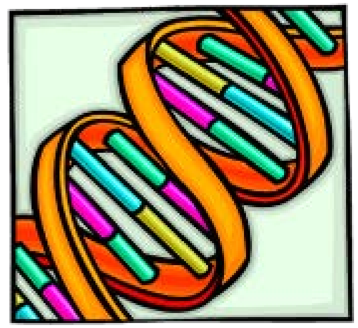


Brown trout: Genetic diversity and its implications for management and conservation

Andy Ferguson

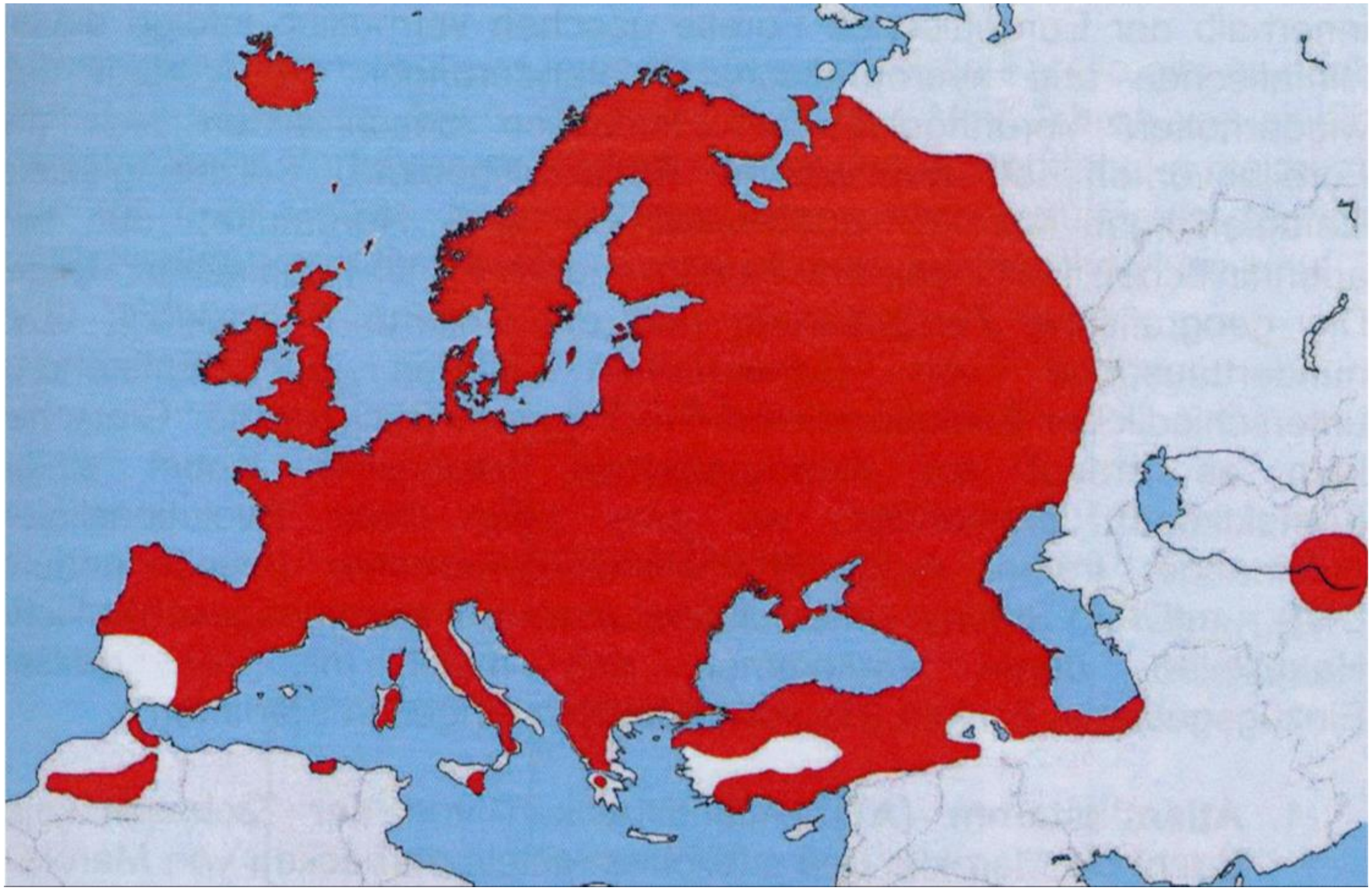
Professor Emeritus, School of Biological Sciences, Queen's University Belfast

QUEEN'S UNIVERSITY BELFAST

Outline of talk

- Brown trout distribution & nomenclature
- Origins of genetic diversity
- Examples of genetic diversity - colouration, morphology and life history (migration, reproduction, feeding)
- Importance of genetic diversity
- Conservation & management

current native trout distribution



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Brown trout *Salmo trutta* sensu lato

- **Brown trout** common name for native trout
  - Some use **brown trout** only for freshwater trout, **sea trout** being used for sea-migratory trout
  - Similar to use of rainbow trout, in freshwater, steelhead, for sea-migratory, in North America
- **Eurasian trout** may be more inclusive name in spite of a few populations in N. Africa
  - Will use brown trout in the broad sense or simply 'trout'

One species or many?

- Many local common names referring to particular geographical types / ecotypes etc
- Breac, spotted trout, speckled trout, ferox, gillaroo, sonaghen (an), dollaghen (an), salmon-trout, buddagh, croneen, white trout, bull trout, slob trout, lake trout, harvester
- Some argue for multiple species
  - 19th C - 50+ species
  - Early 20th C - 1 species
  - 2017 - 40+ species e.g. Kottelat *et al*

BT widely introduced worldwide

- Introduced to North America & many countries in southern hemisphere
- In New Zealand e.g. of considerable importance for angling

Very high variability / diversity

- The adjectives that best describe brown trout are ‘**variable**’ / **‘diverse’**
- BT is one of the most variable vertebrates
  - Klemetsen (2013) claims Arctic charr to be most variable vertebrate species

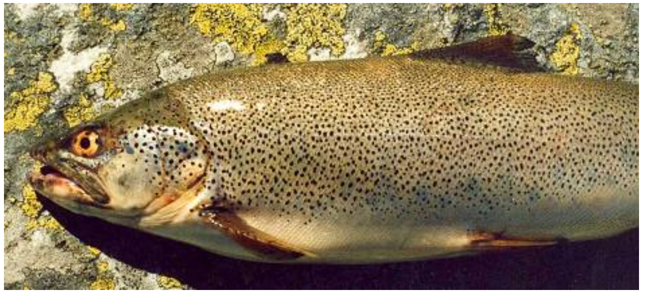
    - geographic range, migration, habitat, adult size, colour, body form, polymorphism, diet, reproduction, genetics
  - Scores rainbow trout & brown trout a bit lower but I would argue with some of the scoring

Much variation present in Ireland

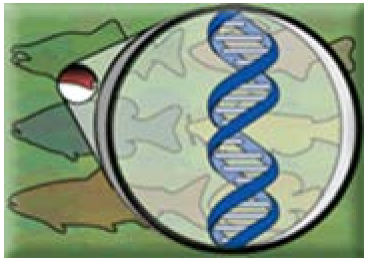
- This diversity presents a considerable challenge for conservation and management
- ‘One size fits all’ approach not appropriate
  - Actions must be tailored to an individual catchment and its populations
- **To what extent are genes responsible for observable (phenotypic) variation in life history & other key biological traits**

