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### **REVIEW ARTICLE**

# Ecology of FRESHWATER FISH WILEY

# Identifying and conserving sympatric diversity in trout of the genus Salmo, with particular reference to Lough Melvin, Ireland

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### Abstract

Salmonid (Salmonidae) sympatric diversity is the co-occurrence, in a lake or river, of two or more reproductively isolated populations/subpopulations, or phenotypes resulting from phenotypic plasticity. Sympatric populations can arise through allopatric and/ or sympatric evolution. Subsequently, allopatric lineages can occur in sympatry due to independent colonisation and/or through anthropogenic introduction. Sympatric divergence is often driven by feeding opportunities, with populations segregating as planktivorous, benthivorous and piscivorous ecotypes ("trophic polymorphism"), and further segregation occurring by feeding depth and body size. Subpopulations evolve by natal homing where a water has two or more discrete spawning areas, often resulting in phenotypically and ecologically cryptic sympatry. Most known sympatric populations/phenotypes in trout of the genus Salmo (Eurasian trout aka brown trout) involve sympatric piscivorous (ferox) and lifetime invertivorous trout. Segregation on the benthic-limnetic axis has been poorly studied in Eurasian trout compared with other salmonids but is likely commoner than currently described. While three sympatric populations/species of Eurasian trout are recognised from Lake Ohrid (Albania/ North Macedonia), limited ecological information is available and there are only two lakes with three or four sympatric populations with described benthic, limnetic and piscivorous trophic segregation: Lough Melvin (Ireland) and Loch Laidon (Scotland), the latter having the only identified case of a sympatric profundal benthic feeding populations, possibly due to the absence of Arctic charr (Salvelinus alpinus) in the lake. Many thousands of waters are yet to be examined. Some sympatric populations are extinct, and others are vulnerable with conservation action being urgently required. This should ideally be based on populations/conservation units, but the lack of recognition of intraspecific units in most legislations in the native Eurasian trout range necessitates a pragmatic approach, with species classification, where appropriate, based on integrative taxonomy. Some sympatric populations clearly merit species status and should be formally classified as such if a valid previous name is not available.

### **KEYWORDS**

conservation units, ecotype, ferox, genetic markers, integrative taxonomy, Salmonidae

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### 1 | INTRODUCTION

### 1.1 | Terminology

Sympatric salmonid (Salmonidae) diversity refers to the occurrence in the same lake or river of two or more distinct groups of individuals that overlap geographically (are syntopic) during part of their life cycle, generally for feeding, but may spatially segregate for breeding. The terminology used for such sympatric groups is diverse (Taylor, 1999) and is often used inconsistently among authors (Clemens & Schreck, 2021). No one term is ideally suitable for all situations, especially when phenotypically cryptic sympatry is included (Jorde et al., 2018). The term populations is used here for groups that are substantially reproductively isolated as shown by their genetic differentiation. Separate breeding groups may occur within a population, for example, due to natal homing, and these are considered as subpopulations. Ecotype refers to a population that shows heritable adaptations to its feeding or breeding habitats (Clemens & Schreck, 2021), although the genetic basis is generally inferred from morphological differences rather than being specifically demonstrated. The terms phenotype, or morphotype when morphologically distinct, are used for phenotypically distinct groups of individuals where the genetic status is not implied, or where the variation may be the result of phenotypic plasticity within the same gene pool. The sympatric occurrence of different migratory life histories involving anadromy, potamodromy and residency are excluded from this review since, although having a heritable component, they do not generally form separate sympatric reproductively isolated populations (Ferguson, Reed, et al., 2019). Note that in Scotland, a lake is referred to as a Loch and, in Ireland, as a Lough.

### 1.2 | Evolution and ecology of sympatric diversity in salmonids

Sympatric diversity appears to occur more in lakes rather than rivers, and in lakes that were formed by the last glaciation relative to older ones (Koene et al., 2020). Lakes typically have a greater diversity of habitats than rivers facilitating ecological segregation; this ecological opportunity and spawning diversity increase with lake size and depth (Doenz et al., 2019; Recknagel et al., 2017). Low species diversity in postglacial lakes results in the availability of diverse ecological niches with limited competition for resources and fewer predators, promoting diversification through trophic specialisation under divergent selection pressures (Schluter, 2000). Multiple spawning areas including inlet and outlet rivers, and the lake substrate result in diversification through spawning habitat specialisation. Sympatric populations and phenotypes of salmonids involve many different species (Salisbury & Ruzzante, 2022; Taylor, 1999). These include rainbow trout (Oncorhynchus mykiss) (Grummer et al., 2021), although more commonly lake-dwelling charrs of the genus Salvelinus, particularly Arctic charr (Salvelinus alpinus), Dolly Varden charr (Salvelinus malma) and Lake charr (Salvelinus namaycush) (Arostegui

& Quinn, 2019; Chavarie et al., 2021; Saltykova et al., 2015; Skúlason et al., 1989; Taylor, 2016). Sympatric charrs are typically morphologically distinct, exploit different food resources, exhibit differences in growth and life history patterns and, in most cases, form genetically distinct populations. However, some sympatric types appear to result from phenotypic plasticity. Arctic charr generally shows from two to five sympatric populations (Adams et al., 1998; Doenz et al., 2019; Ferguson, Adams, et al., 2019; May-McNally et al., 2015; Skúlason et al., 1996; Winfield et al., 2015). Lake Kronotskoe (area 246 km<sup>2</sup>; max. depth 136 m; Kamchatka, Russia), with eight sympatric phenotypes of Dolly Varden charr, is the most diverse lake currently known for salmonid sympatric diversity, excluding subpopulation structuring based purely on natal homing. Six of the eight phenotypes have different feeding habits. Five phenotypes have been shown to be genetically distinct, with the other three comprising one genetic cluster (Esin et al., 2020). Lake versus river spawning, together with spatial isolation in each, is responsible for the genetic divergence of the six known populations (Markevich et al., 2018). Whitefish and ciscoes (Coregonus sp.), both in North America and Europe, also show extensive occurrence of sympatric populations (Rogers & Bernatchez, 2007; Thomas et al., 2017) with up to six sympatric populations in European lakes (Selz et al., 2020).

Lakes have three main discrete resource habitats namely limnetic, littoral benthic and, if deep, profundal benthic zones, although the latter has been much less studied than the other two (Præbel et al., 2013). Each has a characteristic invertebrate fauna: limnetic zooplankton (small crustaceans): littoral benthic macroinvertebrates (molluscs, insects and larger crustaceans); profundal benthic macroinvertebrates (specialised oligochaetes, chironomids, crustaceans and Pisidium sp.). In postglacial lakes, the littoral zone typically provides the best foraging, with the limnetic zone considered to be second best, and the profundal zone least favourable (Præbel et al., 2013). In some lakes, individual fish populations are primarily restricted to particular habitats resulting in resource or trophic polymorphism (Pfennig & Pfennig, 2012; Skulason & Smith, 1995; Snorrason & Skúlason, 2004). Trophic phenotypes can arise via phenotypic plasticity, whereby certain individuals in a population shift to a new foraging behaviour (e.g. from invertivory to piscivory) and their morphology changes as they do so, or more usually via evolutionary diversification constituting genetically distinct populations maintained by reproductive isolation (Klemetsen, 2010).

Often trophic specialisation involves benthic macroinvertebrate versus limnetic plankton feeding, although ontogenetic changes from benthivorous to planktivorous can occur (Jacobs et al., 2019; Snorrason & Skúlason, 2004). Further specialisation entails switching from initial invertivory to piscivory (Hughes et al., 2019). Segregation by feeding depth and adult body size can also occur (Hooker et al., 2016; Piggott et al., 2018). In some cases, size-segregated sympatric populations can arise within the same lake zone with similar feeding habits. Thus, two littoral morphotypes (small benthic and large benthic) found in the Arctic charr of Lake Þingvallavatn (Iceland; area 84 km<sup>2</sup>; max. depth 114 m), both feed mainly on the pond snail (*Lymnaea peregra*), albeit differing in preferred snail size (Sandlund et al., 1992). Along with the sympatric

planktivorous population, and possibly a piscivorous one, they form genetically distinct populations (Guðbrandsson et al., 2019). Similarly, four Arctic charr populations are found in Lake Tinnsjøen (Tinnsjå), one of the largest (51 km<sup>2</sup>) and deepest (460 m) lakes in Norway, including shallow-moderate profundal and deep profundal forms, the latter being highly specialised (Peris Tamayo et al., 2020). While differential feeding and habitat requirements result in selection for morphological changes that improve the ability to obtain specific food organisms in the particular habitat (Adams et al., 2003; Garduño-Paz & Adams, 2010; Knudsen et al., 2006), sympatric populations differing in morphology, colouration, life history traits, physiology and/or ecology can also occur independently of trophic segregation. Feeding on zooplankton in the limnetic zone results in a more streamlined slender body with a narrow, more pointed head, smaller eyes and dorsoventral countershading of the body for camouflage, and an increased number and/or length of gill rakers for better zooplankton filtering (Bernatchez et al., 2016; Roesch et al., 2013). Benthic macroinvertebrate feeders develop larger eyes, subterminal mouths and thicker set bodies with more robust deeper heads that aid consumption of larger prey (Piggott et al., 2018; Skulason & Smith, 1995). Ecomorphological adaptations to the profundal zone include large eyes, pronounced subterminal mouth and few short and widely spaced gill rakers (Harrod et al., 2010). For piscivorous salmonids, natural selection may promote adaptations to this mode of feeding such as a more robust skull, increased musculature, larger jaws and larger teeth (Cawdery & Ferguson, 1988; Mittelbach & Persson, 1998).

Specific environmental conditions (e.g. lake depth and altitude) may also contribute to changes in morphology, especially of the head (Koene et al., 2020). Identical ecomorphological adaptations and associated genetic and gene regulation changes can occur in unconnected lakes as a result of similar selection pressures, and thus, the evolution of similar phenotypes in different lakes is a common phenomenon (Eaton et al., 2021; Jacobs et al., 2020; Rougeux et al., 2019; Taylor, 1999). However, with the possible exception of a few key genes, generally such parallel changes are not accompanied by similar genetic changes suggesting that different genetic pathways can result in similar phenotypes (Salisbury & Ruzzante, 2022). Reproductive isolation involving spatial, temporal, behavioural and/or postmating mechanisms facilitate the development and reinforcement of adaptations. European whitefish show repeated evolution on limnetic-benthic axes in lake environments (Hudson et al., 2017; Østbye et al., 2005; Præbel et al., 2013). Feeding specialisation by discrete populations produces an overall increase in the trophic resources used by a species (Behnke, 1972). Thomas et al. (2017) found that for European whitefish (Coregonus lavaretus), this resource diversity was almost three times greater in a lake where four populations occurred, compared with an ecologically similar lake with a single population.

#### 1.3 Trout of the genus Salmo

Trout of the genus Salmo are native to Europe, central and western Asia, and northwest Africa, although many natural populations Ecology of FRESHWATER FISH -WILEY

are now extinct (Ferguson, Adams, et al., 2019; Lobón-Cerviá et al., 2019; Markevich & Esin, 2019; Rasmussen et al., 2019; Schöffmann et al., 2019). Considerable variation in morphology, life history, genetics, physiology and other characteristics has led to Salmo trout being regarded as among the most variable of the vertebrates (Ferguson, 1989; Klemetsen, 2013). This high variability has resulted in numerous vernacular and scientific names having been applied to individual populations, phenotypes and life histories. Of the English language common names, brown trout is the most widely used (Lobón-Cerviá & Sanz, 2018), although many authors use this name in a restrictive way, both geographically and in terms of life history, with considered membership of the brown trout complex varying widely. Due to this inconsistency, a vernacular name including all Salmo trout is desirable, irrespective of whether individual parts of this diversity merit species status. While Eurasian and Northwest African trout is an accurate descriptor, this phrase is unsuitable as a species name. The most appropriate compromise is Eurasian trout, rather than European trout as previously used (Whiteley et al., 2019). albeit it omits the unique populations in northwest Africa (Doadrio et al., 2015). There are many precedents in birds and mammals, for example, for using the Eurasian epithet even when the breeding range extends into North Africa.

The common ancestor of the salmonids dates to 50-60 million years ago (MYA; Crête-Lafrenière et al., 2012; Lecaudey et al., 2018). The genus Salmo split from the other salmonid genera around 30 MYA. Atlantic salmon (Salmo salar) and Eurasian trout separated from a common ancestor around 9.6-15.4 MYA with extant Eurasian trout diversity having evolved over the past 5 MY. Ohrid belvicia (Salmo ohridanus) and softmouth trout (Salmo obtusirostris) were the first to split from the rest of the Eurasian trout group (Crête-Lafrenière et al., 2012; Lecaudey et al., 2018; Ninua et al., 2018; Pustovrh et al., 2014). Eurasian trout likely originated in the Ponto-Caspian (Caucasus) region (Makhrov and Bolotov, 2019) and expanded west through Turkey to the Balkans. During the Pleistocene glaciations (past 2.6 MY), Eurasian trout survived only in glacial refugia mainly in the south and expanded their range northwards again during interglacials. This had a major impact on Eurasian trout evolution (Ninua et al., 2018). The Balkan Peninsula is recognised as one of the main Pleistocene refugia in Europe (Hewitt, 1999) and exhibits high levels of diversity and endemism in Eurasian trout (Schöffmann et al., 2019). Conversely, in the warmer interglacial periods, Eurasian trout in the southern regions became restricted to cooler higher altitude areas. Eurasian trout colonised the Atlantic region around 0.7 MYA (Bernatchez, 2001), or possibly later 0.2-0.6 MYA (Gratton et al., 2014), but most current northern European populations have only existed since the retreat of the most recent glaciation some 10,000-15,000 years ago. However, colonisation from multiple glacial refuges and substantial reproductive isolation on secondary contact, have resulted in high genetic diversity that predates the last glaciation (McKeown et al., 2010).

