Introduction to population genetics

CRITFC Genetics Training
December 13-14, 2016
What is “population genetics”?  

Population genetics *n.*

**In culture**: study of the genetic composition of populations; understanding how evolutionary forces select for particular genes.

**In science**: study of the inheritance and prevalence of genes in populations, usually using statistical analysis (quantitative).

......or if you prefer Wiki-wisdom

**Population genetics**: the study of the distribution and change in frequency of alleles within populations -used to examine adaptation, speciation, population subdivision, and population structure -based on several main processes of evolution (natural selection, genetic drift, gene flow, mutation).

I know it’s Wiki, but I like this one
Stock identification and its role in stock assessment and fisheries management: an overview

Gavin A Begg, Kevin D Friedland, John B Pearce

Abstract

A symposium on “Stock Identification – its Role in Stock Assessment and Fisheries Management” was held as part of the 128th annual meeting of the American Fisheries Society (AFS), Hartford, Connecticut, USA, 23–27 August 1998, to summarize the current state of knowledge of stock identification issues, problems and methodologies, as well as to identify future directions for stock identification research. With today’s, growing emphasis on stock assessment, this symposium was a timely reminder of the need to identify fish stocks accurately, and the implications of stock identification for fisheries management. The symposium was structured into four general themes: (1) the stock concept; (2) genetic variation; (3) phenotypic variation; and (4) fisheries management. We review the presentations given in each theme session, which form the basis of the proceedings presented in this issue, as well as providing an overview of current issues and directions in stock identification research. We hope that the overall proceedings constitute a text helpful in these directions, useful in the classroom, laboratory, and field.
Importance in fish management

Molecular genetics and the stock concept in fisheries

G. R. Carvalho, L. Hauser

Abstract

The concept of a sustainable yield (SY, Gulland, 1983; Lannan et al., 1989) has dominated fisheries management for almost 50 years. The central idea is that each stock has a harvestable surplus, and that fisheries that do not exceed this will not compromise the stock’s natural perpetuation. A basic assumption is that the fishery targets a unit stock with definable patterns of recruitment and mortality. Although it is difficult to reach agreement on what constitutes a stock (Gauldie, 1991), the notion of population units with varying degrees of temporal or spatial integrity stimulated a quest to characterize and identify such assemblages. It became apparent that few species form single homogeneous populations, but rather that fish species are often composed of discrete stocks, and that these stocks may react to harvesting more or less independently. It was the idea of independent responses of different stocks to exploitation that demanded information on stock structure. Hence, the stock concept was linked strongly, at least in theory, with the desire to balance the impacts of harvesting with efforts to ensure continued economic returns. What was much more difficult to achieve than the theory was: (i) how to actually recognize a stock, and (ii) how to translate stock structure data into fishery practices.
The identification of management units (MUs) is central to the management of natural populations and is crucial for monitoring the effects of human activity upon species abundance. Here, we propose that the identification of MUs from population genetic data should be based upon the amount of genetic divergence at which populations become demographically independent, instead of the current criterion that focuses on rejecting panmixia. MU status should only be assigned when the observed estimate of genetic divergence is significantly greater than a predefined threshold value. We emphasize the need for a demographic interpretation of estimates of genetic divergence given that it is often the dispersal rate of individuals that is the parameter of immediate interest to conservationists rather than the historical amount of gene flow.
Population allele frequencies

Genetic composition of a population

**Allele frequency** - rate of occurrence of a gene variant (*allele*) at a particular locus
Population allele frequencies
Genetic composition of a population

**Allele frequency** - rate of occurrence of a gene variant (*allele*) at a particular locus

**High frequency** - common alleles observed in many individuals in a population
Population allele frequencies
Genetic composition of a population

**Allele frequency** - rate of occurrence of a gene variant (*allele*) at a particular locus

**High frequency** - common alleles observed in many individuals in a population

**Low frequency** - rare alleles observed in few individuals in a population
Population allele frequencies
Genetic composition of a population

**Allele frequency** - rate of occurrence of a gene variant (*allele*) at a particular locus

**Evolution** – change in allele frequencies over time
Population allele frequencies
Genetic composition of a population

**Allele frequency** - rate of occurrence of a gene variant (*allele*) at a particular locus

**Evolution** – change in allele frequencies over time
occurs at the population level.......Individuals do not evolve
Change in AF over time = Evolution