Phenotypic variation can be due to

1. **Environmental plasticity** – same genotype producing different phenotypes in different environments i.e. no genetic variation
2. **Gene variants (alleles) directly determine the variation** - no environmental influence
   – Simple Mendelian inheritance
   – Genotype = phenotype



3. **Multiple genes combined with environmental influences** – continuous & threshold (quantitative) traits
   – Nature & nurture as for many of our own traits



Genotype

+

Environment

=

Phenotype

How is genetic variability studied

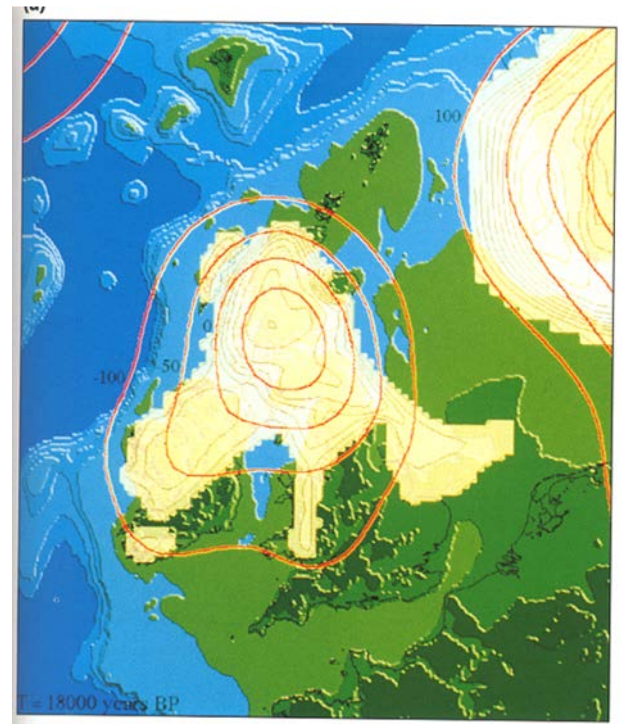
- Variation in **phenotype**
  - Colouration, life history including migrations, feeding, longevity, body structure, physiology, environmental tolerance, disease and parasite resistance, etc
- Natural communal environment situations /'common garden' experiments can be used to identify genetic components

Direct studies of genes (**genotype**)

- Molecular techs – DNA, RNA & proteins
  - 45+ years small number (<50) of **genetic markers** eg. allozymes, mitochondrial DNA, microsatellites
  - **Markers** for spatial population structuring, movements, mixed-stocks analyses, etc
- Recent years have seen development of genome wide (**genomic**) studies
  - Many thousands of genes, often known function
  - Adaptive variation, life history determinants, etc

Postglacial colonisation

- Recolonisation from **glacial refuge areas** after glaciers retreated (c14,000 – 10,000 years ago)
  - Several refugia adjacent to Britain & Ireland due to **lower sea level**



- Colonisation by at least 6 lineages from various parts of NW Europe
  - evolved there during all or part of the ice age
- Several lineages colonised same lake / river at different times
  - lineages mixed by interbreeding in some places but remained distinct in others due to breeding only with members of same lineage

Natal homing

- Adults return to river region of birth for spawning with considerable accuracy
- Results in population structuring even in the absence of physical barriers
  - i.e. separate populations in different tributaries or sub-tributaries
- As populations are the unit of production this population structuring needs to be recognised in conservation & management

Homing allows local adaptation

- Separate populations acquire adaptations to local conditions by **natural selection**
- Local adaptation increases survival & reproductive success (i.e. increases <u>fitness</u>)
- Small populations subject also to random genetic changes (i.e. **genetic drift**)

Genetic diversity today result of

1. Postglacial colonisation by multiple lineages
2. Changes in individual populations since colonisation as a result of natural selection and genetic drift, due to both natural and human-mediated changes