Currently, FishBase (Froese & Pauly, 2021) lists 49 species names for Eurasian trout, and several recently published ones are not included. Notwithstanding current taxonomic uncertainties, some

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species of Eurasian trout are considered as valid, at least by some authors, and are accepted as such here within the context of this review. These are Ohrid belvicia; softmouth trout; marble trout (Salmo marmoratus); Garda carpione (Salmo carpio); Fibreno trout (Salmo fibreni); Ohrid lake spawning trout (Salmo letnica); Ohrid river spawning trout (S. lumi); ferox (Salmo ferox) (Britain & Ireland); Melvin gillaroo (Salmo stomachicus); and Melvin sonaghen (Salmo nigripinnis) (Ferguson, 2004; Hashemzadeh Segherloo et al., 2021; IUCN, 2021; Kottelat & Freyhof, 2007; Meraner & Gandolfi, 2018; Pustovrh et al., 2014; Sušnik et al., 2007; Whiteley et al., 2019). Other Salmo trout considered here are grouped as brown trout (Salmo trutta). That is, the term Eurasian trout is used here to include all Salmo trout species, while brown trout is used for trout populations not falling within the above noted species since in a number of sympatric situations not all populations have accepted scientific species names. However, it is highly likely that more valid species will be recognised within this brown trout complex as further genetic marker/genomic studies are undertaken.

#### Aims of review 1.4

To review the origins and occurrence of sympatric populations of Eurasian trout and their genetic diversity, together with trophic and spawning ecology, and ecomorphological differentiation.

To place the studies undertaken by the authors and colleagues on Lough Melvin in the context of studies on other Eurasian trout sympatric populations, and to provide a pregenomics synopsis of the Melvin populations as a basis for future genomic studies.

To consider the systematics and conservation requirements of the unique sympatric populations in Lough Melvin, within the broader context of other Eurasian trout populations.

To encourage further studies on sympatric populations of Eurasian trout.

#### **DETECTION OF SYMPATRIC** 2 POPULATIONS

Many sympatric populations are known initially from phenotypic diversity such as morphological, ecological, and behavioural differences. Thus, the Lough Melvin sympatric populations (Section 5) have been described by naturalists and anglers since at least the mid nineteenth Century (Günther, 1866; Newland, 1851). Clear size differences often point to the occurrence of sympatric invertivorous and piscivorous ecotypes. Limnetic and littoral benthic feeders frequently differ in body colouration and shape. However, some apparently cryptic sympatric populations have been revealed only through genetic screening (Fišer et al., 2018; Jorde et al., 2018). Genetic differentiation among sympatric populations varies widely and is related to the degree and length of time of reproductive isolation, natural selection and effective population size  $(N_{\rm E})$ , which inversely determines the extent of genetic drift. Given that many sympatric

forms have diverged postglacially, detection of the often low level of genetic differentiation is challenging. However, Haenel et al. (2021) found genomic regions fixed for alternative alleles over a distance of a few hundred metres in the three spined stickleback (Gasterosteus aculeatus: Gasterostidae). This strong divergence is apparently maintained by polygenic selection in spite of high gene flow and low selection on individual loci.

Crucial to detecting sympatric diversity is an adequate fish sampling design to obtain a full representation of all types present in a water. Detecting lake sympatric populations with little or no phenotypic differentiation, for instance, requires detailed sampling covering all available habitats and depths using 3D-stratified random netting techniques (Appelberg, 2000; Verspoor et al., 2019). Thus, sampling based on angler-caught specimens, in most cases, is unlikely to provide sufficient coverage of the diversity present since many angling techniques only target surface or subsurface feeders (Headley, 2019). Comprehensive and nonbiased sampling of juveniles, including temporal components, in all afferent and efferent rivers of a lake may give an indication of sympatric populations. Multiple samples are required in individual rivers since distinct populations may spawn in different parts of the same river (e.g. downstream and upstream; Ferguson & Taggart, 1991). However, river sampling alone will not pick up lake spawning populations, a life history now considered to occur more frequently in Eurasian trout and other salmonids than was previously realised and that cannot be excluded in advance for any lake (Arostegui & Quinn, 2019; Ferguson, Adams, et al., 2019; Heggenes et al., 2009).

Until recently, most detection and confirmation of genetic differentiation and reproductive isolation of sympatric populations have relied on a suite of genetic markers such as allozymes, mitochondrial DNA (mtDNA) restriction fragment length polymorphisms (RFLPs), partial mtDNA sequencing, a limited number of single-nucleotide polymorphisms (SNPs) and microsatellites. It is important when applying these genetic markers that appropriate, and ideally several, marker types and a sufficient number of markers, are used as this can impact on the ability to detect sympatric populations. More importantly, and contrary to common thinking and trends, the more recently developed makers are not necessarily the best. Palmé et al. (2013) found that two cryptic populations could be detected with 14 allozyme markers ( $F_{\rm ST}$  > 0.1) but would have gone undetected with seven microsatellites (Weir & Cockerham's, 1984  $F_{ST}$  is used as a measure of genetic differentiation throughout this review.). For these same populations, Andersson, Jansson, et al. (2017) found that genetic divergence was considerably greater for these 14 allozymes than for 3093 single-nucleotide polymorphisms (SNPs), possibly the result of selection on functional allozymes. Verspoor et al. (2019) reported that one set of microsatellite markers was more effective than another set at detecting sympatric populations.

Increasingly, studies are moving from small sets of markers to genomic approaches involving partial or complete genomic sequencing. In spite of DNA sequencing having decreased considerably in cost, it is still problematic to conduct full genomic sequencing on a large number of individuals and short-cut approaches are still used

(Lou et al., 2021). Restriction site-associated DNA sequencing (RAD sequencing), whereby part of the genome is sequenced extensively in many individuals allowing reliable genotyping, is a popular approach. Using 29,068 SNPs genotyped by RAD sequencing, Ackiss et al. (2020) were able to clearly distinguish among the three most common sympatric populations of Coregonus artedi (Salmonidae) in Lake Superior for the first time, as well as identifying putative hybrids and potentially misidentified specimens. Population assignment rates based on these data were 93%-100%, with the only misassignments being putative hybrids, compared with 62%-77% using nine microsatellites.

Full genome sequencing is often needed to identify adaptive differences, which may be missed with RAD sequencing (Lou et al., 2021). With the availability of a reference nuclear genome for Eurasian trout (Hansen et al., 2021), increasingly DNA resequencing of nuclear DNA (nDNA) is being applied to provide improved resolution on genetic differentiation involving both neutral and functional genes (Saha et al., 2021), with both sequencing of individual DNA and pooled DNA from multiple individuals. Whole-genome resequencing is important in identifying genomic regions underlying phenotypic divergences between sympatric populations (Grummer et al., 2021). Although a reference genome is available for Eurasian trout mtDNA (Sahoo et al., 2016), sequencing is still largely confined to the control region (Hashemzadeh Segherloo, 2021; Sanz, 2018).

Tetraploidy in the early evolution of the salmonids (Macqueen & Johnston, 2014) means that many genes still exist in duplicated state (paralogs) (Lien et al., 2016). Duplicated genes facilitate adaptation when paralogs acquire different functions and can result in reproductive isolation when alternative silencing of paralogs occurs (Arostegui & Quinn, 2019: McKinnev et al., 2018), Salisbury et al. (2020) found different paralogs as outliers between reproductively isolated sympatric resident and anadromous Arctic charr morphs occurring in parallel in three different lakes. Population genetic studies thus need to take account of paralogs and not exclude them as was the case in earlier analyses (McKinney et al., 2018).

Where phenotypic differences exist, these can be used as a basis for a priori grouping of specimens and the resulting groups evaluated for genetic differentiation. Samples from different spawning locations can be analysed in a similar fashion. Other methods rely on treating all specimens from a water as a single sample with sympatric populations being detected by analysis for heterozygote deficiency (Wahlund effect) (Jorde et al., 2018), or by using population structuring methods such as BAPS (Corander & Marttinen, 2006; Corander et al., 2003, 2004), STRUCTURE (Pritchard et al., 2000) and/or discriminant analysis of principal components (DAPC; Jombart et al., 2010). BAPS and STRUCTURE do not rely on a priori information to infer population structuring. On the other hand, DAPC maximises genetic differentiation between groups without the need for assumptions of Hardy-Weinberg equilibrium, linkage disequilibrium and random mating (Dufresne et al., 2014) required in BAPS and STRUCTURE, which are also sensitive to uneven sample sizes (Puechmaille, 2016). STRUCTURE gave more apparent structuring than BAPS when several brown trout populations were marginally

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significantly differentiated but both gave congruent results at higher levels of differentiation, i.e.  $F_{ST}$  >0.03 (Prodöhl et al., 2019). It should be noted, however, that there is no way of validating K = 1 when using the  $\Delta K$  method (Evanno et al., 2005), and it may be that K = 2is reported by default (Janes et al., 2017) resulting in false apparent structuring. The existence of additional sample data (e.g. phenotypes, sampling location) can substantially increase the reliability of inferences compared to genetic data alone in both BAPS (Corander et al., 2003) and STRUCTURE (Hubisz et al., 2009).

In simulation studies, Jorde et al. (2018) found that the power to detect cryptic sympatric populations in STRUCTURE was related to the number of marker loci, the sample size and the relative proportions of the populations in the sample. There was also a threshold of genetic differentiation for detection of structuring. Using 10 microsatellites in STRUCTURE analysis, it was possible to detect two populations with an  $F_{s\tau}$  of 0.0435 with 90% certainty, but this fell to 17.5% with an  $F_{sT}$  of 0.025. The heterozygote deficiency test was able to detect structuring at a slightly lower level of population divergence than STRUCTURE.

### 3 EVOLUTION OF SALMONID SYMPATRIC POPULATIONS

Sympatric populations can arise in four main ways. These are not mutually exclusive, and two or more types of ancestry can result in sympatric populations in a specific water. Thus, both allopatric and sympatric evolution may be responsible for sympatric diversity with an allopatrically derived lineage splitting further in sympatry (Bryce et al., 2016).

### Allopatric origins-natural colonisation and 3.1 anthropogenic introduction

Populations may evolve allopatrically as a result of natural selection and/or genetic drift under different environmental conditions with geographical barriers preventing gene flow. Adaptive evolutionary change can occur in only a few generations among allopatric populations of Eurasian trout (Westley et al., 2013). Isolation in separate refugia during periods of glacial advance was responsible for much divergence in northern populations of salmonids (Taylor, 1999) including Eurasian trout (McKeown et al., 2010). Subsequently, distinct lineages, which evolved in isolation, may naturally colonise the same lake or river and may remain largely reproductively isolated. Reproductive isolation of these allopatrically derived lineages could be reinforced on secondary contact reducing introgression and allowing further divergence and adaptations to reduce competition (i.e. reinforcement selection). Anthropogenic transfers of distinct lineages can take place potentially resulting in sympatry of the native and/or introduced lineages. This can be difficult to differentiate from natural multiple colonisations except where the lineage involved is unlikely to

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have colonised naturally. Thus, Atlantic lineage (sensu Bernatchez, 2001) Eurasian trout have been introduced outside their native range into many waters that contain native trout of other major lineages (Berrebi et al., 2021).

While introgression can often occur as a result of introductions, the long-term impact of this is often less that might be expected from the scale of the stocking (Ferguson, 2007; Schenekar et al., 2014). Lineages can remain distinct especially where the native population has evolved a distinct life history. For example, the genetically distinct native carpione trout, a deep-water lake spawner in Lake Garda (Italy), is sympatric with a lacustrine-adfluvial (see Ferguson, Reed, et al., 2019 for terminology of potamodromous life histories) Eurasian trout derived from a farm trout strain of Atlantic lineage, which were stocked around 1900, with no evidence of interbreeding (Gratton et al., 2014; Meraner & Gandolfi, 2018; Section 4.4). Two lineages of Eurasian trout have been reported as sympatric in several parts of the Plitvice Lakes water system (Croatia), one representing native Danubian trout and the other introduced Atlantic lineage trout (Buj et al., 2021). Mixing of the two lineages appears to be limited, at least as based on mtDNA haplotypes.

#### 3.2 Sympatric origins

Reproductively isolated populations can evolve sympatrically (within the definition used here) from a common ancestral lineage in a water without a physical barrier separating them, even in the presence of high gene flow, through divergent selection on ecologically important traits. Such "sympatric speciation" (adaptive radiation) has become increasingly accepted during recent decades with the link between ecological specialisation and reproductive isolation being particularly apparent in the evolution of postglacial fishes (Schluter, 2009). Adaptive divergence can result in reproductive isolation through several mechanisms. Individuals can become adapted to their trophic mode and/or spawning habitat characteristics resulting in hybrids being selected against due to reduced biological fitness. Assortative mating may be present because individuals may prefer to mate with others of the same phenotype (Garduno-Paz et al., 2020). Divergence may involve only a few genes under selection, possibly clustered throughout the genome (genomic islands), with the rest of the genome remaining largely homogenous as a result of gene flow (Franchini et al., 2013; Jacobs et al., 2018; Nosil et al., 2021).

