and Mori 2016). At the same time, there are also several examples of range expansion. Most documented cases of range expansion involve the colonisation of lakes and streams that were formerly isolated from the ocean, meaning they most likely involve *G. aculeatus*, even if the authors do not differentiate it from *G. nipponicus*. These expansions have typically involved (presumably) unintentional inclusion of stickleback in salmonid stocking efforts (Figure 4). In Lake Towada in the north of Honshu Island, stickleback were first found in 1979 (Mori and Takamura 2004); and, in lakes Kussharo and Shikotsu on Hokkaido Island, they were found in 2003 and 2010, respectively (Adachi et al. 2012). In 2011, due to a tsunami, stickleback colonised Lake Otsuchi and were present in new ponds that were formed by the inundation (Hosoki et al. 2019). Many of these ponds have subsequently disappeared, and so the continued existence of tsunami-origin populations is not certain.

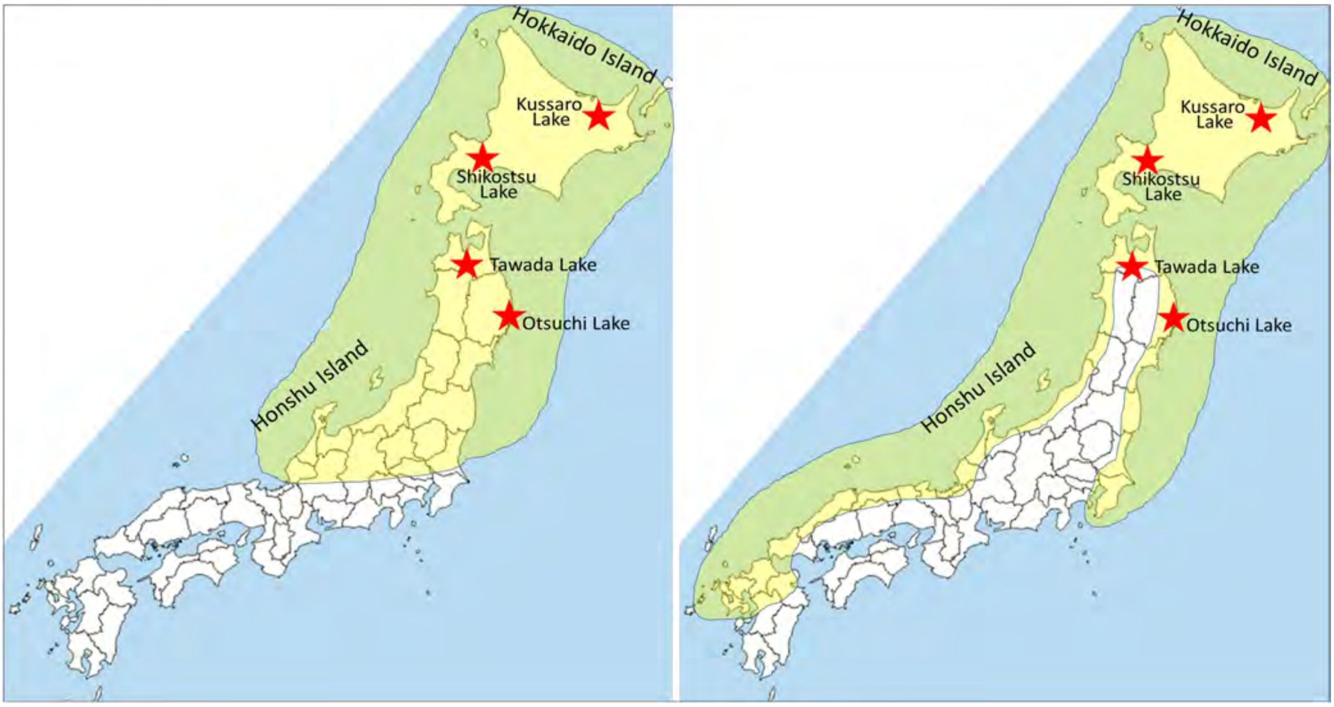

FIGURE 4 | Native range (yellow filling) and new records (red asterisks) of genus *Gasterosteus* in Japan. Left—*G. aculeatus*, right—*G. nipponicus* (based on Higuchi, Sakai, and Goto 2014).