- Illustrate 1 & 2 by studies on Lough Melvin trout

Lough Melvin

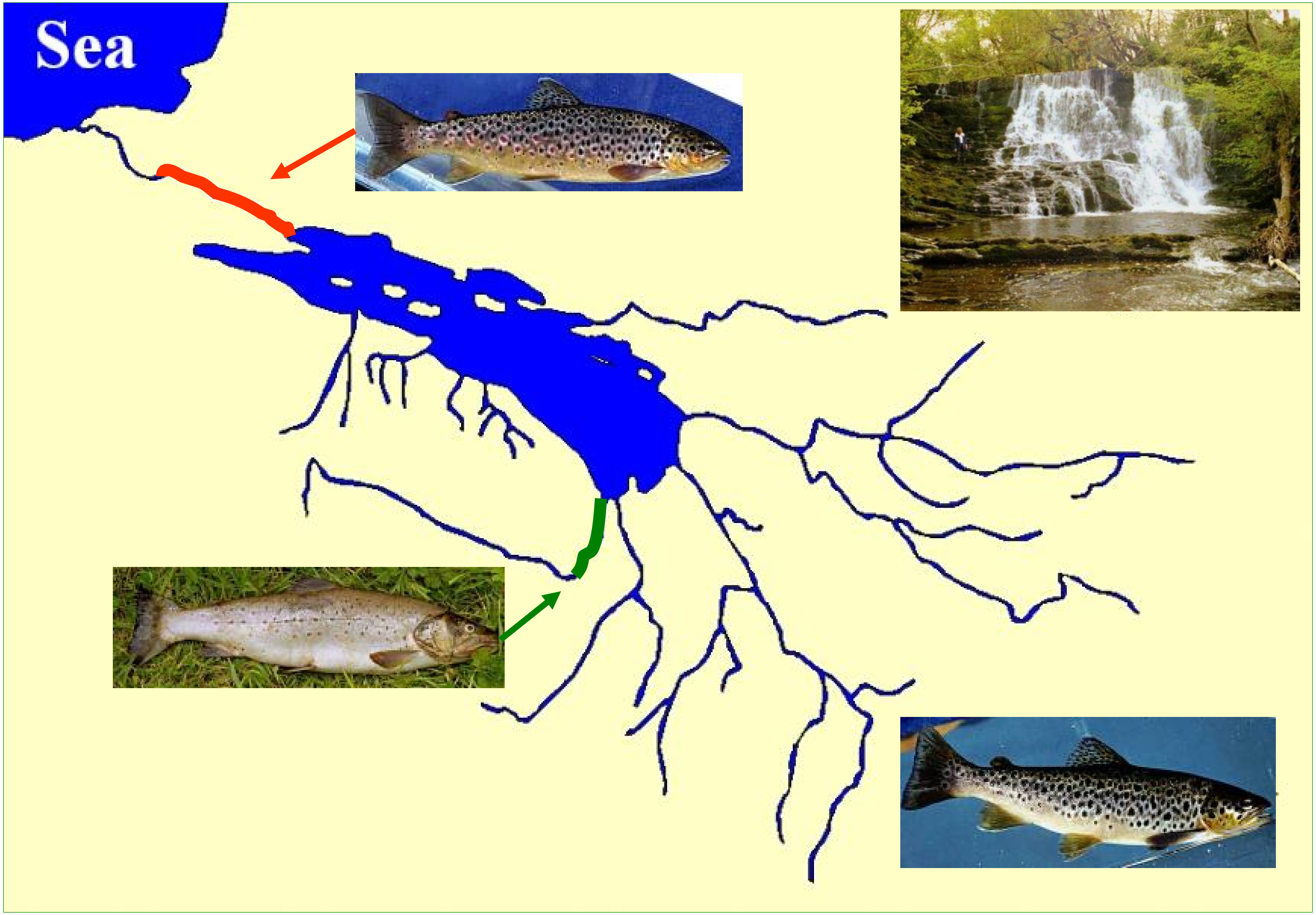
Area: 22km^2 Maximum depth: 45 metres

gillaroo

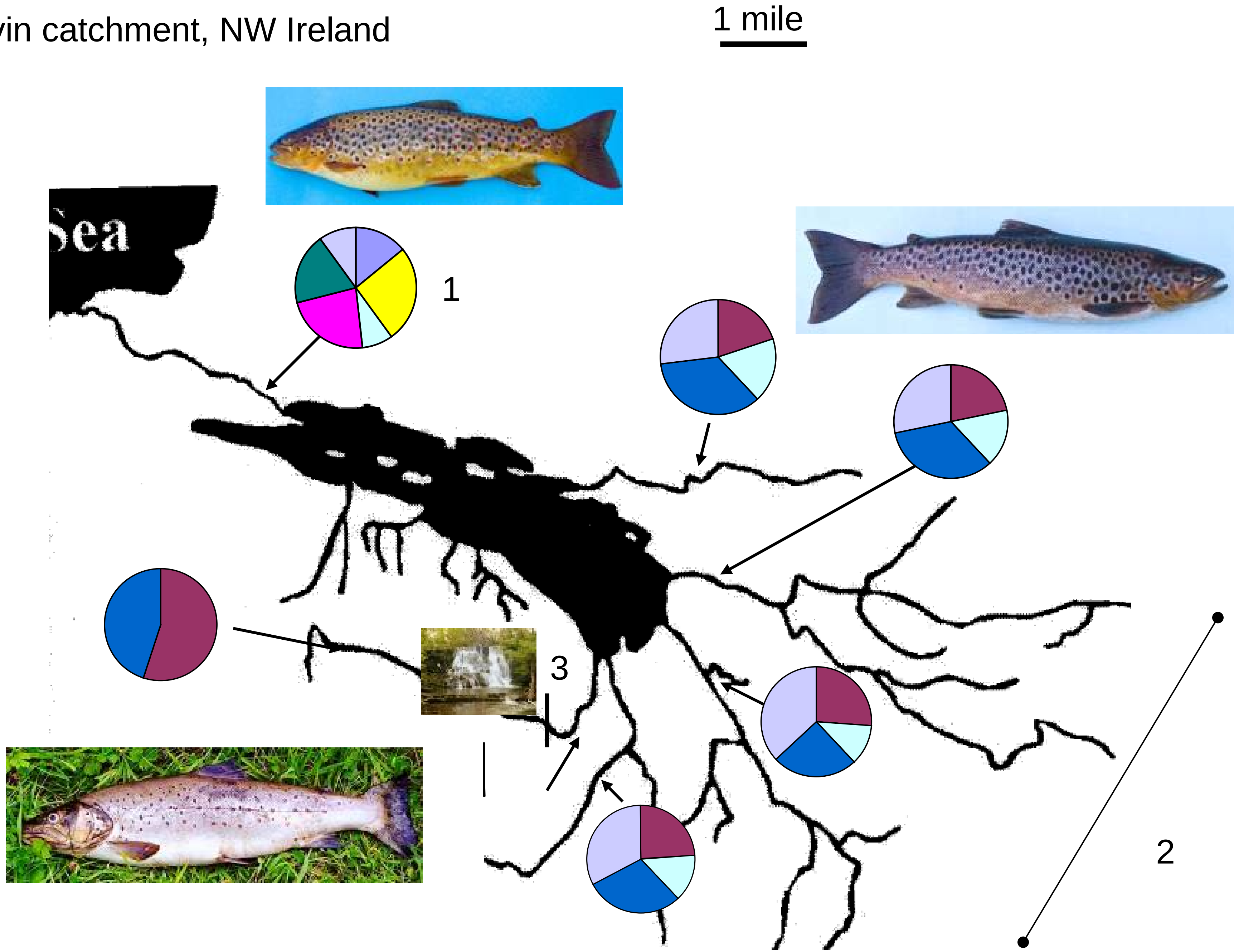
sonaghen

Colonised as 3 genetically distinct lineages

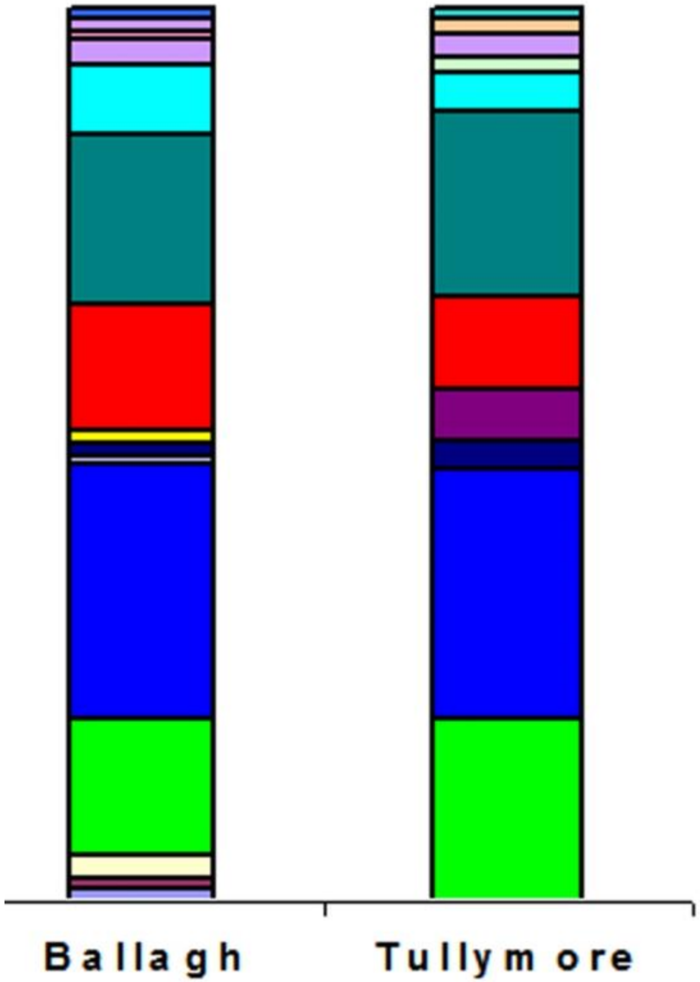
ferox

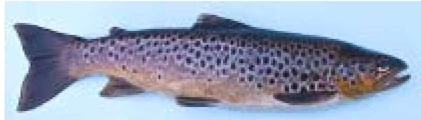

Sea

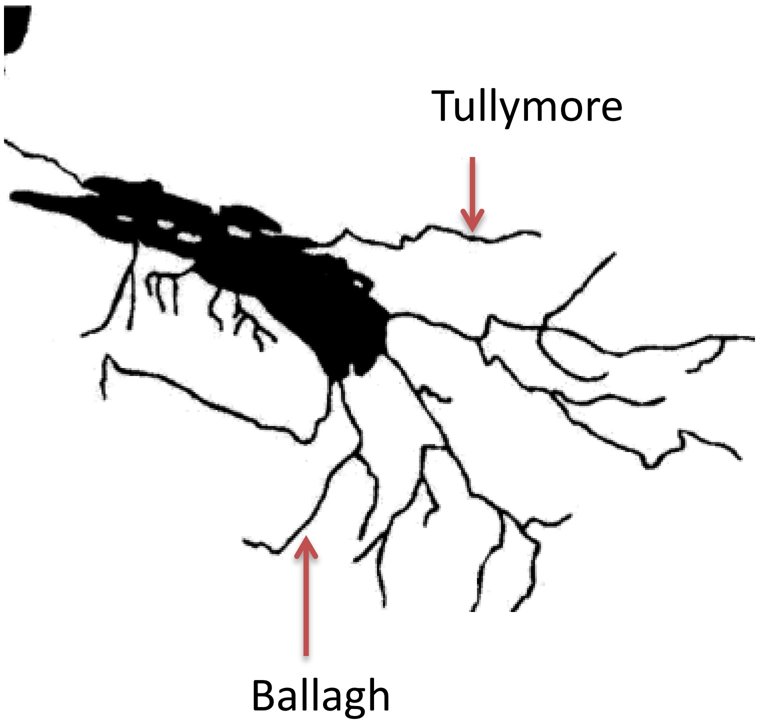
Melvin catchment, NW Ireland



Differences among sonaghen spawning rivers as a result of natal homing



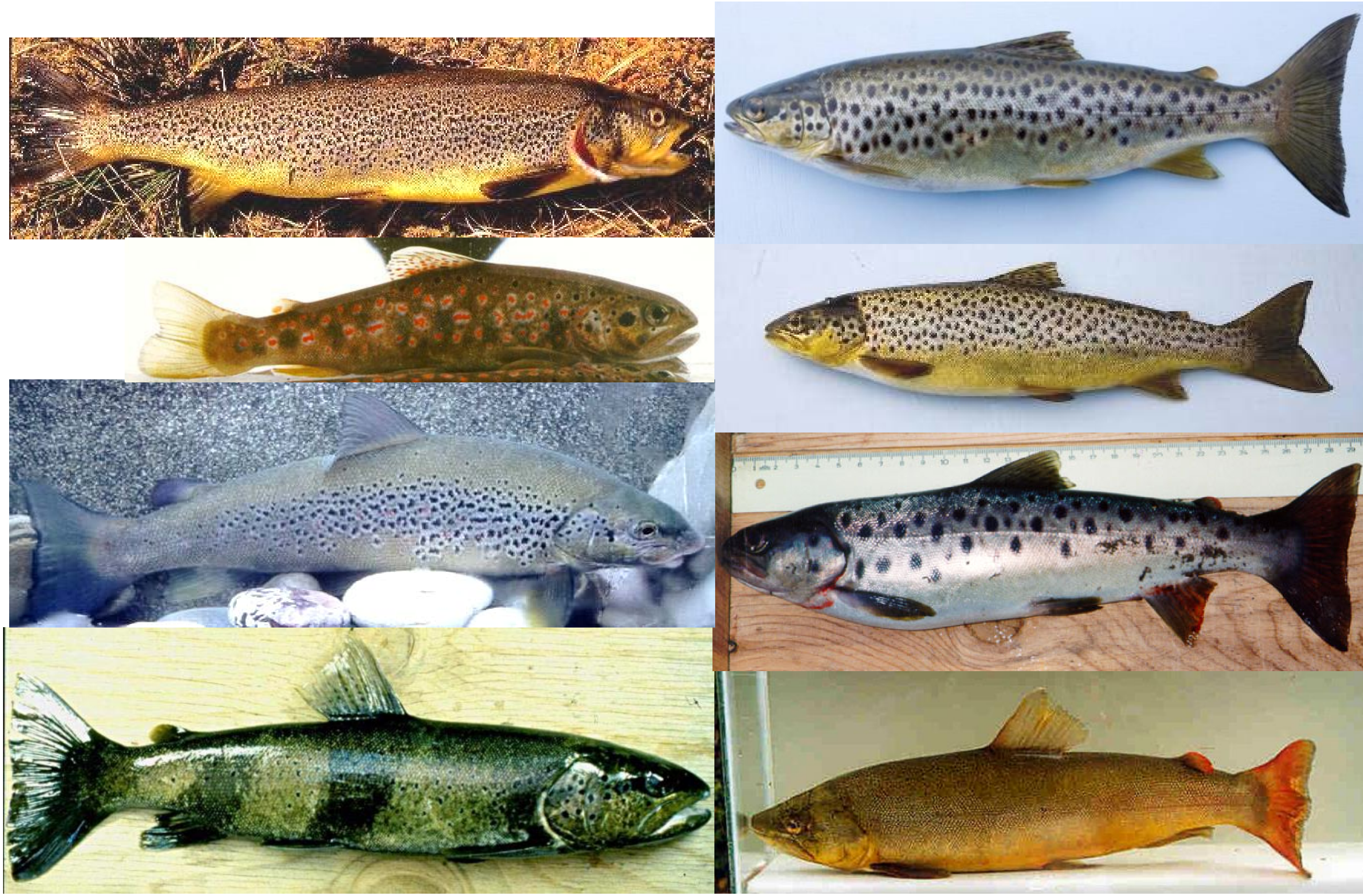




Spatial population structuring

- Significant genetic differentiation between samples from different locations indicates distinct populations, potentially with different adaptations
- Although differences may be small, taken cumulatively over 20+ marker systems they can be sufficient to identify trout taken in the lake as to their river of origin – mixed-stocks analysis / Genetic Stock Identification (GSI)

Brown trout shows considerable colour variation



Trout from 5 lakes in SW Scotland within a maximum of 10 miles apart

How far is this variation simply the result of environmental differences?