Smith and Skúlason (1996) and Skúlason et al. (1999) presented a conceptual model explaining sympatric divergence in general. This involves a single population colonising a new or relatively unexploited environment coupled with a high level of intrapopulation competition. Subsequently, rapid phenotypic shifts occur, especially in behaviour, morphology and life history, primarily brought about by phenotypic plasticity. Divergent selection then results in the evolution of specialised populations and reduced phenotypic plasticity. The final stage is the evolution of prezygotic and postzygotic reproductive isolating mechanisms resulting in reduced gene flow. The model was further extended by Skúlason et al. (2019) by integrating

development with ecology and evolution (eco evo devo). This emphasises the need to consider phenotypic variation generated during the ontogenetic process, together with ecological opportunity and natural selection, to fully understand sympatric speciation.

While in practice, it can be difficult to differentiate between allopatric and sympatric origins, allopatrically evolved lineages might be expected to have colonised multiple waters and populations sharing genetic ancestry could be found elsewhere (Mehner et al., 2021). On the other hand, populations that have evolved in sympatry should share greater genetic ancestry to each other than to similar populations that have evolved in parallel in other waters. Thus, sympatrically derived populations are likely to share an mtDNA clade indicating evolution from a common lineage (Gowell et al., 2012). Populations that have evolved in sympatry in postglacial lakes generally have lower genetic differentiation than allopatric ones due to the shorter period of isolation, although effective population size  $(N_{\rm r})$  will also be important in this respect. However, gene flow on secondary contact of allopatrically derived populations may also result in increased similarity of now sympatric populations.

Unlike Arctic charr and European whitefish, for Eurasian trout, there are few clear-cut examples of sympatric splitting resulting in reproductively isolated populations. Three of the four sympatric populations in Loch Laidon (Scotland) fit the expectations of sympatric divergence (Verspoor et al., 2019; Section 4.2).

#### 3.3 Natal homing subpopulations

Most lakes and rivers have two or more spawning locations resulting in reproductively isolated subpopulations. Natal homing means that subpopulations in these locations can genetically diverge from each other where the strength of genetic drift and/or natural selection producing divergence exceeds the gene flow opposing it. In large lakes, isolation by distance can result in gene flow among adjacent spawning subpopulations but not among more distant ones (i.e. isolation by distance). Subpopulations of Eurasian trout generally do not show obvious morphological and/or trophic segregation, although in most cases studies have not been sufficiently detailed to conclude this definitively. However, in large lakes, with considerable distance among spawning tributaries, there is some evidence of such divergence among subpopulations (Crozier, 1985; Crozier & Ferguson, 1986; Swatdipong et al., 2010, 2013). Natal homing is likely to be responsible for at least some cryptic sympatric "populations" in salmonids.

Restoration stocking of a lake, where Eurasian trout have become extinct, using several distinct lineages with differential contribution of these in the spawning rivers can initiate genetic divergence, which is then maintained by natal homing and potentially differential selection. In Loch Fleet (southwest Scotland; area 0.18 km<sup>2</sup>; max. depth 17 m), restoration stocking with four distinct lineages, following acidification-induced extinction of the native trout, was found to have resulted in genetically different inflow and outflow river populations some six to eight generations later (Prodöhl et al., 2019).

Genetically distinct subpopulations are expected in all waters with two or more spatially segregated spawning areas, although they may only be detected with a limited number of genetic markers where small effective population sizes  $(N_r)$  have resulting in increased differentiation due to genetic drift. Thus, Prodöhl et al. (2019) detected three sympatric subpopulations in Loch Grannoch (southwest Scotland; area 1.15 km<sup>2</sup>; max. depth 21 m) but not in other similar lakes in the same region. The number of brown trout in this particular lake was reduced to a few hundred fish by severe acidification in the 1970s, and thus,  $N_{\rm F}$  in each of the three spawning rivers was undoubtedly very low. Genetic drift likely resulted in sufficient genetic differentiation (mean  $F_{ST} = 0.03$ ) for the structuring brought about by natal homing to be detected with both BAPS and STRUCTURE.

Sympatric subpopulations resulting from natal homing have been widely demonstrated in many waters throughout the Eurasian trout range (Berrebi et al., 2013; Crozier & Ferguson, 1986; Duguid, 2002; Keenan, 2015; Linløkken et al., 2014; Magee, 2017; Skaala, 1992; Swatdipong et al., 2010). Sympatric subpopulations solely as a result of natal homing are not considered further in this review.

#### 3.4 Phenotypic plasticity

Sympatric phenotypes may be environmentally induced, i.e. they represent phenotypic plasticity resulting from epigenetic differences, such as DNA methylation or histone modifications, and consequent modification of gene expression (Crotti et al., 2021; Fargeot et al., 2021). Thus, environmental influences can be converted into gene-regulatory signals resulting in fine tuning of phenotypic variation in ecologically important traits (Heckwolf & Meyer, 2021). Plastic phenotypic differentiation through epigenetic changes can be the first stage in adaptation to changing environmental conditions (Hu et al., 2021; Mäkinen et al., 2018), although the overall importance of this mechanism is still unclear. However, Vernaz et al. (2021) found substantial DNA methylation differentiation, associated with changes in transcriptome activity of ecologically relevant genes, among sympatric Lake Malawi cichlid species, in spite of their low DNA sequence differentiation. Campbell et al. (2021) compared Arctic charr reared at 9°C and 5°C and found significant differences in craniofacial morphology and vertebral number. Environmentally induced phenotypes do not represent separate populations initially, although phenotypic plasticity is considered the first stage in the evolution of genetically based morphological, ecological and behavioural differences (Parsons et al., 2016; Skúlason et al., 2019).

Absence of genetic differentiation between phenotypes, as seen from a limited number of genetic markers, must be treated with caution. Unless they have been reproductively isolated for sufficient time for the accumulation of genetic differences, it is unlikely that there will be genome-wide differentiation that could be detected with such techniques. In some cases of recently diverged populations, a few highly differentiated loci of large effect can be responsible for population-level morphological, ecological or behavioural

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divergence in spite of other regions showing little or no differentiation. Thus, genetic differentiation can be present in a few genes involved with specific adaptations and/or reproductive isolation with divergence involving most genes being very low due to their recent divergence and/or gene flow (Grummer et al., 2021; Jacobs et al., 2018; Nosil et al., 2021). In summary, while differences as seen by genetic markers reflect genetic differences, similarities may not indicate genetic similarity (Ferguson, 1980). The screening of many individuals and comprehensive genomic sequencing are required to identify genes with large effect that are responsible for specific phenotypes (Kardos et al., 2016), particularly for recently diverged populations. Also, reproductive isolation may rely more on regulatory gene changes, producing epigenetic differences, rather than protein coding ones (Hamilton & Miller, 2018). Reproductive isolation and local adaptation can also be produced by chromosomal structural changes and other changes in genomic architecture even in the presence of substantial gene flow that results in uniformity at genetic markers (Cayuela et al., 2020; Hale et al., 2021; Wellenreuther et al., 2019; Wold et al., 2021). Phenotypic plasticity may be responsible for some of the spawning phenotypes of Eurasian trout in Lake Ohrid (Section 4.7) and Lake Sevan (Section 4.8).

#### **OCCURRENCE OF SYMPATRIC** 4 EURASIAN TROUT POPULATIONS

Unlike charr and whitefish most currently known Eurasian trout sympatry involves only two populations. Leaving aside the four spawning phenotypes in Sevan trout, which have not been demonstrated to be reproductively isolated (Section 4.8), three and four sympatric populations are confirmed only from Loch Laidon (Scotland; Section 4.2), Lake Ohrid (Albania/North Macedonia; Section 4.6) and Lough Melvin (Ireland; Section 5).

#### 4.1 **Piscivorous trout**

In Eurasian trout, the commonest occurrence of two sympatric populations/phenotypes involves trout that feed on invertebrates throughout their lives and those that switch to fish feeding after initial invertivory. The ontogenetic transition to piscivory requires both that suitable prey is available within a lake and that the trout, a gapelimited predator (Jonsson et al., 1999), reaches a size sufficiently large to be physically able to consume fish prey (Keeley & Grant, 2001). The timing of the feeding switch varies among individuals and populations and is determined by several factors including fish community structure, body length, trophic position and individual dietary specialisation (Sánchez-Hernández et al., 2017). The presence of small fish such as sticklebacks (Gasterosteus aculeatus/Pungitius pungitius) and minnows (Phoxinus phoxinus) may enable a shift to piscivory earlier and, thus, provide a stepping-stone between invertebrate prey and larger fish such as Arctic charr. Typically, the switch to piscivory in Eurasian trout is at a minimum size of 130-150 mm

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for feeding on sticklebacks and minnows, and 200–300 mm for Arctic charr and European whitefish (Grey, 2001; Jensen et al., 2012; L'Abée-Lund et al., 1992). As the size of the trout increases, so does the size of prey taken, with the assumption that there is an optimum prey size for a given size of trout. Above this, optimum size prey becomes increasingly difficult to capture, and below the optimum size, it becomes energetically less profitable.

In Britain and Ireland, long-lived, late-maturing Eurasian trout that feed predominantly on larger fish such as Arctic charr, European perch (Perca fluviatilis), whitefish and roach (Rutilus rutilus) (not sticklebacks or minnows) are generally referred to as ferox (Campbell, 1979). In practice, ferox are often identified purely on the basis of piscivory. Ferox have been described from many hundreds of lakes in Britain and Ireland, and especially in Scotland (Hardie, 1940; Hughes et al., 2016). In Scotland, 192 lakes show evidence of currently, or historically, supporting ferox, their presence being predicted in logistic models by larger and deeper lakes that also have Arctic charr (Hughes et al., 2016). Applying similar criteria and taking account of known and extinct ferox in northwest England, Wales and Ireland (Gargan et al., 2021; Williams, 2020), this would increase the estimated number of ferox lakes in Britain and Ireland to over 220. The current record rod caught ferox in Britain and Ireland was from Loch Awe (Scotland) in 2002 and had a mass of 14.4 kg (https://www. wildtrout.org/content/ferox-trout). In some lakes, large brown trout can occur as the result of unusual feeding opportunities promoting extremely fast growth (Campbell, 1979). These trout, however, are usually short lived and early maturing and thus do not meet the definition of ferox as used here.

As well as a switch to piscivory and subsequent increased growth rate, ferox are characterised by late sexual maturity (7+ years) and longevity (up to 23 years in Britain) (Campbell, 1979; Hughes et al., 2018; Mangel & Abrahams, 2001), with a positive correlation between size and longevity (Jonsson et al., 1991). Age of sexual maturity in Eurasian trout and other salmonids is influenced by both ecological and genetic factors (Mobley et al., 2021; Palm & Ryman, 1999), and thus, indirectly at least, there is a genetic basis to piscivory, late maturation and longevity, all of which are interlinked requirements for large size. It is likely that older, larger trout have low levels of mortality from predation given the lack of other large predators in postglacial lakes. Thus, delaying sexual maturation may not be disadvantageous and potentially results in large lifetime fitness benefits (Shedd et al., 2015).

In most lakes, given the limit on prey availability, only a small proportion of trout become piscivorous and make up c. 5% of the adult stock (L'Abée-Lund et al., 2002; Mangel & Abrahams, 2001). However, in some lakes in the Nordic region where there is an abundance of fish prey, most, if not all, Eurasian trout can become piscivorous. Piscivory can be seasonal; in lake Fjellfrøsvatn (Norway), for instance, trout >20-cm fork length feed predominantly on juvenile Arctic charr during the period December to May and rarely outside this period as charrs are in the profundal zone (Amundsen & Knudsen, 2009). In Finland, where the prey consists of abundant European whitefish, vendace (*Coregonus albula*) and European smelt

(Osmerus eperlanus), almost all lacustrine trout are piscivorous at a length >30 cm (Huusko et al., 2018). In a Norwegian reservoir where initially only invertivorous Eurasian trout were present, the trout switched to feeding on minnow and Arctic charr after these were introduced (L'Abée-Lund et al., 1992). Surprisingly, few studies have been undertaken on piscivorous trout in the Nordic region. Thus, it is not known if these fish are homologous to ferox as described in Britain and Ireland, i.e. long-lived and late-maturing. Some studies suggest that differences in age of maturation and longevity in the Nordic region may not be as pronounced as in Britain and Ireland (Jonsson et al., 1999).

The genetics of some of the ferox populations in Britain and Ireland have been explored, although, as far as can be determined, no such studies have been undertaken in the Nordic region. Several studies involving genetic markers have shown ferox of Lough Melvin to be genetically highly distinct from sympatric gillaroo and sonaghen (Section 5). Duguid et al. (2006) examined ferox from Loch Awe (Scotland) and Loch Laggan (Scotland) and found them also to be genetically distinct from sympatric brown trout in each lake. In the only genomics study of ferox published to date, Jacobs et al. (2018) found strong genetic differentiation ( $F_{sT}$  between 0.32 and 0.68) in several outlier genomic regions (genomic islands), scattered throughout the genome, between brown trout and ferox trout from Loch Maree (Scotland: area 28.7 km<sup>2</sup>; max. depth 122 m). Several genes with functions potentially involved in life history divergence were identified, which the authors inferred to be under differential selection. Furthermore, their analysis indicates that the two types represent distinct lineages that evolved during the last glaciation with introgression on secondary contact. Jacobs et al. (2018) suggest that size-related assortative mating may be partially responsible for reproductive isolation of ferox and brown trout, although intrinsic barriers may also be present as a result of genetic differentiation.