Forces affecting change in allele frequency:

1. **Natural Selection** – favors alleles offering fitness advantages
2. **Mutation** – introduces new alleles through “mistakes” in DNA copying
3. **Gene Flow** – introduces new alleles through dispersal (immigration/straying)
4. **Genetic Drift** – random change in allele frequency (e.g., demographic isolation)
5. **Genetic Bottleneck** – decreased diversity through culling/decline (e.g., flood)
6. **Sexual Selection** – favoring more “attractive” alleles (e.g., body shape)
Calculating allele frequency

example: 12 Snake River steelhead

suppose there are two alleles $p$ and $q$ at gene $X$, where frequency $p +$ frequency $q = 1$
Calculating **allele** frequency

example: 12 Snake River steelhead

1. How many of each **allele** are observed in the diploid population?

\[(p = 6) + (q = 18) = 24\] total
Calculating **allele** frequency

**example: 12 Snake River steelhead**

1. How many of each **allele** are observed in the diploid population?

\[ (p = 6) + (q = 18) = 24 \text{ total} \]

2. What is the observed **frequency** of each **allele** in the population?

\[ p = \frac{6}{24} = 0.25 \quad q = \frac{18}{24} = 0.75 \quad \text{(sum = 1)} \]
Calculating **genotype** frequency

example: 12 Snake River steelhead

3. How many of each **genotype** are observed in the population?
Calculating **genotype** frequency

example: 12 Snake River steelhead

3. How many of each **genotype** are observed in the population?

\[ p^2 = 1 \]

homozygous type
Calculating **genotype** frequency

example: 12 Snake River steelhead

3. How many of each **genotype** are observed in the population?

\[ p \ p = 1 \]

homozygous type

\[ p \ q = 4 \]

heterozygous type
Calculating **genotype** frequency

example: 12 Snake River steelhead

3. How many of each **genotype** are observed in the population?

\[ p\ p = 1 \]
\[ p\ q = 4 \]
\[ q\ q = 7 \]

homozygous type
heterozygous type
alternate homozygous type
4. What is the observed frequency of each genotype in the population?

\[
\begin{align*}
p p &= \frac{1}{12} = 0.083 \\
p q &= \frac{4}{12} = 0.333 \\
q q &= \frac{7}{12} = 0.583
\end{align*}
\]

\[0.083 + 0.333 + 0.583 = 1\]
Hardy-Weinberg Equilibrium (HWE)

• Fundamental principle (model, theorem, law) of population genetics

**THE LAW:** randomly mating populations maintain constant [allele frequencies](https://example.com) and [genotype frequencies](https://example.com) from one generation to the next.
Hardy-Weinberg Equilibrium (HWE)

- Fundamental principle (model, theorem, law) of population genetics

The HWE equation for “expected” genotypic frequencies

\[ p^2 + 2pq + q^2 = 1 \]

- No natural selection
- No sexual selection
- No mutation
- No migration
- Infinite population size

contingent of these assumptions about evolutionary forces
Is our population in HWE?

example: 12 Snake River steelhead
Is our population in HWE?

HWE equation: \( p^2 + 2pq + q^2 = 1 \)

Our allele frequencies: \( p = 0.25 \) \( q = 0.75 \)

example: 12 Snake River steelhead

5. **answer**: does the observed deviate from the expected under HWE?
Is our population in HWE?

example: 12 Snake River steelhead

5. **answer:** does the observed deviate from the expected under HWE?

Our allele frequencies: \( p = 0.25 \quad q = 0.75 \)

HWE equation: \( p^2 + 2pq + q^2 = 1 \)

\[
\begin{align*}
    p^2 &= (0.25)^2 \quad = 0.063 \quad \text{expected frequency of } pp \\
    2pq &= 2(0.25)(0.75) \quad = 0.375 \quad \text{expected frequency of } pq \\
    q^2 &= (0.75)^2 \quad = 0.563 \quad \text{expected frequency of } qq
\end{align*}
\]
Is our population in HWE?