Parent Lake 1

F5 Lake 2

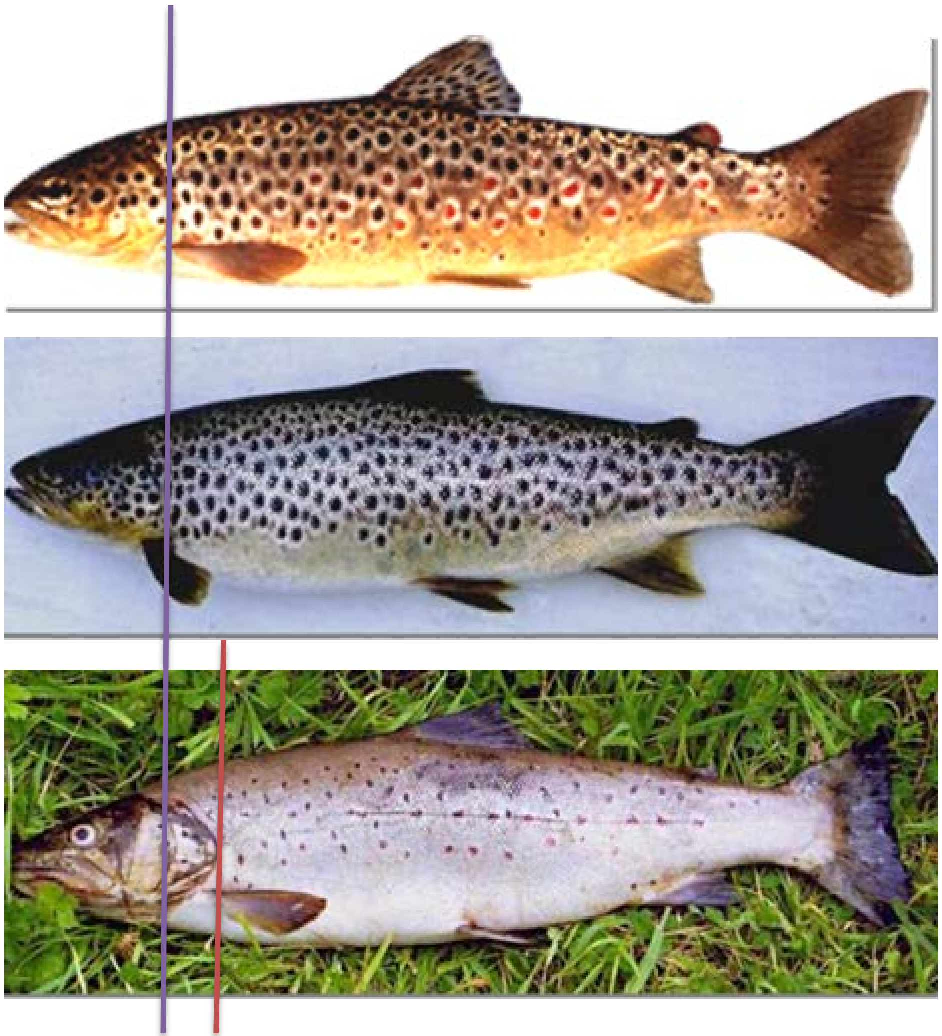
F5 Lake 3

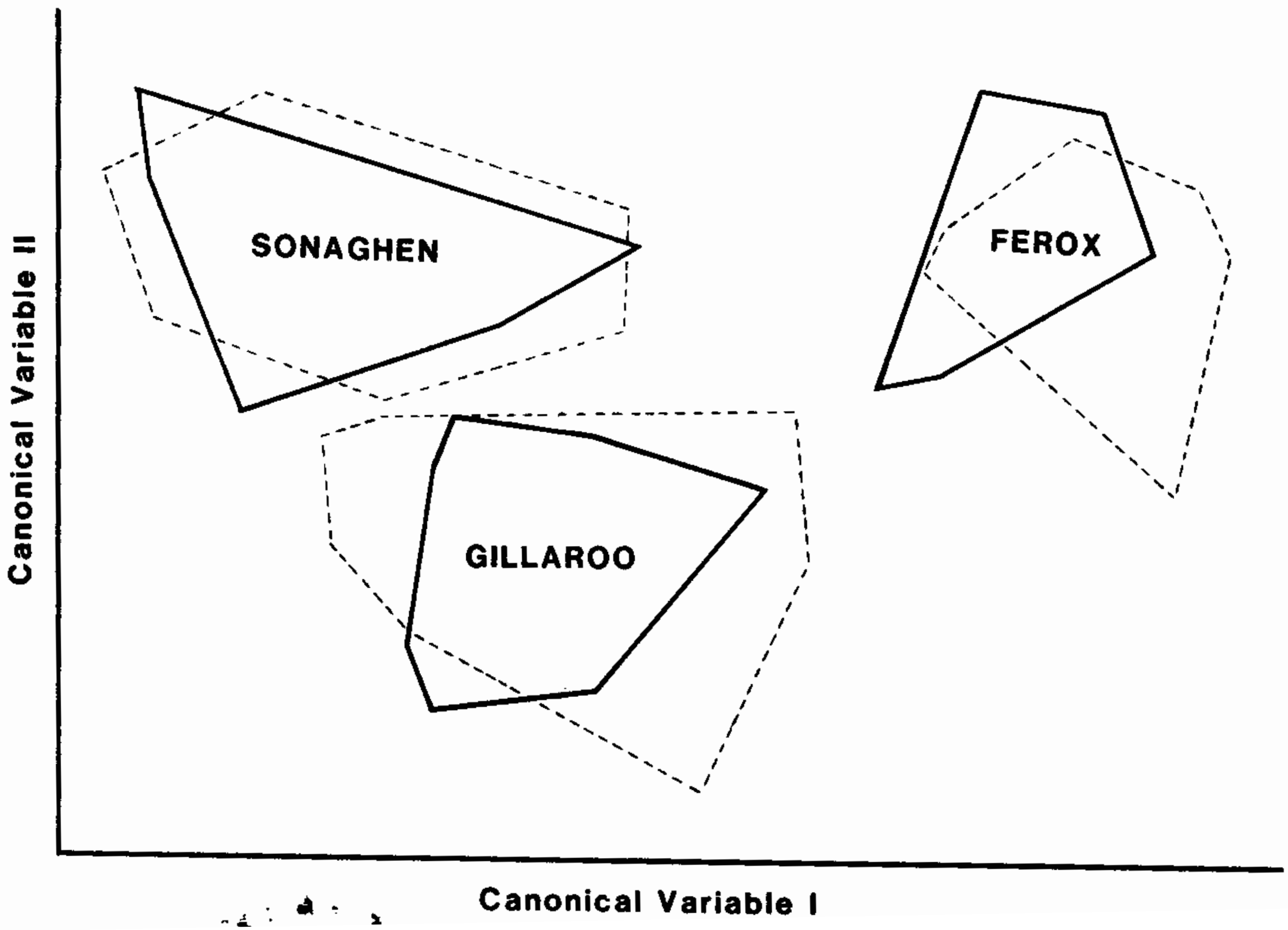
Melvin

Offspring

Reared from eggs and stocked in small lakes in Belfast area

Morphology - Head & fin measurements, gill raker length and number of teeth most discriminatory




SONAGHEN
FEROX
GILLAROO
Canonical Variable II
Canonical Variable I

Life history variation

Three interlinked aspects

- **Migration / residency**
- **Reproduction**
- **Feeding**
- Characterisation of the range of life history types and habitats utilized by trout within a catchment is increasingly recognized as a prerequisite for effective conservation and management

Resident trout

- <u>River resident</u> staying within general area where born – eg where good adult feeding in spawning tributaries or impassable barrier (eg waterfall) preventing upstream return
- <u>Lake resident</u> where entire life cycle is spent in lake (although may be inshore-offshore movement)
  - **Within lake spawning probably more common than currently known**

Within lake spawning

- Upland lakes – diffusive drainage into lake, windy conditions, waterfall at outlet
- Melvin gillaroo

- Lough Mask (P. Gargan pers. comm.Ryan et al. 2016)
- Further studies required to establish extent in large lowland loughs

Migrations

- Migration is movement between discrete spawning, adult feeding and refuge habitats
  - Regular periodicity within life span
  - Directed movement rather than random or passive drift
- **Most trout in Ireland are migratory**