In a common garden experiment, Hughes et al. (2018) found that first generation juvenile progeny of ferox trout from Loch Maree (Scotland) showed increased behavioural dominance and food acquisition relative to the progeny of sympatric brown trout with ferox being dominant in 90% of pairwise contests. Increased exploratory behaviour has also been found in piscivorous rainbow trout (Monnet et al., 2020). Thus, dominance-related differences and increased boldness, of genetic and/or nongenetic (e.g. maternal effects) origin, likely contribute to the maintenance of a piscivorous life history. Relatively high mortality of hatchery-reared hybrids between brown trout and ferox trout from Loch Maree suggests that these life history forms are not only reproductively isolated by extrinsic barriers but also that intrinsic postzygotic barriers may be present (Hughes et al., 2018).

No other lochs have been examined in sufficient detail to determine whether ferox are genetically distinct from sympatric brown trout, or whether some ferox are simply ecophenotypes. Lough Melvin, Loch Awe and Loch Laggan ferox populations share the same mtDNA haplotype (QUB 7.6), distinct from sympatric brown trout, the haplotype being fixed in Melvin ferox and at frequencies of 0.70 and 0.88 in Awe and Laggan, respectively, with significantly lower frequencies in sympatric nonferox trout. This suggests a common ancestry and, thus, genetic predisposition to the ferox life history (Duguid et al., 2006; McKeown et al., 2010). This haplotype is also present at high frequencies (0.84-1.0) in trout from Loughs Corrib, Erne and Mask in Ireland, and in moderate frequencies (0.42-0.56) in Lochs Maree, Rannoch and Shin in Scotland, all of which are known to have ferox trout (Duguid, 2002; Gargan et al., 2021; McKeown et al., 2010).

While this is not a universal diagnostic feature (Hughes et al., 2018), some ferox populations are also characterised by a high frequency of the LDH-C1\*100 allele, which is typically absent or at low frequency in other populations and is thought to represent a distinct ancestral trout lineage (Hamilton et al., 1989). Thus, Melvin ferox share a high frequency (0.65) of the LDH-C1\*100 allele with Awe (0.65) and Laggan (0.96) ferox populations (Duguid et al., 2006). The genotype of the record rod caught ferox from Loch Awe in 2002 was LDH-C1\*100/100 (R. Hynes, pers. comm.). Of the 12 trout >42 cm, and presumably ferox, as other trout there rarely exceed 40 cm. obtained from Melvin, nine were LDH-C1\*100/100 homozygotes (and three heterozygotes) even though, based on the overall frequencies of this allele in Melvin trout (0.06), the expected number of such homozygotes would be 0.04 if there was no association of ferox and LDH-C1<sup>\*</sup> genotype (Ferguson & Taggart, 1991). However, ferox from Loch Rannoch were found to have a low frequency (0.10) of the LDH-C1\*100 allele while ferox samples from five other Scottish lochs known to have ferox were fixed for the LDH-C1\*90 allele (Duguid, 2002). Differential introgression on secondary contact between ferox and other lineages, together with genetic drift and/or selection, may explain the disparities in the degree of contemporary genetic differentiation in various lakes.

Melvin ferox 1+ parr from the spawning river could be identified on head measurements further supporting a genetic basis as piscivory does not start until at least 3+ (Cawdery & Ferguson, 1988). In Melvin, Laggan, and Awe, ferox recruit from a single river, the largest inflow in the case of Melvin and Laggan and the outflow in the case of Awe. However, there is evidence that, in the immediate postglacial period, the current Awe outflow could have been an inflowing river with the outflow being at the opposite end of the lake (Duguid et al., 2006). Loughs Corrib and Mask (western Ireland) contribute over 75% of ferox caught in Ireland (Gargan et al., 2021). Ferox have been shown to spawn predominately in the Cong River and Cong Canal, although overall, these contribute only c 1% and c 4% of trout recruitment to these lakes respectively (Gargan et al., 2021). The Cong River/Canal is the outflow of Mask and an inflow into Corrib, construction of the canal having been attempted to bypass subterranean parts of the river but was never completed. However, it serves as an overground connection during high flow conditions (Gargan et al., 2021).

Similar piscivorous and insectivorous rainbow trout ecotypes occur sympatrically in western North America, although the piscivorous type is rare across the native range of lacustrine rainbow trout (Keeley et al., 2005). One example involves these two ecotypes in Kootenay Lake (British Columbia, Canada; area, 400 km<sup>2</sup>) where the

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piscivorous type historically matured at greater than 60 cm and 5 kg, while the insectivores matured at smaller sizes. They are genetically distinct and spawn in different rivers (Taylor et al., 2019). Grummer et al. (2021) found high genomic divergence ( $F_{ST} = 0.188$ ) between these two ecotypes i). However, unlike the Jacobs et al. (2018) study of ferox, they found that the piscivorous rainbow trout ecotype is controlled by multiple genes with small effects on growth and related metabolic activities.

#### Loch Laidon 4.2

Loch Laidon (westcentral Scotland; area 4.83 km<sup>2</sup>; max. depth 39 m) is an upland lake at 282 m above sea level that lies in Rannoch Moor, one of the last parts of Scotland to be deglaciated (Bromley et al., 2014). Eurasian trout were collected in 2008 by stratified random three-dimensional Nordic survey gill netting (Appelberg, 2000) and, together with angler-caught loch and electrofished river specimens. were screened for mtDNA RFLP variation (cytochrome-b, D-loop and 16sRNA-ND1) and microsatellite variation (22 loci) (Verspoor et al., 2019). DAPC analysis of the genetic data indicated four distinct groups with two individuals forming one group. These two individuals appeared to be morphologically similar to ferox as described from other Scottish lochs (Section 4.1). STRUCTURE at K = 4placed these two putative ferox individuals, together with two other smaller individuals, in a single cluster. The distribution of the three clusters of nonferox trout in the lake was nonrandom and associated with net depth.

Given that only two individuals were caught, the putative ferox were not studied further. For the other individuals, the dietary habits of the three genetically assigned population types were consistent with their distribution in the lake, although there was considerable overlap in feeding. The profundal type showed stomach contents dominated (>90% of prey items) by profundal prey such as Pisidium sp. and chironomid larvae (Chironomidae). In the limnetic population, 51% of individual stomach contents were dominated by zooplankton and adult insects. In contrast, the analysis of individuals in the shallow benthic population had a mixed diet with 21% of individuals having stomach contents dominated by profundal prey, 21% by pelagic prey and 14% by littoral prey items while the remaining individuals showed no dominance by any prey group, suggesting this population was, overall, a trophic generalist. Thus, collectively the analyses provided clear evidence of divergence in the trophic ecology of the different populations and support the separation of the nonferox trout of Loch Laidon into profundal macrobenthos, shallow benthic generalist and limnetic planktivore feeding groups (Piggott et al., 2018).

Detailed morphological analysis of the trout genetically assigned to the profundal benthic, shallow benthic and limnetic populations showed differences in body morphology, albeit with some overlap (Piggott et al., 2018). The profundal form had a deep body with a relatively large head and eye, together with relatively short and widely spaced gill rakers, and pale skin colouration, characteristics

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consistent with those also found in Arctic charr showing a profundal ecology (Hooker et al., 2016; Skoglund et al., 2015). The limnetic form had a more streamlined body and contrasting dorsoventral shading, with relatively long and closely spaced gill rakers, as typical of other limnetic Eurasian trout (Cawdery & Ferguson, 1988). Although significantly different in morphology from the other two groups, the shallow benthic form was intermediate in morphology and did not show clear ecomorphological differences in keeping with its generalist feeding ecology (Piggott et al., 2018).

The profundal benthic population ecotype is unique in that it is the first time this ecotype has been documented in sympatry with shallow benthic and limnetic populations of Eurasian trout. The DAPC analysis showed the ferox population to be highly divergent from the other three populations, consistent with ferox having an allopatric origin as in other lakes (Duguid et al., 2006). The low level of genetic differentiation of the three nonferox populations ( $F_{ST}$  across groups as defined by STRUCTURE 0.037 and DAPC 0.038) would suggest recent and likely sympatric origins, or alternatively a high level of gene flow. The lack of profundal benthic trout in other lakes would also argue for its sympatric origin.

### 4.3 | Lakes Bunnersjöarna

Lakes Bunnersjöarna (central Sweden; total area 0.67 km<sup>2</sup>, max. depth ~2 m) are connected twin lakes located at an elevation of 955 m. Two genetically distinct cryptic populations were found in both lakes, with the populations showing fixation for alternate functional and null alleles at the LDH-A1\* locus, together with statistically significant differences in allele frequency at five other enzyme coding loci (Allendorf et al., 1976; Ryman et al., 1979). Saha et al. (2021) extended these allozyme studies by examining 96 SNPs, through whole-genome pooled sequencing of DNA from 50 individuals from each LDH-assigned population, and individual sequencing of two individuals per population. Genome-wide divergence between the two populations was found to be the outcome of both genetic drift and diversity selection and was similar to lower values found between reproductively isolated allopatric populations in the same geographical region ( $F_{ST}$  based on SNPs = 0.24 and on pooled sequencing = 0.13). There were differences in the amount of genetic variation within each population, based on both allozymes and SNPs, with the population characterised by the null allele being considerably lower (expected heterozygosity 0.27 and 0.08 respectively). Without prior grouping of individuals, STRUCTURE suggested that the data were consistent with 2 groups (K = 2), which on the basis of membership were almost entirely consistent with the LDH-based groups. The study identified two LDH-A1\* alleles and found divergence between the populations in a regulatory section of one of these alleles. However, the exact genomic backgrounds to the two LDH-A1\* alleles (i.e. genomic location of gene locus encoding for this polymorphism) remain unresolved. Given that Melvin gillaroo is also characterised by a moderate frequency of an LDH-A1\* null allele (Section 5), it is of interest to speculate as to the role of such

regulatory variants in reproductive isolation. As Saha et al. (2021) note, regulatory genes have been implicated in the divergence of dwarf and normal whitefish in Canada (Hebert et al., 2013).

While significant differences were detected in growth rate between the two populations, no other phenotypic differences were observed, albeit no detailed morphometric and meristic studies have been published. Saha et al. (2021) found that genes involved with growth were associated with high  $F_{ST}$  values, suggesting diversifying selection. Several other genes potentially under selection were associated with reproduction, implying that the reproductive isolation between the populations is under genetic control. As with Lough Melvin (Section 5) there is some indication of separate inlet and outlet spawning populations (Ryman et al., 1979). No differences in feeding were observed between the two populations (Ryman et al., 1979).

Preliminary analysis of the mtDNA sequences of the populations do not indicate that they were derived from separate postglacial lineages (Saha et al., 2021). While Svärdson and Fagerström (1982) suggest human translocation was involved for one of the populations, whether this or natural processes produced the sympatry is still unknown (Saha et al., 2021). There are other lakes c 20 km away, however, where the *LDH-A1*\* null allele has also been observed (Allendorf et al., 1984), thus both hypotheses are feasible. Irrespective, following natural or anthropogenic sympatry little, if any, hybridisation has occurred. Natural or anthropogenic origins of these populations do not impact on their conservation importance – it is what is currently present that is important. The high degree of genome-wide differentiation without any obvious morphological or trophic differences makes these populations of particular evolutionary and management importance.

### 4.4 | Lakes Trollsvattnet

Two genetically isolated cryptic sympatric populations of Eurasian trout, in roughly equal occurrence, have been reported in two small, interconnected lakes – Lakes Östra and Västra Trollsvattnet (central Sweden; area 0.10 km<sup>2</sup> and 0.17 km<sup>2</sup>) (Andersson, Jansson, et al., 2017; Andersson, Johansson, et al., 2017; Jorde & Ryman, 1996; Palmé et al., 2013). Genetic differences, as detected by allozyme variation, have remained stable over at least 28 years (4+ generations), with allozymes showing significant greater differentiation than microsatellites or SNPs ( $F_{\rm ST}$  allozyme 0.1, microsatellite 0.02, SNP 0.03 and pooled sequencing 0.03) (Andersson, Jansson, et al., 2017). STRUCTURE analysis of SNPs indicated K=2 as the most likely number of clusters explaining the data, with mean assignment probability Q to each of the two clusters of 0.95 and 0.81 respectively (Andersson, Jansson, et al., 2017).

One population shows close genetic similarity with trout in the connected small upstream Lake Hästskotjärnen. The other population shows high genetic similarity to trout from several downstream lakes. Each population is more similar to trout samples from other lakes in the area than they are to each other, suggesting allopatric/ parapatric origins. There are some indications that different spawning sites maintain structuring. No significant morphological differences were found between the two populations within each of the lakes (Andersson, Johansson, et al., 2017). Furthermore, examination of the stomach contents revealed no evidence of trophic differences between the two sympatric populations although there were differences between the two lakes. The specimens were obtained in late August when food was likely to be most abundant. There were also no differences between the sympatric populations in carbon or nitrogen isotope signatures, which would be expected to be influenced over a longer period of feeding especially as slower turnover muscle tissue was used.