4 | Discussion

We summarised available information on the historical and contemporary ranges of threespine stickleback, with the goal of inferring recent range expansions and—in some cases—dramatic increases in abundance. Any such effort is subject to uncertainty about whether a species was historically present even if it was not reported. That is, the apparent historical absence of a species at a given site might simply reflect a lack of relevant surveys, low-quality surveys or inadequate reporting. Additionally, some material is likely missed due to it only being available in the local language. Although we acknowledge such ambiguity, it is nevertheless clear that sticklebacks have undergone massive range expansions and some dramatic increases in abundance. Here, we leverage information from our literature survey to infer the primary vectors of stickleback range expansion, the sources of those expanding populations, the contemporary evolution of new populations, and the ecological consequences of stickleback colonisation and abundance increases.

4.1 | Vectors

When stickleback colonised a new area, how did they get there? When documented, the vectors fell into several categories: (i) natural ocean migrations, (ii) artificial canals connecting drainages, (iii) extreme events (e.g., earthquakes, tsunamis and floods) and (iv) translocation by humans. The translocations were sometimes unintentional through inclusion with intentional introductions of salmonids, via their use as bait in recreational fishing, or in ship ballast waters. Other translocations have been intentional, such as the dumping of unwanted organisms during restoration efforts, and experiments by scientists or aquarists. In the latter case, it is due to beliefs in humane release, ritualistic practices and unintentional escapes from tanks, breeding farms or drainage systems (Padilla and Williams 2004). We provide clear examples of each category while noting that multiple factors are likely at play in many instances.

4.1.1 | Sea Migrations

Range expansion of stickleback in the Arctic is likely due to climate warming and has been facilitated by the species' ability to undergo long migrations in the open ocean, as suggested by the finding of stickleback in Greenland and Svalbard (Nielsen, Hamerlik, and Christoffersen 2012; Svenning, Aas, and Borgstrøm 2015). These long-distance movements by individuals in recent range expansions of stickleback are likely facilitated by climate change (Panov et al. 2007; Paukert et al. 2021). At the same time, climate warming is probably not the sole environmental factor driving natural range expansions; for instance, the first reports of stickleback in the Severnaya Zemlya Archipelago occurred in 1985 (Chernova et al. 2021), before climate warming in the region became pronounced.

4.1.2 | Artificial Canals

In North America, the invasion of stickleback into the upper Great Lakes (above Niagara Falls) was likely facilitated by the construction of canals for ship movement. These canals made available a drainage basin of 684,000 km^2 for potential occupation by stickleback. In Europe, range expansions have been similarly facilitated along the so-called 'Invasion Corridors', a system of canals connecting different river basins (Garcia-Berthou et al. 2005).

Although range expansions along this corridor are usually northwards, probably due to climate change (Panov et al. 2007), sticklebacks have expanded in both directions. For instance, southward expansion took place as Baltic Sea stickleback invaded the upstream part of the Volga River basin (Bardukov et al. 2024) and the Dnieper River basin (Grochmalicki 1920; Zhukov, Kunitsky, and Rizevsky 1986). Eastward expansion took place when stickleback penetrated from the Black Sea basin to the Caspian Sea basin through the canal connecting the Don River and East Manych River (Bardukov et al. 2024). These observations fit the expectation that stickleback range expansion in temperate freshwater is mainly limited by barriers to migration. That is, following the last glacial maximum, freshwater stickleback populations have naturally arisen only when a lack of barriers allowed upstream colonisation by marine/anadromous populations (Bell and Foster 1994; Taylor and McPhail 2000).