Migratory trout

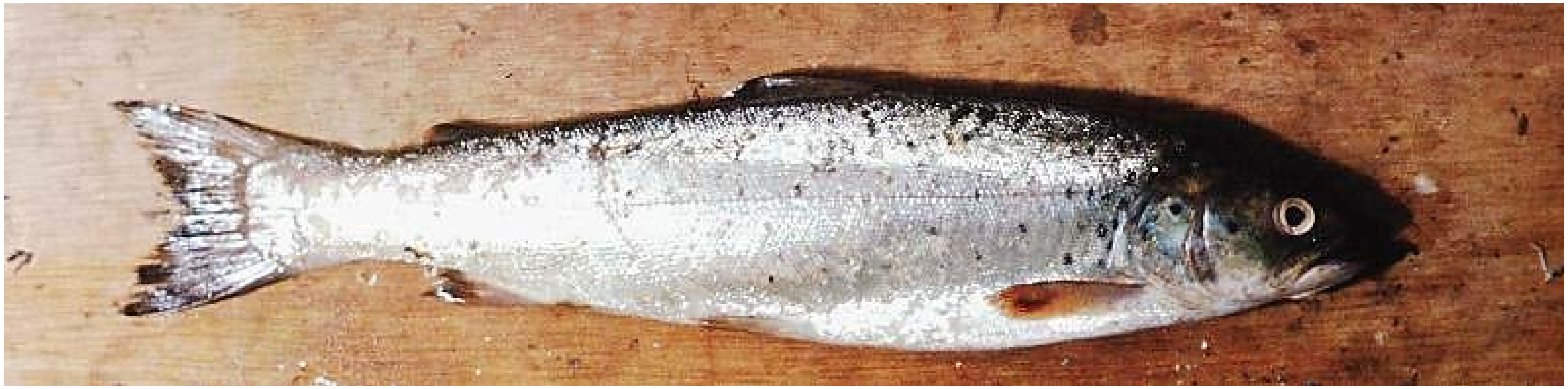
1. Migration from spawning tributary to main stem of river (**fluvial potamodromous**)
2. Migration from spawning river to lake (**adfluvial potamodromous**)
   - <u>Numerically commonest LH in Ireland and most important for angling – 12,000+ loughs</u>
3. Migration from spawning river to sea (sea trout – **anadromous**)

Why are sea trout considered differently from other migratory trout?

- Legislation treats sea trout differently
- Sea trout is simply one migratory tactic and **does not differ fundamentally** from the other migratory types
  - Main difference is that ionic & osmoregulatory changes are required when moving between freshwater & sea- water

- Recent study (Leitwein et al 2017) on rainbow trout / steelhead found same **Migration Associated Genes** in lake-migratory as in sea-migratory, but not resident trout
  - Indicative of same genetic control for both types of migration & independent genetic control of migration and physiological changes

- Silvering is also found in lake-feeding trout – it is simply open water camouflage



Not about size either

- Piscivorous lake trout (ferox) in Britain & Ireland are larger than sea trout
  - GB record rod-caught lake trout
    - ferox (L Awe) 32¾lb

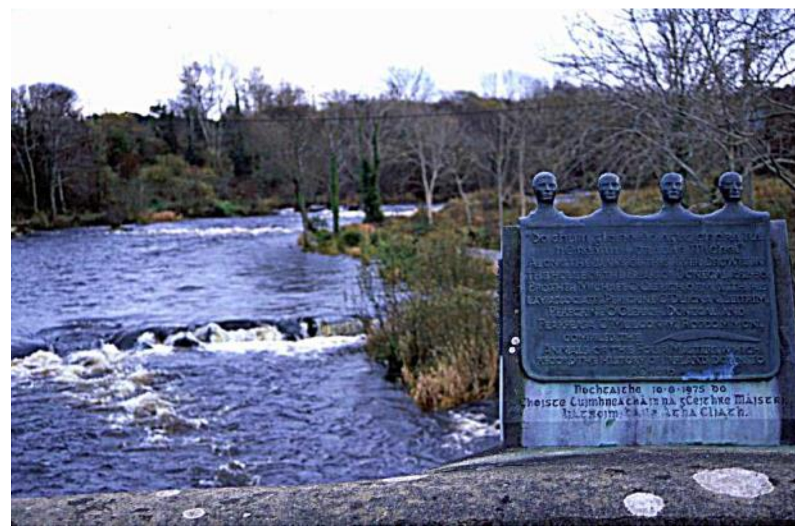
  - GB record rod-caught sea trout (S. England) 28¼lb
  - Ireland ferox L. Ennel 26 lb
  - Ireland river trout R. Shannon 20lb
  - Ireland sea trout R. Shimna 16½ lb

- Some individuals can change migratory pattern alternating between sea and a lake
  - In Loch Lomond trout repeatedly move between the lake and estuarine / marine environments
- All native freshwater trout in Ireland derived in last 14,000 yrs from sea trout ancestors
  - At end of last ice age no freshwater connection to rest of Europe

Inlet & outlet spawning

- Lake migratory trout are of two groups
  - Inlet river spawners
  - Outlet river
- Outlet spawning relatively common
- Requires different direction of parr migration
  - Experiments have shown this to be genetically determined
  - Forms a local adaptation