#### 4.5 Lake Garda. Italy

Lake Garda (area 368 km<sup>2</sup>, max. depth 350 m) is an alpine lake dating from the end of the last glaciation in the southern Alps, some 15,000-18,000 ybp (Meraner & Gandolfi, 2018). The genetically distinct carpione trout has been described as occurring in the lake since the mid-16<sup>th</sup> Century. It is thought to have originated from an ancestral Italian peninsular trout within Garda after postglacial colonisation (Meraner & Gandolfi, 2018). The species status of carpione S. carpio is supported by the phylogenomics study of Hashemzadeh Segherloo et al. (2021). Analyses of mtDNA and nDNA sequences, together with microsatellite data, (Gratton et al., 2014; Meraner & Gandolfi, 2018) showed no evidence of population substructure within carpione in spite of the fact that there are two spawning periods, December to February, and July to August (Melotto & Alessio, 1990). In addition, no significant difference in the proportion of sibship relationships within and between these winter and summer spawning groups was observed and it would appear that individuals are plastic with respect to spawning time with possible biannual spawning (Meraner & Gandolfi, 2018). Their diet is mainly zooplankton (principally Bythotrephes longimanus) in the summer with benthic crustaceans (Crustacea) and chironomid larvae in the winter (Melotto & Alessio, 1990).

Carpione is sympatric with an introduced farm strain brown trout of Atlantic lineage that were stocked around 1900. However, based on mtDNA and microsatellites, there is no evidence of any interbreeding of the introduced trout with carpione (Gratton et al., 2014; Meraner & Gandolfi, 2018). Carpione spawn on submerged gravel ridges close to underwater springs at depths of 50-300 m, while sympatric introduced brown trout are lacustrine-adfluvial spawners (Lunelli et al., 2012). Kess et al. (2021) identified a number of diverged genomic regions in deep-water Arctic charr relative to those inhabiting shallower water (>50 m) of the same lake. Various genes, likely to be involved in deep-water adaptation, were identified as well as putative copy number variants that are potentially involved in gene expression differences. It might be expected that deep-water adaptations would similarly be present in carpione. If this is the case it is possible that hybrids between carpione and introduced brown trout would be selected against. Thus, both prezygotic

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(place of spawning) and post zygotic mechanisms could be responsible for the isolation of carpione from introduced brown trout.

#### 4.6 Lake Posta Fibreno

Two genetic and morphologically distinct sympatric populations, Fibreno trout and native brown trout, occur in Lake Posta Fibreno (central Italy; area 0.29 km<sup>2</sup>; max. depth 15 m). The brown trout has been variously classified as Salmo cettii (Kottelat & Freyhof, 2007), S. macrostigma (Meraner & Gandolfi, 2018), or S. trutta (Delling et al., 2020). The Fibreno trout has been classified as S. fibreni (Meraner & Gandolfi, 2018). The two populations differ in meristic characters, parr marks and pigmented spots, and size at maturity, with Fibreno trout maturing at the end of its first year at a length of >12 cm for males and >14 cm for females (Gratton et al., 2013). The brown trout individuals mature at a larger size. The distinctive colour patterns and the size of mature individuals have been used to identify the two populations for management and conservation (Meraner & Gandolfi, 2018).

Spawning of Fibreno trout occurs in underground pools fed by karstic springs, either directly accessible from the lake or from the south-eastern tributary river. The brown trout are river spawners with a typical lacustrine-adfluvial life history. STRUCTURE assignment Q values for Fibreno trout were >0.98, except for a sample from the south-eastern river (mean Q = 0.89) where adjacent spawning of the two types occurs and a low level of introgression is present. The program NewHybrids (Anderson & Thompson, 2002) provided evidence that introgression between the Fibreno trout and brown trout gene pools occurs beyond  $F_1$  (Gratton et al., 2013). Introgression by stocked Atlantic lineage brown trout has also been noted, although, due to the cessation of stocking, this latter introgression is now reduced (Gratton et al., 2013). Both Fibreno trout and the native brown share a fixed mtDNA haplotype supporting the recent sympatric origin of the two forms. However, Gratton et al. (2014) found that their data lacked the power to discriminate between allopatric and sympatric origins. Ecological specialisations for adaptations to cave spawning in Fibreno trout, in the presence of ongoing gene flow, may have resulted in isolation being maintained by selection (Gratton et al., 2013). For example, Fibreno trout females produce very large eggs typical of other cave adapted fish (Poulson, 2001).

#### Lake Ohrid 4.7

Lake Ohrid (Albania/North Macedonia; area 347 km<sup>2</sup>, max. depth 289 m), a karstic lake, is the oldest lake in Europe, having originated some four to ten MYA as a result of tectonic shifts (Banarescu, 1991). In Ohrid the belushka (Albania)/belvica (North Macedonia) is now accepted as the most genetically distinct of the Eurasian trout species (Pustovrh et al., 2014; Whiteley et al., 2019). It probably split from a common ancestor of Eurasian trout >4 MYA (Sušnik et al., 2006). It is

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a slender, silvery, plankton-feeding trout that inhabits deeper parts of the lake around 40 m–60 m and spawns in the lake littoral zone.

Sympatric with belvica trout is Ohrid trout, referred to as *S. letnica* although this likely comprises at least two species (Hashemzadeh Segherloo et al., 2021). While hybrids between belvica and Ohrid trout have been produced artificially, there does not appear to be any natural hybridisation between the two species (Sušnik et al., 2006). Sušnik et al. (2007) examined Ohrid trout using 12 microsatellites and sequencing of mtDNA control region and found it to be a distinct part the wider Adriatic trout lineage. Moreover, sequencing of 22 nDNA genes show the separation of Ohrid brown trout from those in adjacent river catchments, thus supporting its genetic distinctness (Pustovrh et al., 2014).

Ohrid trout is previously known to have had four distinct spawning phenotypes differing in time and place of spawning; typicus is a winter lake littoral spawner, and aestivalis a summer lake spawner around bottom springs at c10.5°C. Balcanicus spawned in the outlet river now obstructed by a weir, and lumi is a winter river spawner (Kottelat & Freyhof, 2007; Spirkovski, 2004). Kottelat and Freyhof (2007) retain these as four species, albeit acknowledging that relevant data are limited - S. letnica (typicus), S. balcanicus, S. aphelios (aestivalis) and S. lumi. Balcanicus has shown considerable declines in the number of mature individuals and may now be extinct (IUCN, 2021). Both typicus and aestivalis are now largely maintained by stocking of around 15 million individuals per year (Sell & Spirkovski, 2004; Sušnik et al., 2007). The phenotypes have similar trophic ecology (Sell & Spirkovski, 2004) but are reported as differing in morphometric and meristic characters (Dimovski et al., 1992 cited by Sell & Spirkovski, 2004). Sušnik et al. (2007) failed to find any significant genetic differentiation between samples of typicus and aestivalis using 12 microsatellites and sequencing the mtDNA control region, although the other two types were not examined. This lack of difference between typicus and aestivalis is surprising given their highly distinct spawning times and locations in the lake. The situation may be similar to the winter and summer spawning carpione in Lake Garda with plasticity in spawning time and perhaps biannual spawning (Meraner & Gandolfi, 2018). However, Sell and Spirkovski (2004) found a significant difference in the frequency of mtDNA haplotypes between typicus and aestivalis, mostly resulting from variation found in the mtDNA control region 3' end. This variation was absent in the samples examined by Sušnik et al. (2007). Moreover, Sušnik et al. (2006) argue that variation in this region is likely due to instability caused by intramolecular mechanisms, making it unreliable for phylogenetic inference. A phylogenomics study revealed separate clusters of lumi and the other spawning types indicating that it merits species status, S. lumi (Hashemzadeh Segherloo et al., 2021). Thus, there are/were at least three sympatric species of Eurasian trout in Ohrid, albeit the current status of lumi is unknown.

### 4.8 | Lake Sevan

Lake Sevan (Armenia; area 1240 km<sup>2</sup>, max. depth ~79m) is known to have had four phenotypes of Sevan trout, which are generally

assigned to one species *Salmo ischchan* (Osinov, 1989). Two phenotypes known as bodzhak and winter ischchan (winter bakhtak, Markevich & Esin, 2019) have been extinct since the 1980s due to loss of their spawning grounds resulting from irrigation withdrawal causing a drop in water level of 18.5m, and the other two phenotypes, gegarkuni and summer ischchan (summer bakhtak) are considered critically endangered being largely supported by farm-reared trout (Levin et al., 2018, 2021). The phenotypes differ/differed in time and place of spawning, colouration and maximum size (Levin et al., 2021). Thus, gegarkuni are river spawners with a lacustrine-adfluvial life cycle. Summer ischchan are summer spawners within the lake, and also in the river mouths and immediately upstream. Bodzhak and winter ischchan were winter spawners within the lake.

While the four phenotypes have been assigned species status (Levin et al., 2021), this is questionable based on the available molecular information. Studies based on allozymes (Osinov, 1989) and mtDNA, including use of archived scales for the extinct types found a low level of genetic diversity and no clear genetic differentiation among the four phenotypes (Levin et al., 2018; Osinov & Bernatchez, 1996). Levin et al. (2021) carried out a more detailed study involving complete mitogenomes and genome-wide nDNA SNPs. Gegarkuni was found to be significantly genetically differentiated (mean  $F_{sT}$  0.06) from the other three phenotypes, which formed a single cluster. Thus there are two distinct genomic clusters, the lacustrine-adfluvial form and the primarily lacustrine spawners. The three phenotypes within the lacustrine spawning group are possibly the result of phenotypic plasticity and may not represent reproductively isolated populations. In Lake Garda (Section 4.5) winter versus summer spawning appears to be a plastic trait with the same individuals being involved. A more detailed genomic study is required before definitive conclusions on lack of reproductive isolation among the lacustrine spawning group can be reached. However, as two of these are now extinct this means that archived scales are the only source of DNA for such studies (Levin et al., 2018, 2021). Sympatric subpopulations, with moderate degrees of genetic differentiation, resulting from natal homing have been widely demonstrated in many waters throughout the Eurasian trout range (Section 3.3) and hence they do not represent a "species flock" as referred to by Levin et al. (2021) for Lake Sevan.

### 4.9 | Adriatic rivers

Although in many rivers distinct populations are parapatric or allopatric in distribution, or form highly introgressed populations, there a few situations of sympatric populations. Distinct populations represented by softmouth trout, marble trout and native brown trout coexist in the River Neretva (Croatia/Bosnia-Herzegovina), and River Zeta (Montenegro) (Pustovrh et al., 2014; Schöffmann et al., 2019). Mrdak et al. (2012) found a microsatellite-based  $F_{ST}$  of 0.305 between softmouth trout and marble trout, and 0.363 between softmouth trout and brown trout, sympatric in the River Zeta. Snoj et al. (2008) noted a microsatellite-based  $F_{ST}$  of 0.323 between

FIGURE 1 Photographs of trout from Lough Melvin and of  $F_1$  offspring reared in three small lakes near Belfast, c. 150 km from Melvin. 1. Melvin gillaroo; 2. Melvin sonaghen; 3. Melvin ferox; 4.  $F_1$  gillaroo lake A; 5.  $F_1$  gillaroo lake B; 6.  $F_1$  sonaghen lake C. For  $F_1$  offspring eggs and milt were taken from mature gillaroo from the Drowes river and sonaghen from the Ballagh river. Fertilised eggs were reared under standard conditions in a trout farm and 0+ juveniles planted out in August. Adult sampling was as 3+



sympatric softmouth trout and brown trout in the River Neretva. Different spawning times, and possibly separate spawning areas, prevent hybridisation or limit it to a low level, with softmouth trout spawning mainly in March-May compared to October-January for sympatric brown trout. Habitat and feeding analyses showed that softmouth trout avoid competition with brown trout by feeding predominantly on benthic macroinvertebrates, especially *Gammarus* spp. (Gammaridae) (Mrdak et al., 2012). Marble trout and native brown trout are also sympatric in most of the seven rivers in northern Italy and the two in Slovenia where the marble trout occurs (Schöffmann et al., 2019).

### 5 | LOUGH MELVIN

Since the mid-19th Century three distinct morphotypes of trout in Lough Melvin (northwest Ireland; 21 km<sup>2</sup>; max. depth ~45 m) have been widely reported in the angling and scientific literature (Day, 1887; Houghton, 1879; Newland, 1851). Locally these are known as gillaroo, black-finned trout or sonaghen, and ferox. The name gillaroo has been widely applied to mollusc feeding trout in other Irish lakes (Thompson, 1856; Went, 1951). As noted above (Section 4.1), ferox is the name given to large, long-lived, late-maturing and piscivorous trout found throughout Britain and Ireland. The name sonaghen appears in several early 20th century publications (Cosgrave 1912 as recorded by Howell, 1948; Went, 1952) and has uniquely been applied to Melvin trout. (Sonaghan, as used by some, is a late 20th century spelling artefact.) Of 457 trout taken in a survey in 2001, 61% were morphologically identified as sonaghen, 8% as gillaroo, 7% as ferox and 24% were unassignable on morphology (Central Fisheries Board, 2002, unpublished internal report). These Melvin populations appear to have remained stable based on no statistically significant differences in catch per unit effort in surveys carried out in 2008, 2011, 2014 and 2017 (Connor et al., 2018).

The Lough Melvin morphotypes have been studied in most detail of all sympatric situations to date, with the exception of genomic sequencing, although this is currently in progress (P. A. Prodöhl, unpublished data).