4.1.3 | Extreme Events

The Fukushima tsunami in 2011 created many new ponds along the coast of Japan, and these were rapidly inhabited by stickleback (Kume et al. 2018). Similarly, the massive earthquake in Alaska in 1964 caused the creation of new ponds and lakes that were occupied by stickleback, a process particularly well documented on Middleton Island (Lescak et al. 2015) where the land rose by 14 mm per year (Savage et al. 2014). In both situations, the extreme event probably entrained marine stickleback in the new habitats, which then decreased in salinity through time as a result of precipitation and run-off. The process in these cases is akin to human-generated barriers (e.g., roads and railways) that isolate small bays from the rest ocean. Further, both natural and climate-accelerated glacial retreats have generated new lakes and ponds that are sometimes quickly colonised by stickleback. In the latter case, the fish may reach the new habitat either via connecting streams (Milner et al. 2011) or through translocation by humans, which should be considered a vector per se.

4.1.4 | Unintentional Translocations

In some lakes (Japan and North America), sticklebacks have colonised through inadvertent inclusion with deliberate introductions of salmonids (Crossman 1991; Van Zyll de Jong, Gibson, and Cowx 2004; Adachi et al. 2012). For instance, sticklebacks are sometimes present in the hatcheries or habitats from which salmonids are captured for stocking, and this 'by-catch' is then carried with the salmonids and released into the target habitat. Moreover, it is not only salmonid introductions that can have this ancillary effect. In the Dnieper River, invasion by stickleback was associated with an intentional introduction of carp, *Cyprinus carpio* (Zhukov, Kunitsky, and Rizevsky 1986). Further, the use of stickleback as a bait fish by recreational fishers probably contributed to its' spread in the Great Lakes of North America (Stedman and Bowen 1985). Transport of fish with ballast water in ships is another potential contributor to the Great Lakes introductions, although this vector has not been specifically tied to stickleback (Crossman 1991).

4.1.5 | Intentional Translocations

Some translocations of stickleback are intentional. Release by aquarists was the most likely reason for the appearance of stickleback in the upstream reaches of the Danube River near Vienna and Munich (Grote, Vogt, and Hofer 1909; Gaschott 1928). In such cases, the release of fish was intentional even if the goal was not to establish new populations. In other cases, the goal was specifically to restore populations or establish new ones. A particularly common situation is the intentional release of stickleback for lake restoration following Rotenone treatment to remove other invasive fish species (Bell, Aguirre, and Buck 2004; Bell and Foster 1994; Bell et al. 2016; Wund et al. 2016). Another situation is the release of stickleback into artificial or natural ponds for research (Ziuganov 1991; Terekhanova et al. 2014, 2019) or into isolated habitats for conservation purposes. For example, the incipient collapse of the benthic/limnetic species pair—where stickleback forms two distinct populations within the same lake, one inhabiting the inshore zone (benthic) and the other the open water (limnetic)—in Enos Lake, British Columbia (one of just a few such sympatric species pairs; see Schluter and McPhail 1992), led to fish from that lake being introduced into several other small ponds in the Vancouver area (D. Schluter, pers. comm.).

Stream enclosure experiments should be considered translocations as well. In these experiments, individuals bred in the lab were placed into stream enclosures with holes that allowed local fish to enter. The lab-reared fish bred freely in the enclosures, and some individuals likely escaped into the wild (Moser, Kueng, and Berner 2015). These same populations have also been referred to as invasive in the Constance drainage (Rösch, Baer, and Brinker 2018; Hudson et al. 2021), though this translocation did not expand their range. These intentional translocations are often used as a model to understand the factors shaping contemporary evolution (Laurentino et al. 2020).

4.2 | Sources

When stickleback colonised a new area, where did they come from? In some cases, the evidence is based on recorded information (e.g., scientists report the source population used in an introduction) or geographic information (e.g., a canal linking two drainages). As such, no ambiguity attends the origin of stickleback in ponds in Haida Gwaii (Leaver and Reimchen 2012; Marques et al. 2022), restored lakes in Alaska (Bell et al. 2016), experimental lakes in Greenland (B. Matthews, pers. comm), inundations in Fukushima (Kume et al. 2018) or land upheavals on Middleton Island (Lescak et al. 2015). In many other cases, however, genetic studies are necessary to understand the origin of new stickleback populations.