Direction of parr migration

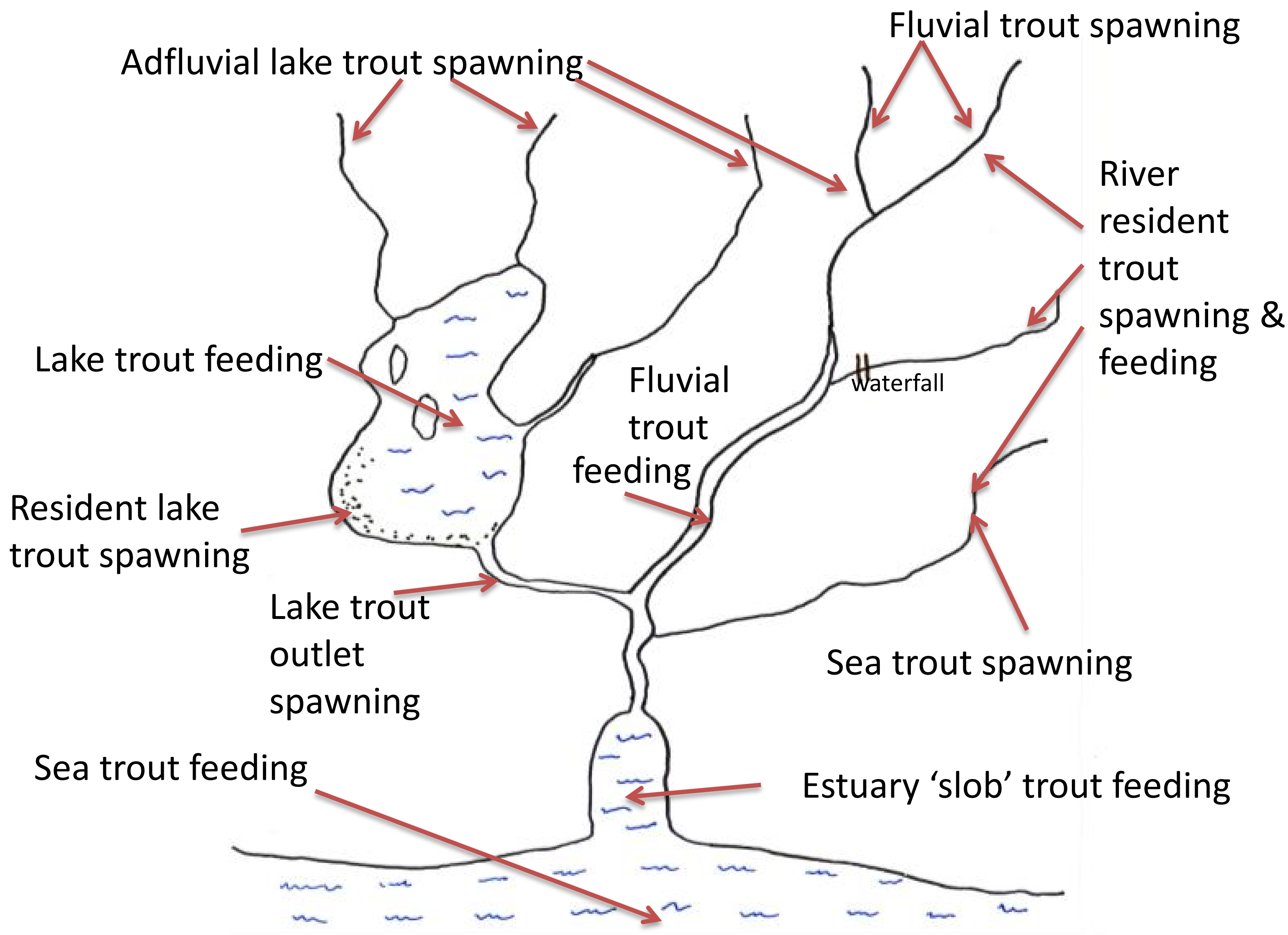


L Fleet – inlet & outlet populations

- L Fleet re-established by stocking 1988+ but now shows **genetically distinct inlet river and outlet river populations**

- **Reproductive isolation** and genetic divergence acquired within c8 generations since stocking took place

All can be present in one river system with a lough

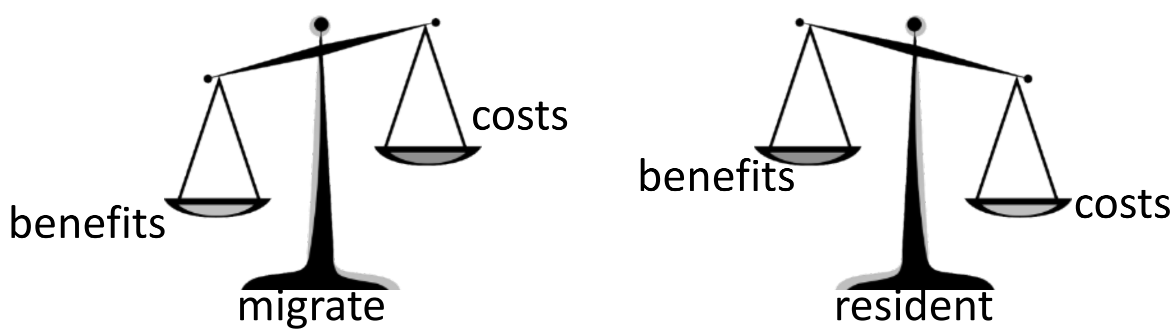


Obligate vs facultative migration

- In some small spawning streams all trout migrate, often in first summer (obligatory migration)
- In larger spawning rivers some individuals in the population migrate while others complete their entire life cycle as residents - facultative (optional) migration

Benefits / costs of migration

- **Better feeding** in main river / lake / sea - larger body size giving
  - More eggs - eggs buried deeper, less overcutting
  - Improved competition for mates
- **Greater risk of predation**
- **Higher energy costs** of migrations & physiological changes required for sea



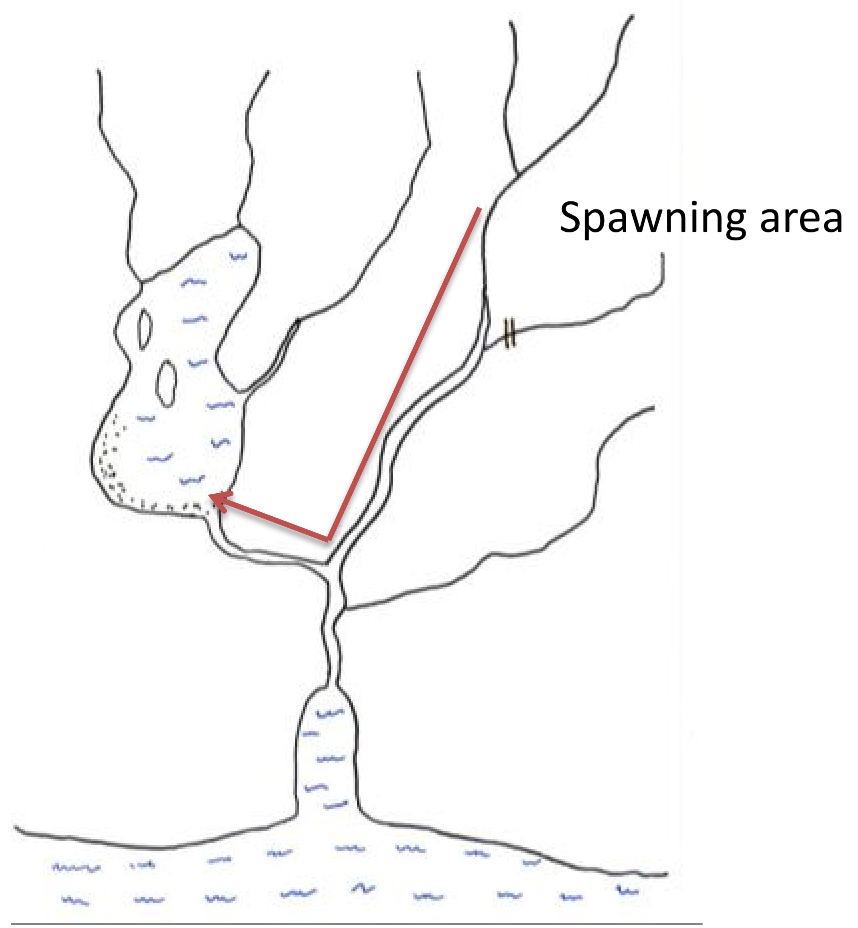
Should I stay or should I go?

- The decision for a juvenile trout in its natal river is **'Should I stay or should I go?'** i.e. remain in the river until maturity or migrate to the main stem of the river / a lake / the sea
- Decision is informed by **both** its <u>physiological (nutritional) condition</u> and by its <u>genes</u> as influenced by relative success of migration for its ancestors, through natural selection

But where to migrate to – main river, lake or sea?

- **Must be largely genetically determined**
  - Direct movement to ultimate location
  - Repeatable over generations
  - In sea trout physiological changes necessary for water & ionic regulation start to occur in river
- Natural selection can change
  - Dams have resulted in change from migrating to sea to migrating to a lake instead

Inherited map of migration route



Age & timing variation

- Within each category of migration there is considerable variation in the age / time of year that both outward & return occurs
- Age & timing has been shown to be under genetic control
- Single gene variation explains 39% in age of maturity of Atlantic salmon – same gene likely in trout as well