### 5.1 | Morphological differentiation

Gillaroo, sonaghen and ferox can be readily recognised on the basis of colouration (Figure 1), especially in living or recently dead fish, and other morphological features (Ferguson & Mason, 1981; Ferguson & Taggart, 1991). These authors used an indeterminate 'brown trout' category for individuals not readily identifiable. F1 offspring of gillaroo and sonaghen reared in separate small lakes s c150 km from Lough Melvin demonstrate the stability of their pigmentations patterns even under distinct environmental and feeding conditions (Figure 1). Genomic data are increasingly demonstrating the genetic bases of colouration differences in Eurasian trout (Valette et al., 2020). Stepwise discriminant analysis based on 12 meristic counts and 19 morphometric measurements from the three morphs correctly assigned 100% of the ferox, 98.8% of gillaroo and 98.7% of sonaghen (Cawdery & Ferguson, 1988). Principal components analysis also showed the morphs to be clearly distinct with head measurements, gill raker length, number of teeth and fin measurements being the most important diagnostic characters. All of these are potentially associated with feeding adaptations and habitat, that is they form distinct ecotypes as well as morphotypes.

### 5.2 | Genetic differentiation

Allozyme studies (Ferguson & Mason, 1981; Ferguson & Taggart, 1991) showed major differences in the occurrence and frequency of alleles, indicating that the three morphotypes are reproductively

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isolated populations. This genetic distinctness was extended by examination of mtDNA RFLPs (Hynes et al., 1996; McKeown et al., 2010; McVeigh et al., 1995), multi-locus DNA fingerprints and single-locus minisatellite variation (Prodöhl et al., 1992), and microsatellite variation (Magee, 2017; McKeown, 2005). Allozyme showed higher differentiation than microsatellites as measured by  $F_{ST}$ : gillaroo – sonaghen 0.1 versus 0.06; gillaroo – ferox 0.28 versus 0.17; sonaghen – ferox 0.27 versus 0.15. MtDNA  $F_{ST}$  showed the highest values–0.18, 0.54 and 0.38 for these three pairwise comparisons.

BAPS analysis, based on 23 microsatellites (reanalysis of data in Magee, 2017), support the existence of three genetically distinct groups (K = 3) within Lough Melvin. BAPS individual clustering followed by admixture analysis grouped each lake-caught gillaroo, sonaghen and ferox separately with BAPS assignment probability Q values of 1.0, with the exception of two hybrids (Figure 2). Lake individuals had been previously morphologically identified, and this was found to be 84% accurate. However, individuals that were morphologically difficult to identify were excluded originally, as noted above. With the exception of a few individuals and hybrids, parr from the outflowing River Drowes clustered with gillaroo, lower River Glenaniff parr with ferox and upper Glenaniff, River Ballagh and River Tullymore parr with sonaghen confirming the allozyme findings that these are the main spawning rivers for the three populations (Ferguson & Taggart, 1991). There is clearly some very limited straying among the rivers as seen by the occurrence of gillaroo juveniles in the Glenaniff and Ballagh, and a sonaghen juvenile in the Drowes (Figure 2). BAPS admixture analysis showing significant admixture (p < .01) in only four individuals. The assignment probability Q values of these are all around 0.5 (0.45-0.55) suggesting  $F_1$  hybrids: two ferox  $\times$  sonaghen and two gillaroo  $\times$  sonaghen. It is interesting to note that there is no evidence of other admixture that would be expected if backcrosses had occurred. Thus, reproductive isolation of ferox, gillaroo and sonaghen appears to result both from prezygotic isolation, especially natal homing, and possibly temporal and behavioural differences such as assortative mating (Auld et al., 2019), as well as postzygotic isolation possibly involving F<sub>4</sub> hybrid sterility and /or backcross inviability. The latter mechanism has been demonstrated for brown trout x Atlantic salmon hybrids (Galbreath & Thorgaard, 1995) where mortality of backcrosses between hybrid males and female Atlantic salmon, at the initiation of feeding, was found to be almost 100%, the exception being a spontaneous triploid individual. Progeny of hybrid females backcrossed to male Atlantic salmon were viable but were triploids, hence effectively sterile. Hybridisation between the Melvin populations occurs at a similar frequency to that observed between brown trout and Atlantic salmon (Matthews et al., 2000).

Gillaroo spawn predominantly in the outflowing Drowes river, with fry being found at least 3 km downstream from the lake, below which it was too deep for the electrofishing technique used (Ferguson & Taggart, 1991). This means that juvenile gillaroo have to move upstream to the lake unlike ferox and sonaghen, which move downstream in the inflowing rivers. Experiments on inlet and outlet spawning brown trout have shown that such differences in



**FIGURE 2** Bayesian Analysis of Population Structure (BAPS) admixture analysis (K = 3) based on the output of the mixture clustering of individuals using microsatellite data. Q values are shown on the y-axis. The admixture analysis involved 100 iterations to estimate admixture coefficients for individuals, 200 simulated reference individuals per population, and 20 iterations to estimate admixture coefficients for the reference individuals. Samples were adult trout (sonaghen, ferox, gillaroo) from Lough Melvin and juveniles (0+ and 1+) from four rivers. Lower and Upper sections of the inflowing Glenaniff River are shown separately being the spawning areas for ferox and sonaghen respectively. The outlet Drowes river, where gillaroo spawn, was sampled in 1990 and 2002. The inflowing Tullymore and Ballagh rivers are the other principal spawning rivers for sonaghen

migratory behaviour are genetically controlled (Jonsson et al., 1994). The observation of numerous redds in the bay leading to the outlet river, and the ease with which gillaroo parr could be obtained by seining in this bay, suggest that this area is also a spawning and nursery area for gillaroo. Day (1887) states that the gillaroo breed in the shallower parts of lakes so possibly spawning occurs elsewhere in Melvin as well.

### 5.3 | Allopatric versus sympatric evolution

Mid-19th Century accounts of trout in Lough Melvin (Day, 1887; Houghton, 1879; Newland, 1851) closely matching the current situation, provide strong evidence that this situation of three sympatric populations is a natural one and not the result of artificial stocking. Generally brown trout stocking in Britain and Ireland was not widely undertaken until the latter part of the 19th Century (Armistead, 1895; Maitland, 1887).

On the basis of morphology, especially colouration, and mollusc feeding, gillaroo have been reported from many lakes in Ireland including Lough Derg and other lakes in the Shannon system, as well as Loughs Conn, Corrib, Mask and Neagh (Bickerdyke, 1897; Kennedy & Fitzmaurice, 1971; Pennant, 1812; Thompson, 1856; Yarrell, 1841). Ordnance Survey maps identify a sandy bay in Lough Conn as Gillaroo Bay, a habitat typical of gillaroo in Melvin. Old photographs of gillaroo from Lough Conn show them to be remarkably similar in colouration to Melvin gillaroo, and local anglers report that, while previously common, trout of this type have been very rarely caught since the 1970s (A. Ferguson, unpublished data). In Melvin, the LDH-A1\*Q0 allele (formerly Ldh-1(n)) is unique to gillaroo. Hamilton (1987) screened 356 trout from Lough Conn, netted in August 1984 and found an overall LDH-A1\*Q0 frequency of 0.04. Hamilton (1987) also found the LDH-A1\*Q0 allele at a frequency of 0.03 in juveniles from the Tourmakeady River, Lough Mask. The overall frequency in Melvin trout was 0.06 and the frequency in morphologically identified gillaroo was 0.17 (Ferguson & Taggart, 1991). McKeown et al. (2010) found a mtDNA haplotype specific to gillaroo within Melvin and also in Lake Cumshingaun (southeast Ireland), but other than for widespread haplotypes there was no sharing with Conn or Mask. Coumshingaun and gillaroo samples also cluster together on the basis of microsatellites (McKeown, 2005). These genetic similarities may indicate Comshingaun trout and gillaroo were derived from a glacial refuge in the ice-free part in the southernmost part of Ireland or the Celtic Sea. In a comprehensive snorkel survey of Coumshingaun at spawning time, trout were found spawning only in the outlet river (F. Igoe, personal communication), thus this life history characteristic may be typical of gillaroo, possibly having evolved in the putative refuge population rather than within Lough Melvin.

Black-finned trout similar to sonaghen were reported by Günther (1866) to occur in Llyn Beguilin (now Bugeilyn) and Llyn Gadr in Wales. However, no genetic similarity was found between sonaghen and Bugeilyn trout sampled in 1983 and 2007 (Hamilton, 1987; P. A. Prodöhl, unpublished data), although black pectoral fins were evident (A. Ferguson, unpublished data). This is likely to be a case of morphological convergence as has been seen with other genetically controlled colour characteristics in brown trout (Delling, 2002; Skaala & Solberg, 1997). However, it is possible that the original 19th Century trout of that lake were no longer extant when recent specimens were obtained, although the remote location of the lake makes that improbable. Unlike gillaroo, sonaghen do not possess any allozyme alleles that are not widely shared with brown trout populations in Ireland and elsewhere. A moderate frequency (0.29) mtDNA haplotype (QUB 2.6) in Melvin sonaghen was also found in Lough Corrib brown trout, as well as in several populations in east Scotland and northeast England, but not elsewhere in Ireland. In addition this haplotype was also found in farm brown trout strains of Loch Leven origin (McKeown et al., 2010). Anecdotal information suggests that such farm trout were stocked into Lough Melvin and interbreeding may have resulted in the introduction of this haplotype into sonaghen, as well as into Corrib brown trout, this lake being also subject to stocking with farm strain trout in the past. In general, such supplemental stocking has limited genetic impact due to the low fitness of the farm trout in the wild (Ferguson, 2007) but a mtDNA haplotype could be more easily incorporated into the wild population by genetic drift compared to nuclear genes. This may explain the disjunct distribution of the haplotype. If this is the case, there is nothing currently to differentiate sonaghen genetically from many other brown trout populations in western Ireland and sonaghen appears to be equivalent to brown trout from these other catchments, all arising from a western Ireland refuge (McKeown et al., 2010). The morphological

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and ecological features that differentiate it from the others probably having evolved within Melvin following colonisation.

Ferox from Lough Melvin, Loch Awe and Loch Laggan have considerable genetic similarities and indeed they are genetically more similar to each other than they are to sympatric brown trout (Duguid et al., 2006). There are also some similarities with ferox in other lakes as well (see Section 4.1 for more details).

For ferox, and to a lesser extent for gillaroo and sonaghen, there is strong evidence that these morphs evolved allopatrically, with some current characteristics probably the result of postcolonisation ecological competitive character displacement in sympatry. Distinct mtDNA clades further supports allopatric origins (McKeown et al., 2010). Detailed genomic studies, especially on other Irish populations and making use of 19th Century museum specimens could likely resolve the issue of allopatric versus sympatric origins of gillaroo and sonaghen.

#### 5.4 **Trophic segregation**

Feeding segregation in Lough Melvin was examined based on stomach contents analyses. Since this is the most detailed study of feeding in sympatric Eurasian trout populations to date, and since Ferguson (1986) is "grey literature" and hence not easily accessible, a more detailed account is given here compared to other sections. For gillaroo (total N = 159 of food containing stomachs) and sonaghen (N = 178), lake-caught specimens were accumulated over several years (1981–1984, but mainly 1982) from February (32 gillaroo, 11 sonaghen), April (28, 27), May (27, 15), June (32, 25), July (8, 23), August (7, 25), September (16, 42), and November (9, 10). These involved day-time (c10.00-17.00) angler-caught fish at competitions supplemented by overnight (c16.00-10.00) netting outside the main angling period. All sonaghen and gillaroo were morphologically identified (Ferguson & Mason, 1981), although there was the potential for some errors in assignment for specimens that had been dead for some time, as noted above. Ferox specimens (N = 34) were caught by anglers from February to September 1978-1984. Ferox were identified by their captors mainly on the basis of their size (>40 cm), with again the potential for some errors in assignment. A range of ages, as determined by scale-reading, was included but primarily 2+ to 4+ for gillaroo and sonaghen and 5+ upwards for ferox. Due to the small number involved, ferox are not separated by month of capture.

All ferox stomachs contained food items. All gillaroo and sonaghen stomachs obtained in May, June, July, August and September contained food items. Empty stomachs in other months were as follows: February-20% gillaroo, 68% sonaghen; April-0%, 25%; November-18%, 29%. Food items were identified to the lowest taxonomic level feasible. The main food items found and taxonomic groups, separated by developmental stage where appropriate, are shown in Table 1. Dietary importance was assessed in two ways as recommended by Hyslop (1980). First, the number of stomachs containing one or more items of each food category expressed as a proportion of all food containing stomachs. Second, the proportion

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that the volume of food category comprised of the total food volume in an individual stomach. Volume was determined by water displacement using subsamples of each food type.

To examine differences in individual diet among sonaghen, gillaroo and ferox, a nonmetric multidimensional scaling (NMDS) analysis, was carried out using the function "metaMDS" within the R-package vegan (Oksanen et al., 2020). The dissimilarity distance matrix (Bray-Curtis) was generated from the matrix of volume proportions, although not all individual data as used by Ferguson (1986) were available for analysis. Stress was minimised following preliminary trials with a different number of dimensions. A solution (i.e. convergence) was reached with five dimensions. The R-package vegan was also used to test putative statistical difference in diet among Melvin ecotypes ("anosim" function with 9999 permutations), and to identify the main food items contributing to putative differences in feeding preference ("envfit" function with 999 permutations). Sonaghen, gillaroo and ferox showed statistically different diets (anosim: R = 0.072, p < .001) (Figure 3). Of the 12 diet categories s found in the stomachs, 11 were identified by NMDS as significantly contributing to the observed differences in feeding preferences of the three ecotypes (Table 1).