example: 12 Snake River steelhead

6. Compare **numbers** of each genotype (observed & expected)

<table>
<thead>
<tr>
<th># expected</th>
<th># observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>(0.063) x 12  pp = 0.8</td>
<td>(0.083) x 12  pp = 1.0</td>
</tr>
<tr>
<td>(0.375) x 12  pq = 4.5</td>
<td>(0.333) x 12  pq = 4.0</td>
</tr>
<tr>
<td>(0.563) x 12  qq = 6.8</td>
<td>(0.583) x 12  qq = 7.0</td>
</tr>
</tbody>
</table>
Is our population in HWE?

example: 12 Snake River steelhead

1. No Natural Selection
2. No Sexual Selection
3. No mutation
4. No migration
5. Infinite population size

likely not absent but nominal or static

\( P\text{-value} = 0.70 \)

7. Yes, statistically the population is in HWE, and we assume random mating
Combining two or more forces: complicates things somewhat. In general, combining two opposing forces (such as selection and migration) produces an equilibrium in the population. Combining two complimentary forces amplifies their effect.

The DeFinetti diagram is useful when determining if a population is in H-W Equilibrium. The curve through the diagram represents the H-W Equilibrium genotypic frequencies. Assortative mating or Genetic drift causes the population to deviate noticeable from this line.
Deviation from HWE expectations

The absence of equilibrium indicates **real** or **perceived** non-random mating and/or the influence of one or several evolutionary forces...

- Natural Selection – new or elevated adaptive pressures
- Sexual Selection – factors affect mate pairing (e.g., *allee*)
- Mutation – elevated rate from introduced causes (unlikely culprit)

- Gene flow – immigration (strays), and/or introgressive interaction
- Bottleneck – population culling or range expansion

- Admixture – a population sample actually contains multiple populations
- Demographic bias – disproportionate family (kinship) representation

* density dependence operating in small populations. The per capita birth rate declines at low densities, because of (for example) the increased difficulty of finding a mate.
Genetic diversity/variation

**Genetic Variation** - The phenotypic and genotypic differences among individuals in a population. Facilitates ability to adapt to changing environments.

**Heterozygosity (H_0 or H_E)** - A measure of genetic variation across the genome. The proportion of heterozygous (pq) individuals in a population.
Genetic diversity/ variation

- Relevance in fisheries harvest & management, supplementation & conservation
  - Identification of stocks in mixtures
  - Inbreeding, domestication, effective population size in hatcheries
  - Diversity in life history and growth characteristics
  - Difference in adaptive potential
Genetic distance: \( (F_{ST}) \)

- Amount of genetic variation between sub-populations:

  **High** \( F_{ST} \) : divergence (restricted gene flow / isolation)
  **Low** \( F_{ST} \) : similarity (gene flow / common origin)
Genetic distance: \( F_{ST} \)

- Amount of genetic variation between sub-populations:
  
  **High** \( F_{ST} \): divergence (restricted gene flow / isolation)
  
  **Low** \( F_{ST} \): similarity (gene flow / common origin)

\[
F_{ST} = \frac{H_T - H_S}{H_T} = \text{value 0-1}
\]

\( H_T \) = Total expected heterozygosity: sub-populations treated as one

\( H_S \) = Average sub-population heterozygosity: \( ((2p_1q_1 + 2p_2q_2)/2) \)
Genetic distance: sockeye example

suppose we have 2 sub-population (n=12; 24 alleles)
Genetic distance: sockeye example