Sticklebacks in the Caspian Sea basin appear to have originated from several different sources. Analysis of haplotypes at the mitochondrial gene cytochrome oxidase I (COI) shows their similarity to Black Sea stickleback (Denys et al. 2015; Bardukov et al. 2024); yet the population in the Volga River (Kuibyshev Reservoir) is genetically similar as populations in the Baltic basin (Bardukov et al. 2024). The Black Sea basin is inhabited mainly by stickleback carrying mitochondrial DNA haplotypes typical of southern European populations; yet populations in the Dnieper River show some genetic similarity to Baltic populations (Mäkinen and Merilä 2008; Bardukov et al. 2024).

Similar complexities and ambiguities are associated with other range expansions around the globe. In Switzerland, molecular genetic studies found that new stickleback populations originated both from adjacent native populations and also from populations in the Baltic and Mediterranean basins (Lucek et al. 2010; Roy et al. 2015; Marques et al. 2016). By contrast, molecular genetic studies have not yet been able to pinpoint the source of fish in Hasse Lake, Alberta (Rezansoff et al. 2015), which is geographically disjunct from other stickleback populations and was either introduced from an unknown source or is vestige of a glacial refuge.

In summary, stickleback populations in new areas result either from nearby local sources, specific distant sources, or a complex admixture of different phylogenetic lineages from nearby and distant sources. Further, native populations might experience natural or human-induced secondary contact with invading lineages. Such novel introgression can result in changes in the adaptive traits of native populations. For instance, introgression with invasive genotypes might have contributed to the disappearance of the 'golden phenotype', considered a subspecies of stickleback in the Romanian Lake Techirghiol near the Black Sea (Bănărescu 1994).

4.3 | Contemporary Evolution

Sticklebacks have a remarkable ability to quickly adapt to new conditions and, as such, the species has become one of the key model systems for understanding contemporary evolution (Hendry and Kinnison 1999; Reznick and Ghalambor 2001; McKinnon and Rundle 2002; Hendry, Farrugia, and Kinnison 2008; Hendry et al. 2013). Much of the insight has come from studies of stickleback introduced into—or that naturally colonise—new habitats. In many such cases, if the year of colonisation is known, researchers can obtain good estimates of the rate and trajectory of adaptive changes at the phenotypic and genomic levels.

One example comes from a new freshwater stickleback population in Loberg Lake, Alaska, where anadromous stickleback found their way into a lake that had been treated with Rotenone. In the subsequent years, a series of morphological changes were documented (Arif, Aguirre, and Bell 2009), with the most striking being a shift in the frequency of fully plated individuals from 95.9% in 1990 to 11.2% in 2001 (Bell, Aguirre, and Buck 2004). During this period, partial reproductive isolation evolved between the Loberg Lake population and its putative anadromous ancestor (Furin, von Hippel, and Bell 2012)—a pattern also documented on Middleton Island in Alaska (Lescak et al. 2015). Remarkably, the rapidity of these changes meant that the new populations closely resembled typical freshwater sticklebacks within only a few decades (Bell, Aguirre, and Buck 2004; Gibson 2005). These cases are among the most rapid instances of evolution in natural environments known across all organisms.

Dramatic phenotypic and genetic changes have been documented not only when anadromous stickleback colonise freshwater (as above), but also in other contexts. The introduction of well-defended (against bird predators) limnetic-type Mayer Lake stickleback into a small pond on Haida Gwaii (British Columbia) led to the rapid emergence of numerous trait and genomic changes reflecting adaptation to a more benthic environment with fewer bird predators (Leaver and Reimchen 2012; Marques et al. 2018). Further, a study of new lake and stream populations in Lake Constance and Lake Geneva revealed substantial recent divergence in numerous traits (Berner et al. 2010; Lucek et al. 2013). In this latter case, hybridization and introgression influenced the diversity of adaptive phenotypic traits, and it may have increased evolutionary potential and promoted further range and habitat expansion (Lucek 2016; Marques et al. 2019; Hudson et al. 2021). One can only agree with Hudson et al. (2021), who consider the Swiss stickleback system to be a good model for understanding invasive species in general and for studies of contemporary evolution.