The dominant food items by volume in gillaroo stomachs were Trichoptera larvae and pupae followed by molluscs (500+ individuals in some stomachs) and *Gammarus*. Both Trichoptera and molluscs occurred in large numbers attached to rocks and on sandy substrates in the lough. Sonaghen feeding was dominated by Cladocera (*Bythotrephes longimanus* followed by *Daphnia* by volume with vice versa by number), with several thousand individual *Daphnia* estimated in some stomachs, together with Chironomid pupae. Cladocera formed <1% of the diet of idividuals morphologically identified as gillaroo. Small numbers of molluscs were found in four fish morphologically assigned as sonaghen but overall comprised <1% of food volume for that morphotype. Most of the ferox stomachs examined contained fish, with, in terms of number and volume of items, perch *Perca fluviatilis* being more important than Arctic charr *Salvelinus alpinus*. Two fish morphologically assigned as gillaroo had unidentifiable trout in their stomachs. Again, it has to be borne in mind that morphological identification of these fish was not 100% accurate. Overlap among the three ecotypes occurred in respect of insect feeding of various life stages (Figure 3) with gillaroo and sonaghen not showing significant difference in the proportion of Ephemeroptera subimagos and adults (Table 1).

The similarity in diet composition on a monthly basis was also calculated using Schoener's (1970) index of dietary overlap. The index gives values from 0 to 1, where 0.00 and 1.00 indicate no overlap and complete overlap in diet, respectively. The diet is considered to be significantly different at values <0.60 (Wallace, 1981). The Schoener (1970) index, by volume, between gillaroo and sonaghen is shown in Table 2 for each sampling month and overall. Gillaroo and sonaghen showed distinct diets in all months with the Schoener index ranging from 0.01 to 0.47, and an overall value of 0.13. The overall value for gillaroo versus ferox was 0.18 and for sonaghen versus ferox 0.12. The greatest overlap between gillaroo and sonaghen occurred in April when sonaghen fed extensively on benthic insect larvae, the abundance at this time likely reducing competition (Knudsen et al., 2019). Some overlap also occurred in August and September with gillaroo taking mid-water Chaoborus larvae and some surface items such as Ephemeroptera and other insects as noted above. August and September specimens were solely from angling competitions, and this may have biased the sampling against benthic feeders.

TABLE 1 Mean proportion (food volume) of different taxa and life stages in the individual stomachs of sonaghen, gillaroo and ferox, and nonmetric multidimensional scaling (NMDS) results

	Mean proportion per ecotype			NMDS		
Food category	Sonaghen	Gillaroo	Ferox	MDS1	MDS2	r <sup>2</sup>
Cladocera (Bythotrephes, Daphnia)ª	0.674	0.005	0.003	0.874	0.486	.908***
Asellus	0.001	0.076	-	-0.667	0.746	.118***
Gammarus	0.004	0.154	0.009	-0.64	-0.768	.088***
Ephemeroptera nymph	0.003	0.055	0.064	-0.559	-0.829	.042**
Ephemeroptera subimago and adult	0.042	0.045	-	0.631	0.776	.003
Trichoptera larvae and pupae	0.008	0.321	0.033	-0.578	0.816	.611***
Chironomidae larvae	0.05	0.073	0.002	-0.45	-0.893	.048**
Chironomidae pupae	0.109	0.002	-	0.498	-0.867	.107***
Chaoborus larvae and pupae	0.056	0.009	0.012	0.537	-0.843	.047**
Other adult insects incl. terrestrial	0.054	0.019	0.018	0.3	-0.954	.031*
Mollusca (Limnaea, Planorbidae, Potamopyrgus, Bithynia, Valvata) <sup>a</sup>	0.001	0.241	-	-0.861	0.509	.285***
Fish (Perca fluviatilis, Salvelinus alpinus)ª	-	-	0.859	-0.07	-0.998	.520***

<sup>a</sup>Listed in order of volume dominance. Only main food items are included. Individual data from the authors' unpublished results. MDS1 and MDS2 are the variable loadings on each derived axis and  $r^2$  is the coefficient of determination for the linear correlation of each diet category as a function of the axis scores. Significant diet categories are those explaining the majority of the variance among the Melvin ecotypes. Significance levels are designated as follows: \*p < .05, \*\*p < .01 and \*\*\*p < .001.

FIGURE 3 Plot of nonmetric multidimensional scaling (NMDS1 and NMDS2) for stomach contents of individual gillaroo, sonaghen and ferox from Lough Melvin. Individual fish are shown by dots and polygons enclose each ecotype



TABLE 2 Schoener (1970) index of dietary overlap in gillaroo and sonaghen

Month of sampling	Gillaroo vs. sonaghen
February	0.13
April	0.47
May	0.08
June	0.10
July	0.04
August	0.18
September	0.16
November	0.01
Overall	0.13

*Note*: Values were calculated from overall proportional volumes of each food category, and values <0.6 are considered as indicating no significant overlap (Wallace, 1981). Based on Ferguson (1986) and the authors' unpublished data.

Food items were categorised into those of bottom, midwater and surface origin as follows. Bottom: *Asellus, Gammarus,* Molluscs, insect larvae/nymphs. Mid-water: Cladocera, *Chaoborus,* Chironomid pupae, fish. Surface: emerging aquatic and terrestrial insects. Segregation between gillaroo and sonaghen is again clearly demonstrated (Table 3).

In the  $F_1$  experimental allopatric populations of gillaroo and sonaghen (July and August sampling) there was much greater overlap in food items with gillaroo feeding on zooplankton and sonaghen feeding to a greater extent on benthic insect larvae than in Melvin. The Schoener (1970) index between the two artificial gillaroo populations and the sonaghen one was 0.42 and 0.3 respectively with that between the two gillaroo populations being 0.59. The main difference was that only gillaroo stomachs contained molluscs even though these were observed to be present in the sonaghen lake. Molluscs comprised 32% and 35% of the gillaroo diet in the two lakes, respectively. Other studies have noted that brown trout do not take molluscs even when abundant in a lake (Ball, 1961). Possibly mollusc feeding is a heritable trait of gillaroo. Several studies have shown genetically based differential feeding behaviour in sympatric Arctic charr morphs (Adams & Huntingford, 2002; Klemetsen et al., 2006; Skúlason et al., 1993). In Atlantic salmon genetic variation partly underlies variation in prey utilisation among individuals (Aykanat et al., 2020).

# 6 | DIFFERENTIAL OCCURRENCE OF SYMPATRIC POPULATIONS

Sympatry of piscivorous and lifetime insectivorous Eurasian trout has been more commonly reported than for charr and whitefish species. In all lakes studied so far in sufficient detail, ferox have been shown to be reproductively isolated from sympatric trout, i.e. this life history is genetically determined and not the consequence of phenotypic plasticity in these studied situations. It is likely that reproductive isolation will be found to be the rule rather than the exception as more situations are subject to detailed analyses, although the occurrence of phenotypic plasticity in some lakes cannot be excluded as yet. Piscivory appears to have evolved in at least one distinct lineage of Eurasian trout rather than independently in each lake after colonisation. That is, members of the lineage appear to have a genetic predisposition to be ferox, with this life history being expressed when suitable prey is present in a lake. Eurasian trout anatomy may be more suited to the adaptations of larger jaws and teeth with strong skulls that are required for piscivory. On the other hand, Arctic charr is normally considered to be an inferior piscivore and has morphological limitations in features associated with piscivory, having shorter jaws and a smaller head (L'Abée-Lund et al., 1992; Mittelbach & Persson, 1998). Thus, it is not able to compete with piscivorous trout, often being displaced into the profundal zone (Knudsen et al., 2016).

TABLE 3	Contribution of bottom,	mid-water and surface	food items to the month	ly diet of gillaroo	and sonaghen
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		Bottom		Mid-water		Surface	
Ecotype	Sample month	%Occur.	%Vol.	%Occur.	%Vol.	%Occur.	%Vol.
Gillaroo	February	100	99	3	<1	0	0
	April	100	96	36	4	7	<1
	May	96	99	4	<1	0	0
	June	100	94	29	<1	52	5
	July	100	90	33	9	33	1
	August	100	78	50	12	50	10
	September	75	74	38	25	10	1
	November	100	99	11	<1	0	0
	All samples	96	92	23	6	15	2
Sonaghen	February	82	15	55	85	0	0
	April	78	58	26	38	19	4
	May	36	21	86	75	21	4
	June	52	5	96	79	36	16
	July	30	4	100	92	30	4
	August	68	8	100	59	68	32
	September	29	3	100	83	42	14
	November	70	2	100	96	20	2
	All samples	48	8	84	82	35	10

*Note:* Based on Ferguson (1986) and the authors' unpublished data. Occur. = % of food containing stomachs in this ecotype with at least one item from this food category. Vol. = volume of this food category as a % of the overall food volume for this ecotype.

Eurasian trout would appear to show fewer examples of sympatric populations of benthic and limnetic trophic segregation than charr or whitefish, where such populations are widespread. including benthic segregation by depth (for example: Chavarie et al., 2015; Hooker et al., 2016; Markevich et al., 2018; Østbye et al., 2006; Rogers & Bernatchez, 2007; Skoglund et al., 2015). Thus, benthic versus limnetic invertebrate feeding sympatric populations have, to date, only been described for Eurasian trout in Lough Melvin and Loch Laidon, with the latter being the only example of sympatric benthic segregation by depth. However, feeding ecology has not been reported in detail for Eurasian trout sympatric populations in Lake Ohrid and Lake Garda. The occurrence of profundal benthic trout in Loch Laidon but not in Lough Melvin may be due the absence of Arctic charr in Laidon and its presence in Melvin. In netting surveys of Lough Melvin Eurasian trout were rarely caught below 14 m but Arctic charr were generally caught in summer surveys in nets set at 20 m to 35 m (F. Kelly, IFI, personal communication).

Piggott et al. (2018) argue that the trout genetic architecture may make trophic divergence more difficult, with genes functionally relevant to this adaptive radiation being required (Berner & Salzburger, 2015; Schneider et al., 2019). As with other salmonids, Eurasian trout shows many duplicated genes due to its tetraploid ancestry (Macqueen & Johnston, 2014), such paralogs being important for producing phenotypic diversity and local adaptations (Salisbury et al., 2020). However, Macqueen and Johnston (2014)

that climate-linked ecophysiological factors, rather than wholegenome duplication, have been more important to salmonid diversification. Thus, environmental conditions rather than genetic architecture are important and in this respect Eurasian trout occupies a wide range of such conditions. In addition, the fact that Eurasian trout has been successfully introduced worldwide, making it the world's most invasive fish (Budy et al., 2013), may also suggest that it is unlikely that its genetic architecture is limiting its trophic divergence. The authors of this review contend that the lack of reports on benthic versus limnetic sympatric populations is due simply to the lack of relevant studies rather than lack of actual occurrence. Although Eurasian trout has been widely investigated using molecular genetic techniques over the past 45 years, most of these studies have involved allopatric populations (Bekkevold et al., 2020; Ferguson, 1989) and have not usually looked for evidence of sympatric populations. Indeed, one of the aims of this review is to promote more investigations of sympatric populations in Eurasian trout.

For Arctic charr the number of known sympatric populations has been shown to increase considerably where detailed surveys have been undertaken (Ferguson, Adams, et al., 2019; Woods et al., 2012a, 2012b). For example, Wilson et al. (2004) examined Arctic charr from 43 lakes in northwest Europe, primarily from Iceland and Scotland. They found STRUCTURE evidence of two sympatric populations in 10 lakes and heterozygote deficits, potentially indicating sympatric populations, in a further 13 lakes. No

such extensive surveys have been reported for Eurasian trout. In Scotland alone most of the >30,000 lakes, all formed after the Last Glacial Maximum c.18,000 YBP, have species-poor native fish communities dominated by Eurasian trout, allowing ecological opportunity for evolution of sympatric populations. Of these, 172 have a surface area >1 km<sup>2</sup> (Standing Waters Database, 2020), although sympatric populations are known from considerably smaller lochs than this in Sweden. Aside from studies of ferox, the nature and extent of sympatric trout Eurasian trout diversity has been little characterised in Scotland, albeit negative findings may not generally be published. Angling accounts could give indications of potential lochs for study as anglers are generally aware of zooplankton ("Daphnia") feeding and of colouration differences between limnetic and benthic feeding trout. For example, Headley (2019) refers to Loch Arkaig (northwest Scotland; area 16 km<sup>2</sup>; max. depth 91 m) as having distinct mid-water and benthic feeders together with ferox, making this loch a prime target for study. Elsewhere in Europe, especially in the Nordic countries and the Alpine region, there are many thousands of lakes >1 km<sup>2</sup> with Eurasian trout present. Ancient literature apparently indicates the presence of profundal feeding trout, which spawned in the littoral zone, in several subalpine lakes in Austria, Germany and Switzerland (Kottelat & Freyhof, 2007). It is not known if any of these are extant since, as with most other European lakes, there have been no recent investigations in these lakes specifically focussed on sympatric forms of Eurasian trout. Angling and fisheries management accounts could provide indications of priority lochs for investigation.