outmigrating smolts were sampled at a downstream weir
12 individuals
24 alleles

<table>
<thead>
<tr>
<th>Location</th>
<th>#</th>
<th>freq.</th>
<th>(p)</th>
<th>(q)</th>
<th>obs. genotypes</th>
<th>obs. alleles</th>
<th>freq.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wenatchee</td>
<td>7</td>
<td>0.75</td>
<td>0.25</td>
<td></td>
<td>0.583 0.333 0.083</td>
<td>7 0.75 0.25</td>
<td>0.583 0.333 0.083</td>
</tr>
<tr>
<td>Osoyoos</td>
<td>1</td>
<td>0.25</td>
<td>0.75</td>
<td></td>
<td>0.083 0.333 0.583</td>
<td>1 0.25 0.75</td>
<td>0.083 0.333 0.583</td>
</tr>
<tr>
<td>weir</td>
<td>8</td>
<td>0.50</td>
<td>0.50</td>
<td></td>
<td>0.333 0.333 0.333</td>
<td>8 0.50 0.50</td>
<td>0.333 0.333 0.333</td>
</tr>
<tr>
<td>Location</td>
<td># Individuals</td>
<td># Alleles</td>
<td>Observed Genotypes</td>
<td>Observed Alleles</td>
<td>Expected Genotypes</td>
<td></td>
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</tr>
<tr>
<td>Wenatchee</td>
<td>12</td>
<td>24</td>
<td>pp  p q  qq</td>
<td>(p) (q)</td>
<td>(p^2 + 2pq + q^2)</td>
<td></td>
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</tr>
<tr>
<td>freq.</td>
<td>0.75 0.25</td>
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<td>6.8 4.5 0.8</td>
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| Osoyoos   | 12            | 24        | pp  p q  qq        | (p) (q)          | (p^2 + 2pq + q^2)  |
| freq.     | 0.25 0.75     | 0.083 0.333 0.583 | 0.8 4.5 6.8        |

| weir      | 12            | 24        | pp  p q  qq        | (p) (q)          | (p^2 + 2pq + q^2)  |
| freq.     | 0.50 0.50     | 0.333 0.333 0.333 | 6 12 6          |

“expected” as per HWE
**Genetic distance: sockeye example**

**Wahlund effect:** A reduction in heterozygosity caused by subpopulation structure

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<tr>
<td>Wenatchee</td>
<td># freq.</td>
<td>0.75, 0.25</td>
<td>0.583, 0.333, 0.083</td>
</tr>
<tr>
<td></td>
<td></td>
<td>7, 4, 1</td>
<td>6.8, 4.5, 0.8</td>
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<td>1, 4, 7</td>
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<tr>
<td></td>
<td></td>
<td>8, 8, 8</td>
<td>6, 12, 6</td>
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“expected” as per HWE

(p^2 + 2pq + q^2)
**Wahlund effect:** A reduction in heterozygosity caused by subpopulation structure

- When two or more subpopulations have different allele frequencies the overall heterozygosity is reduced even if the subpopulations are in HWE (excess homozygotes, and loss of variation)

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"expected" as per HWE

\( p^2 + 2pq + q^2 \)
\[ F_{ST} = \frac{H_T - H_S}{H_T} = \text{value 0-1} \]

\[ H_T = \text{Total expected heterozygosity: sub-populations treated as one} \]

\[ 2(pq) = 2 \times (0.5) \times (0.5) = 0.5 \]

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\[ F_{ST} = (H_T - H_S) / H_T = \text{value 0-1} \]

\( H_T \) = Total expected heterozygosity: sub-populations treated as one

\[ 2(pq) = 2 \times (0.5) \times (0.5) = 0.5 \]

\( H_S \) = Average sub-population heterozygosity

\[ ((2p_1q_1 + 2p_2q_2)/2) = (2 \times 0.375) + (2 \times 0.375)) / 2 = 0.375 \]

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\[ F_{ST} = \frac{(H_T - H_S)}{H_T} = \text{value 0-1} \]

\[ F_{ST} = \text{genetic distance (among sub-populations):} \]
\[ (H_T - H_S)/ H_T = (0.5 - 0.375)/0.5 = 0.25 \]

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**Pairwise F<sub>ST</sub>: sockeye example**