Recent divergence between littoral and invasive pelagic populations in Lake Constance was not accompanied by substantial genome-wide genetic differentiation or the emergence of phenotypic differences. However, multiple outlier loci were identified between littoral and pelagic individuals across the genome, potentially suggesting early signs of adaptation (Dahms et al. 2024).

An interesting example of addressing genetic temperature adaptations (thermal traits evolution) is provided by the study of Smith et al. (2022). They modelled the projected distribution of marine stickleback in the Northwest Pacific by 2100 under different temperature scenarios and various realistic rates of thermal trait evolution. They found that significant range increases were observed in all cases, but taking into account the evolution of thermal traits resulted in much more substantial increases. This underscores the critical role of evolutionary biology in improving the accuracy of climate change impact projections on species distributions.

The stickleback's ability for contemporary evolution and adaptive species radiation is an important factor in the success of the species—both naturally and in introduced/invasive contexts. At the same time, it is important to recognise that stickleback evolution is not always rapid or complete (Berner et al. 2010; Hendry, Hendry, and Hendry 2013) and that many stickleback introductions fail to generate sustainable populations. That is, sticklebacks are not capable of adapting to all habitats or all forms of habitat change—as seen perhaps most obviously in their extirpation when faced with particular predatory invasive species—especially northern pike (Haught and von Hippel 2011).

4.4 | Ecological Effects

4.4.1 | Changes in Range and Abundance

Increases in stickleback range and abundance were most frequently observed by our literature review. However, some stickleback populations have also experienced declines, extirpations and range contractions. Foster, Baker, and Bell (2003) reviewed threats to stickleback populations, highlighting invasive species, water table declines, habitat loss and climate change, particularly in industrially developed regions such as Spain, the Netherlands, Japan and the United States. For instance, the Californian subspecies *G. a. williamsoni* experienced a decline and range contraction resulting from urbanisation and the introduction of exotic species (Ono, Williams, and Wagner 1983; Turba et al. 2022). In other areas near the southern border of the species range—such as Spain, Italy and Japan—some stickleback populations have gone extinct (Vila et al. 2017; Kitano and Mori 2016; Sharda and Argenti 2018).

Further, no changes in the range have been documented in some areas, such as Portugal (Moreira et al. 2022) and the Aleutian Archipalgo, Alaska (Kenney and von Hippel 2017). Certain stickleback populations exhibit different trends in various parts of their range. For instance, in the Baltic Sea, their abundance increased in the central part (Olsson et al. 2019) and decreased in the southern part (Morozińska-Gogol 2015). Fluctuations in abundance approaching not just times but orders of magnitude are observed in the White Sea stickleback; this represents the longest time series for this species, exceeding a century (Lajus et al. 2021).

Numerous studies have analysed the effects of abiotic factors such as temperature, salinity, acidification, oxygen concentration and their variability on stickleback under experimental conditions (Wootton 1984; Östlund-Nilsson, Mayer, and Huntingford 2007; Shama 2017; Devergne et al. 2023). However, extrapolating these experimental results to wild populations often presents challenges, and so these were not covered by the present review.

4.4.2 | Ecosystem Complexity

Low diversity and altered ecosystems are often more susceptible to stickleback invasion. McPhail (1994, 436) noted that '*Gasterosteus* may resemble a weed: an excellent colonizer but a poor competitor'. These 'weedy' traits include rapid sexual maturation, parental care, high phenotypic plasticity, euryhalinity and euryphagy (Wootton 1976; Bell and Foster 1994). Drastic increases in stickleback abundance may be observed in artificial systems, such as in the Proletarskoye Reservoir following increased salinity (Poznyak and Frolenko 1998). They also often increase in water bodies with naturally low fish species diversity. For instance, this was observed in Lake Takvatn, northern Norway, where only three fish species are present (Amundsen et al. 2013), and in the Dyurso River in the Caucasus, where most other fish species were devastated by catastrophic flooding, leading to stickleback becoming the most abundant species (Artamonova et al. 2014; Reshetnikov, Pashkov, and Makhrov 2015).