It could also be that more Eurasian trout sympatric diversity has been lost compared to that in charr and whitefish. Phenotypes in Lake Ohrid and Lake Sevan have been lost as a result of changes in water level impacting on littoral spawning grounds. Gillaroo in Ireland appears to have been formerly more numerous in various lakes (Section 5.3). If outlet spawning was characteristic then such rivers have been more often modified for drainage and hydroelectric schemes than inlet rivers. For example, the Lough Conn outlet river was drained in the 1960s, which coincides with the reported rapid decline of gillaroo in that catchment (anecdotal information from local anglers).

### 7 | SYSTEMATICS AND CONSERVATION

Sympatric Eurasian trout populations are a significant component of biodiversity as well as being of significant economic importance, especially for angling. Individual sympatric populations, as with allopatric populations, can possess a substantial and unique genetic heritage and due to their limited distribution may have a threatened status. Conservation requires identification of the entities involved, which include species, conservation units (CUs) and management units (MUs). These form a hierarchical series with potentially several CUs within a species, and several MUs within a CU. Subspecies are also sometimes described but in salmonid fishes have largely been replaced with CUs.

### 7.1 | Species designations

Most biodiversity studies, conservation activities, ecological and behavioural investigation, and legislative aspects are based on species. Eurasian trout populations within the genus *Salmo* are relatively young (4 MY-<15,000 Y; Bernatchez, 2001; Lecaudey et al., 2018; Pustovrh et al., 2014) and, since most speciation is continuous, they are mostly still in the grey zone of limited divergence where there is limited scientific criteria for deciding the taxonomic status of two populations (Roux et al., 2016; Zachos, 2018). This is especially so for sympatric populations that have split after postglacial colonisation Thus, application of different species criteria leads to various outcomes as to the number of species recognised.

Reproductively isolated sympatric populations potentially qualify as distinct species under the Biological Species Concept (Mayr, 1969, 2000). However, the natal homing of salmonids means that reproductive isolation can occur among subpopulations within and among tributaries (Section 3.3). Even though these subpopulations may be important from a management perspective, to recognise all such reproductively isolated groups as distinct species would be nonsensical and lead to chaos in salmonid taxonomy (Behnke, 1972). It is argued that prezygotic geographical reproductive isolation alone is insufficient for the recognition of distinct Eurasian trout species.

In general species are viewed as independently evolving lineages (De Queiroz, 2007). Recent classification of Eurasian trout species has explicitly or implicitly involved the evolutionary species concept (ESC) (Kottelat & Freyhof, 2007). The ESC, as originally proposed by Simpson (1951) and modified by Wiley (1978). regards species as being "groups of organisms than maintain their identity over time and space" and have their "own independent evolutionary fate". A corollary of this is that a fixed character state, or combination of states, used to establish species boundaries must have a genetic basis, as only such differences can maintain identity and evolve producing local adaptations. Differences in a single character can theoretically result in the designation of separate species under the ESC, providing this difference is genetically based, unique and adaptive. However, this is frequently not recognised, and to date most Eurasian trout species taxonomy has been based on morphological characters, in spite of the many issues with this approach.

### 7.1.1 | Environmental influence on morphology

Morphometric and meristic characters can be substantially influenced by the environment resulting in phenotypic differences that don't reflect genetic differences (Etheridge et al., 2012). Morphometric characteristics such as body and fin shape, as well as meristic characters, including gill rakers, can be affected by the age of the individual as well as temperature and population density during early development (Campbell et al., 2021; Greenberg WILEY FRESHWATER FISH

et al., 2021; Lindsey, 1981, 1988; Ross et al., 2006). Eurasian trout raised in an enriched hatchery environment differ in their colouration and spotting patterns from siblings reared in a conventional hatchery set up (Yaripour et al., 2020). When Eurasian trout populations are examined for morphometrics on a multivariate basis almost all populations are generally found to be distinct (Koene et al., 2020). Unfortunately, *Salmo* species are still being described based solely on environmentally labile characters, without demonstration of heritability and adaptation, and ratios to standardise for size, which are long known to be inappropriate due to allometric growth (Phillips, 1983).

### 7.1.2 | Integrative taxonomy

More recently, an integrative taxonomy approach has been favoured for many different organisms (Dayrat, 2005; Hashemzadeh Segherloo et al., 2021; Ottenburghs, 2019). In this, different species concepts and pluralistic information are integrated to reach an informed decision on species taxonomy. Complementary sources of information potentially include genomics, genetic markers and phylogeny, together with proven genetically based differences in morphology, behaviour, ecology and life history. It is important to distinguish heritable from environmentally determined variation, as well as neutral from adaptive variation, irrespective of the characters used. Not all information is of equal value, and some is potentially misleading. MtDNA sequences and restriction fragment length polymorphisms have been used in many taxonomic studies. However, reticulate evolution of mtDNA (Pustovrh et al., 2014), the existence of pseudogenes (Bensasson et al., 2001), and incomplete lineage sorting (Hashemzadeh Segherloo et al., 2021), means that mtDNA characters need to be used with appropriate caution. Relationships among recently evolved Eurasian trout species are more appropriately resolved with nDNA (Hashemzadeh Segherloo et al., 2021). Neutral markers (e.g. microsatellites not linked to genes under natural selection) are valuable for detecting reproductively isolated sympatric populations, and for assignment of individuals to their population/species of origin. However, the degree of genetic differentiation of neutral markers, as measured, for example by  $F_{ST}$ , is of little value as it reflects genetic drift, which is determined by  $N_{\rm F}$ . Bottlenecked populations can show unusually high  $F_{\rm ST}$  values relative to large populations even when they share a common postglacial ancestor. Thus, adjacent, and likely common origin, but now physically isolated populations in southwest Scotland, bottlenecked due to severe acidification, showed  $F_{ST}$  values >0.5 (Prodöhl et al., 2019). Partial or full genomic data, the ultimate source of evidence for species delimitation can provide evidence of the genetic basis of reproductive isolation and identify key local adaptations. Some have argued that species should be a monophyletic group of populations or an exclusive coalescence of gene trees. However, genomic data used to identify key adaptations make these criteria obsolete (Ottenburghs, 2019). In addition, phylogenetic trees produced by different genes, or groups of genes, are frequently discordant,

especially those based on mtDNA versus nDNA (Pustovrh et al., 2014; Wallis et al., 2017). Thus, phylogenetic trees should only be used as one line of evidence in an integrative framework.

### 7.1.3 | Lough Melvin trout

Is designation of the three Melvin populations as distinct species justifiable under an integrative approach? Both prezygotic and, more importantly, postzygotic isolating mechanisms are present in the form of natal homing and apparent sterility of F<sub>1</sub> hybrids and/ or inviability and/or infertility of backcrosses and F<sub>2+</sub> hybrids. The Melvin populations are genetically highly distinct) and 100% of individuals can be correctly identified to population, or as hybrids, using multiple microsatellite loci in a BAPS admixture analysis (Figure 2). Identification on colouration and other aspects of morphology of fresh-caught specimens exceeds 90% but the exact diagnosability on this basis has not been quantified. However, a multivariate analysis of meristic and morphometric characters correctly assigned 100% of the ferox, 98.8% of gillaroo and 98.7% of sonaghen (Cawdery & Ferguson, 1988). There is clear evidence of adaptation of various morphological features including head structure, gill raker length, number of teeth and fin and body shape. Ferox represents an allopatric derived lineage, with homologs in some other waters being identifiable (Duguid et al., 2006). On current evidence, gillaroo and sonaghen are the result of independent colonisation of allopatrically derived lineages although at present homologs in extant Eurasian trout populations are unclear. All three populations are ecologically distinct. Spawning behaviours are also different with adult gillaroo moving downstream for spawning and juvenile gillaroo having to move upstream to reach the lake, the opposite of ferox and sonaghen. Thus, overall, an integrative approach confirms the species status of the three Melvin sympatric populations, as previously designated (Ferguson, 2004; Kottelat & Freyhof, 2007; Whiteley et al., 2019).

### 7.2 | Conservation units

The existence of sympatric populations presents a significant challenge to fishery managers (Leider et al., 1984) as they cannot be subject to uniform management and conservation actions. It has been recognised for some 50 years that conservation of such sympatric populations of salmonids should be population-based and not reliant on the designation of species and other taxa (Behnke, 1972). Others have reiterated this position down the years (Splendiani et al., 2019; Taylor, 1999). Use of CUs based on populations, or groups of populations, rather than species highlight intraspecific diversity without the taxonomic inflation resulting from the designation of new species (Coates et al., 2018; Guinand et al., 2021). Commonly discussed CUs are the Evolutionarily Significant Unit (ESU), which was originally introduced as a replacement for subspecies (Ryder, 1986), and the Designatable Unit (DU), both of which are designated on the basis of discreteness of genetically based characters and adaptive evolutionary significance (Waples, 1991; Waples et al., 2013). That is, the aim is to conserve the adaptive potential of a species as represented by its constituent CUs (Fraser & Bernatchez, 2001). Such units are given legal protection in some countries including the USA with the Endangered Species Act (ESA) under which Distinct Population Segments of vertebrate species such as ESUs can be protected as if they are species. Similarity in Canada, the Species at Risk Act (SARA) allows protection of DUs, which are assigned by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Waples et al., 2013). COSEWIC (2018) guidelines recognise sympatric populations that are reproductively isolated as justifying DU status since they are discrete and evolutionarily significant. As not all conservation units are equally unique in terms of adaptations, prioritisation may be necessary to ensure targeting of limited resources (Muhlfeld et al., 2019).

In spite of many calls for population-based conservation, as far as almost all countries in the native range of Eurasian trout are concerned there is no recognition of intraspecific units and intraspecific variation is not taken seriously (Laikre, 2010; Mimura et al., 2017). Thus, the European Union countries, other than Germany (Coates et al., 2018), only consider endangered species, not intraspecific CUs. The exact taxonomic status can therefore be a key factor for conservation initiatives (Berrebi et al., 2013). While the authors of this review strongly support a CU approach, it is acknowledged that this is not feasible under current conservation legislations in most jurisdictions and that a pragmatic approach needs to be taken in practice. Thus, if only species are recognised then biologists wishing to promote conservation of unique populations, or groups of populations, need to consider whether species status is warranted along the lines discussed above. That is, conservation should take priority over the semantics of taxonomy!

### 7.3 | Management units

Management units (MUs) are demographically independent units that are not evolutionarily significant entities and lack significant local adaptations yet are substantially reproductively isolated and demographically independent (Palsbøll et al., 2006). Sympatric populations arising due to natal homing can qualify as MUs where they require independent management actions but do not represent a significant evolutionary legacy of the species.

### 7.4 | Conservation actions

Freshwater fish are under increasing threats including environmental changes, introduction of non-native species and overfishing, which have caused an 83% decline in species abundances since 1970 (Grooten & Almond, 2018). Sympatric populations are of particular interest as they contribute to the diversity and productivity of freshwater ecosystems with intraspecific genetic variation having FRESHWATER FISH -WILEY

similar effects as species diversity on ecosystem function (Mimura et al., 2017), including the portfolio effect (Schindler et al., 2015). In some cases, sympatric populations may represent the early stages of sympatric speciation or may already be sufficiently distinct to merit designation as distinct species and are important in the study of speciation processes (Salisbury & Ruzzante, 2022). Irrespective of their taxonomic status it is important that the local community take "ownership" of such unique Eurasian trout assemblages in their area. Certainly this is the case for both Melvin and Laidon where local people proudly tell visitors of their unique trout.

As well as identifying sympatric populations it is also important to identify the key risk factors involved for particular populations. Some ferox populations have been shown to have small population sizes (Thorne et al., 2016) making them particularly vulnerable to extinction through stochastic demographic changes (Goodman, 1987). Age at maturity has also been identified as a major positive correlate of risk status (Parent & Schriml, 1995), of particular relevance to ferox. Eurasian trout populations, including sympatric populations, have declined in all parts of the native range (Ferguson, Adams, et al., 2019; Lobón-Cerviá et al., 2019; Markevich & Esin, 2019; Rasmussen et al., 2019; Schöffmann et al., 2019) as a result of multiple factors (Muhlfeld et al., 2019). Stocking of hatchery-reared trout has been identified as a particular major threat to native populations, and sympatric populations may be particularly vulnerable to such activities. Stocking of non-native or farm strain Eurasian trout represents a threat as such stocked trout have no natal home. They may thus breed at random and form a bridge between the sympatric populations promoting the breakdown of reproductive isolating mechanisms and widespread introgression. This can lead to "reverse speciation" (Feulner & Seehausen, 2019) and the merging of previously reproductively isolated populations. Supportive breeding using broodstock obtained from the water that is subsequently stocked with the hatchery-reared offspring (Ferguson, 2007) can also be potentially damaging. Thus, artificial mixing of separate populations can occur in the hatchery especially where sympatric populations spawn in the same river, for example, ferox and sonaghen (Section 5.2). Stocked fish, since they have no early juvenile experience of their river of origin may breed at random in other rivers as above potentially resulting in introgression. Stocking with other species is potentially detrimental resulting in direct and indirect competition and predation. Reverse speciation has also been noted following the introduction of a competitor species (Bhat et al., 2014).

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### CONFLICT OF INTEREST

The authors declare no conflict of interest.

### AUTHORS CONTRIBUTION

This review derives from AFs and PAPs research interest and collaboration, over 30 years, in the genetics of Eurasian trout, which is a topic now being actively researched by PAP. AF prepared the first draft of the review, which was added to and revised by PAP and AF through several further drafts. Both authors approved the final manuscript.

### DATA AVAILABILITY STATEMENT

Unpublished/grey literature data used in this review are available from the corresponding author on reasonable request.

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