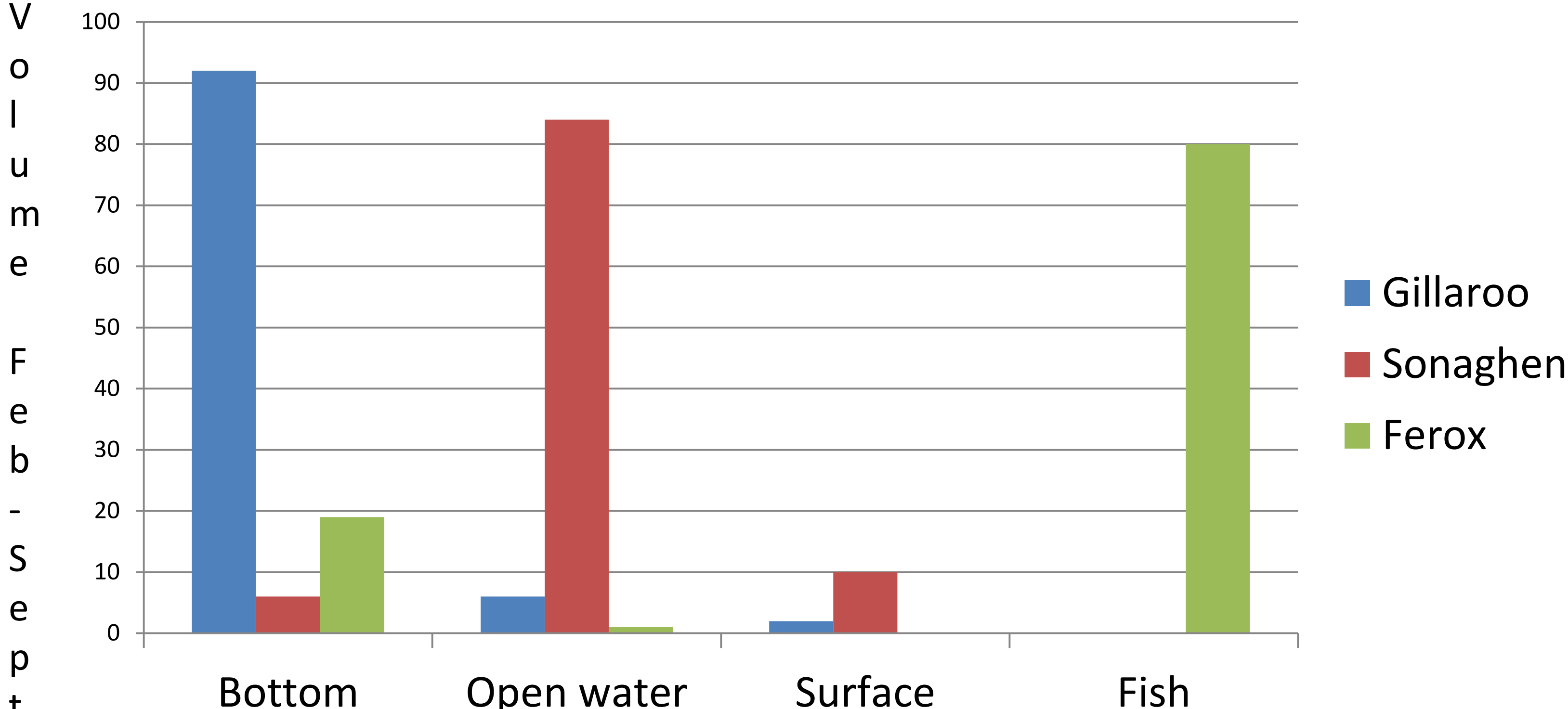
Feeding variation

- Trout are often generalist feeders
- In some lakes, individual trout specialise on one of three main food groups
  - Specialisation allows greater feeding efficiency by adaptations of gill rakers, teeth, head structure etc
  - Requires stable conditions & lack of competitors to evolve

Lake trout feeding ecotypes

- Primarily bottom feeding
  - Macroinvertebrates
- Primarily open-water feeding
  - Zooplankton
- Fish eating – large size – <u>ferox</u> trout
  - Charr, pollan, roach, perch

Melvin trout feeding segregation



- Two or three feeding ecotypes found in many lakes with suitable conditions
- The extent to which this segregation occurs in Irish lakes merits investigation
  - Requires detailed netting survey at range of depths
  - The gillaroo phenotype was reported in the past in a number of loughs as well as Melvin, e.g. Neagh, Conn, Mask, Corrib.
  - A gene unique to gillaroo in Melvin has been found in trout from L. Conn

- Feeding segregation can occur as a result of colonisation by different lineages already adapted to particular food resources.
- Alternatively it can occur within a lake, with or without reproductive isolation of the ecotypes.

Piscivorous trout - ferox

- Ferox are genetically distinct from other trout in 6 lakes studied

- Ferox are genetically more similar to each other, in different lakes, than they are to the co-occurring trout of their own lake
- Thus derived from a common lineage in lakes studied to-date – piscivory innate

Experimental populations

- On their own in a lake both gillaroo & sonaghen widened feeding spectrum
- **Only gillaroo fed on snails** although apparently similarly available in both lakes
  - Genetic basis?

Loch Harray (Orkney)

Heritable basis to most, if not all, life history & other diversity in trout

- If we loose the underlying genetic variation we loose this life history diversity
- Life history diversity results in fuller use of environmental resources and thus greater productivity (more fish) than fixed LH
- Insurance policy if one life history fails - greater long-term stability for the population / species
  - 'portfolio effect'
- Gives diversity of angling opportunity, techniques and interest

Maintenance of life history diversity requires

- Full range of appropriate habitats
  - spawning, nursery, feeding and refuge habitats
- Requires trout to be able to move freely downstream and upstream
  - no barriers
  - sufficient water flow

Genetic diversity determines the abundance of trout

- Genetic components to survival & reproduction (fitness) which directly influence number of trout
- Reduced population size results in loss of genetic diversity and inbreeding with consequent inbreeding depression and loss of fitness (i.e. fewer young produced)
  - 80% reduction in survival in inbred rainbow trout

Adaptation to changing conditions

- Genetic diversity is important in allowing trout to continue to adapt to changing environmental conditions e.g. global warming and new diseases
- Important for practical management
  - In SW Scotland, trout in one lake survived even at pH4, while others in the area became extinct
  - Genetically based tolerance of low pH
  - Offspring used to stock and restore populations in lakes where trout became extinct due to acidification

Integral component of biodiversity

- Genetic diversity among trout populations is an integral component of biodiversity – Governments have statutory duty to protect
  - Trout genetic diversity has arisen over past 2 million years
  - Once lost cannot be regained (in meaningful time period)

Loss of genetic diversity

- Any loss of a population, or reduction in population numbers results in the loss of genetic diversity
- Supplemental stocking with fertile domesticated trout or **even with hatchery reared offspring derived from native broodstock** can also result in detrimental genetic changes

Supplemental stocking

- Interbreeding between wild trout and stocked ones can result in
  - Reduced survival and reproductive capacity
  - Changes in life histories
- Can result in fewer trout than if no stocking
- Fortunately <u>fertile</u> domesticated farm trout supplemental stocking no longer permitted in most jurisdictions

But why is the use of native broodstock a problem?

- **Hatchery environment very different** from wild & rearing - can result in behavioural, physiological and genetic changes which adversely impact future survival, life history tactic and reproduction
  - **Epigenetics** - heritable changes in gene expression
- Often does not take account of natural population structure – mix broodstock from different populations / life histories

Native broodstock schemes last resort

- Native broodstock schemes should only be used when there is a clearly identified problem (bottleneck) limiting number of trout produced
  - Problem cannot be solved in short-term
- High survival in hatchery **does not** result in high life time survival!
  - Overall life time survival, & reproduction, may be lower than if left to breed naturally

Conclusions

- While substantial progress has been made in our understanding of genetic diversity in brown trout, many challenges remain
  - Recent molecular & statistical methodology make further understanding within reach
- Requires full integration of molecular genetic analyses with field & experimental studies
  - Genetics should be integral part of, not separate, from conservation & management activities