The Arctic White Sea can also be considered a low-diversity ecosystem where the stickleback outbreak was not associated with changes in its main forage item, plankton. In this case, population growth is attributed to increasing temperatures and, more specifically, to the reduction of the ice coverage period. This pattern was also observed during the warm period of the 1920s–1940s (Lajus et al. 2021).

In ecosystems with higher species diversity, introduced sticklebacks engage in complex interactions with native species, leading to difficult-to-interpret changes. For instance, in Lake Constance, where the ecosystem effects of stickleback growth have been intensively studied, the recent stickleback population growth coincided with the notable reduction of whitefish *Coregonus wartmanni* biomass (Roch et al. 2018). Two primary hypotheses have been proposed to explain this: competition for key dietary resources (primarily *Daphnia*) and predation on juvenile whitefish by adult stickleback. Experiments have shown stickleback preying on whitefish larvae, although field surveys have found contradictory results regarding predation on whitefish larvae. Analyses conducted by Bretzel et al. (2021) studied hundreds of stickleback guts and found no evidence of wild whitefish larvae presence. Similarly, Roch et al. (2018) reported that no fish larvae were found in the stomachs of sticklebacks during their field sampling. Nonetheless, whitefish larvae were observed in stickleback stomachs near whitefish stocking release sites in the same study. Baer et al. (2021) conducted foraging trials in various parts of the lake and concluded that there is clear evidence of stickleback predation on whitefish larvae. Stable isotope analysis of stickleback stomach contents also suggests their feeding on whitefish larvae and eggs (Gugele et al. 2023). However, additional studies still need to be performed to produce more confident conclusions on how stickleback impacts whitefish populations through competition and predation (Roch et al. 2018; Rösch, Baer, and Brinker 2018; Hudson et al. 2021).

Predation by stickleback on embryos and juveniles, as discussed above in the Lake Constance case, is typical for this species. In the Baltic Sea, sticklebacks prey on eggs and juveniles of their predators, such as European perch *Perca fluviatilus* and northern pike, contributing to their decline (Eklöf et al. 2020). This was also reported in the Sea of Azov (Troitsky and Frolov 1949), Caspian (Niksirat, Hatef, and Abdoli 2010) and Baltic, where stickleback prey on herring eggs (Kotterba et al. 2014). Predation on their own species, that is, cannibalism, is also common in sticklebacks (Whoriskey and FitzGerald 1985; Östlund-Nilsson, Mayer, and Huntingford 2007). Males engage in filial cannibalism by eating their own eggs, while females prey on other eggs. Cannibalism reaches large scales in the White Sea with its extremely high densities of adult fish in the spawning grounds. The eggs were by far the most important component of the adult fish diet during the spawning period, composing 95%–100% of their diet (Genelt-Yanovskaya et al. 2023). High cannibalism likely results from high fish density in spawning grounds, although whether it is an adaptation remains unclear.

Predation from other species is also an important factor, influencing the extent of stickleback invasions. Dramatic decreases in stickleback abundance have occurred following the introduction of predators such as northern pike (Patankar, von Hippel, and Bell 2006; Haught and von Hippel 2011). Stickleback can also be outcompeted by pumpkinseed sunfish *Lepomis gibbosus* (Kynard 1979). The decline in stickleback numbers along the Polish coast of the Baltic Sea is likely attributable to increased pressure from predators and competitors (Morozińska-Gogol 2015). In the White Sea, an abundance of stickleback clearly positively correlates with their presence in the stomachs of predatory fish during the last several decades (Bakhvalova et al. 2016).

The rapid growth of stickleback populations in the Baltic Sea is likely due to the interaction of several factors, which have substantially altered the food web (Bergström et al. 2015; Olsson et al. 2019; Eklöf et al. 2020). Predation pressure likely plays here a crucial role in this ecosystem. The reduction in predator pressure, particularly from species such as perch and pike in coastal areas, and Atlantic cod (*Gadus morhua*) in offshore regions, has been largely influenced by fisheries (Eriksson et al. 2011, 2021; Bergström et al. 2015; Donadi et al. 2017; Olin et al. 2022). Other important factors include increased availability of food resources (Lefébure, Larsson, and Byström 2014), eutrophication facilitated by stickleback predation on consumers that control filamentous algae growth via a trophic cascade, and changes in the foraging behaviour of their competitors, such as the invasive shrimp *Palaemon elegans* (Candolin 2019; Candolin, Bertell, and Kallio 2018). Additionally, rising water temperatures (Lefébure, Larsson, and Byström 2014) have contributed to these population changes.

Parasites are potentially significant players in ecosystem changes, especially when host densities are high, but empirical data on parasites associated with stickleback invasions are currently limited. For example, the stickleback parasite *Schistocephalus solidus* increased in abundance following stickleback introduction in Lake Towada, Japan (Adachi et al. 2012). It is also considered an important factor in the decline of stickleback in the southern Baltic Sea (Morozińska-Gogol 2015).

These examples are a small subset of the likely changes that occur when stickleback colonise new locations or habitats. Contemporary evolution of stickleback in these habitats (see previous section), combined with strong ecological effects, is then predicted to result in eco-evolutionary dynamics (Harmon et al. 2009; Moosmann et al. 2023; Hendry 2017; Eriksson et al. 2021; Hendry et al. 2024). For starters, contemporary adaptation to new environments is expected to increase stickleback abundance, which should then have density-mediated effects such as those described above. In addition, adaptation is expected to change stickleback traits, resulting in different per-capita trait-mediated effects on their prey (e.g., via changes in trophic traits) and predators (e.g., via changes in their defensive traits). However, these eco-evolutionary dynamics have yet to be formally tested in introduced stickleback populations.

5 | Conclusion

In recent decades, threespine stickleback has undergone important increases in geographic range, forming numerous new populations in various water systems, both freshwater and marine. In some cases, the species has become re-established in locations from which it had previously disappeared. Moreover, evidence has accumulated of dramatic population increases in stickleback in areas where the species is native. Some of these range expansions and increases in abundance have occurred 'naturally', whereas many other instances have been driven by human-mediated disturbances, such as the highly developed canal system across Central Europe, intentional or unintentional introductions, pollution or climate change and changes in the abundance and distribution of other species. In marine ecosystems without physical obstacles, migration in the open sea is an important factor for range expansion, especially in combination with the effects of climate change. Increases in stickleback abundance, either in situ within a native habitat or through the introduction and range expansion, can cause ecosystem-level effects through trophic cascades, predation on eggs and juveniles of other fish species, and the spread of parasites. The stickleback is considered a 'supermodel' of evolutionary biology (Gibson 2005) and we suggest it could also be a 'supermodel' in ecology and invasion biology.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study (exact geographical coordinates, factors driving invasions and some other data that were not included in the text due to room limitation) are available from the corresponding author upon reasonable request.

Endnotes

[1] Spisok zoologicheskim predmetam, prislannym ego Prevoskhoditelstvom Akademikom g-nom fon-Berom i khraniaschimsia pri Zoologicheskom muzee Akademii Nauk [The list of Zoological Objects Sent by His Excellency Academician Mr. von Baer and Stored at the Zoological Museum of the Academy of Sciences]. Archiv Rossiiskoy Akademii Nauk, Sankt-Peterburgskiy filial [The archive of the Academy of Sciences, Saint-Petersburg branch]. Fund 129, opis 1. № 612. L. 1–2.

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