*Intermediate genetic distance* – in the form of a half matrix

|              | Alturas-Lake | Fishhook-Creek | Pettit-Lake | Redfish-Lake | Warm-Lake | Wenatchee | Suttle10sock | Suttle11sock | Suttle09sock | Pelton10unk | Billy10sock | Billy11sock | Metol10KOK | Metol09KOK | Meadow | TUM04 | TUM09 | WELLS04 | WELLS09 | WHATCOM |
|--------------|--------------|----------------|-------------|--------------|-----------|-----------|--------------|--------------|--------------|-------------|------------|------------|------------|------------|------------|--------|-------|-------|--------|--------|---------|
| Alturas-Lake | 0.000        |                |             |              |           |           |              |              |              |             |            |            |            |            |        |       |       |        |        |         |
| Fishhook-Creek | 0.014        | 0.000          |             |              |           |           |              |              |              |             |            |            |            |            |        |       |       |        |        |         |
| Pettit-Lake  | 0.178        | 0.179          | 0.000       |              |           |           |              |              |              |             |            |            |            |            |        |       |       |        |        |         |
| Redfish-Lake | 0.078        | 0.090          | 0.261       | 0.000        |           |           |              |              |              |             |            |            |            |            |        |       |       |        |        |         |
| Warm-Lake    | 0.080        | 0.088          | 0.225       | 0.155        | 0.000     |           |              |              |              |             |            |            |            |            |        |       |       |        |        |         |
| Wenatchee    | 0.133        | 0.143          | 0.226       | 0.199        | 0.172     | 0.000     |              |              |              |             |            |            |            |            |        |       |       |        |        |         |
| Suttle10sc   | 0.079        | 0.076          | 0.098       | 0.142        | 0.130     | 0.166     | 0.000       |              |              |              |             |            |            |            |            |        |       |       |        |        |         |
| Suttle11sc   | 0.114        | 0.115          | 0.151       | 0.141        | 0.164     | 0.181     | 0.070       | 0.000        |              |              |             |            |            |            |            |        |       |       |        |        |         |
| Suttle09sc   | 0.130        | 0.134          | 0.049       | 0.192        | 0.165     | 0.182     | 0.043       | 0.098        | 0.000        |              |             |            |            |            |            |        |       |       |        |        |         |
| Suttle08sc   | 0.123        | 0.126          | 0.060       | 0.187        | 0.162     | 0.180     | 0.036       | 0.088        | 0.004        | 0.000        |              |             |            |            |            |        |       |       |        |        |         |
| Suttle07sc   | 0.123        | 0.128          | 0.056       | 0.185        | 0.161     | 0.181     | 0.037       | 0.094        | 0.003        | 0.002        | 0.000        |              |             |            |            |        |       |       |        |        |         |
| Suttle06sc   | 0.103        | 0.107          | 0.098       | 0.156        | 0.149     | 0.181     | 0.026       | 0.051        | 0.030        | 0.022        | 0.023        | 0.000        |              |             |            |        |       |       |        |        |         |
| Suttle05sc   | 0.094        | 0.099          | 0.093       | 0.143        | 0.142     | 0.171     | 0.024       | 0.048        | 0.030        | 0.020        | 0.024        | 0.007        | 0.000        |              |             |        |       |       |        |        |         |
| Suttle04sc   | 0.096        | 0.099          | 0.092       | 0.148        | 0.140     | 0.167     | 0.023       | 0.050        | 0.028        | 0.019        | 0.022        | 0.007        | 0.003        | 0.003        | 0.000        |        |       |       |        |        |         |
| Suttle03sc   | 0.095        | 0.101          | 0.098       | 0.146        | 0.139     | 0.168     | 0.024       | 0.045        | 0.032        | 0.022        | 0.026        | 0.007        | 0.003        | 0.003        | 0.003        | 0.000        |        |       |       |        |        |         |
| Suttle02sc   | 0.093        | 0.097          | 0.094       | 0.144        | 0.139     | 0.166     | 0.023       | 0.047        | 0.030        | 0.020        | 0.024        | 0.006        | 0.003        | 0.002        | 0.002        | 0.000        |        |       |       |        |        |         |
| Suttle01sc   | 0.093        | 0.090          | 0.124       | 0.181        | 0.155     | 0.192     | 0.030       | 0.107        | 0.083        | 0.078        | 0.077        | 0.070        | 0.067        | 0.065        | 0.064        | 0.066        | 0.000        |        |       |       |        |        |         |
| Suttle00sc   | 0.117        | 0.119          | 0.153       | 0.135        | 0.165     | 0.187     | 0.076       | 0.003        | 0.100        | 0.091        | 0.097        | 0.056        | 0.051        | 0.053        | 0.048        | 0.050        | 0.111        | 0.000        |        |       |       |        |        |         |
| Meadow       | 0.114        | 0.114          | 0.147       | 0.136        | 0.164     | 0.179     | 0.073       | 0.002        | 0.098        | 0.089        | 0.095        | 0.054        | 0.050        | 0.052        | 0.047        | 0.049        | 0.110        | 0.002        | 0.000        |        |       |       |        |        |         |
| TUM04        | 0.054        | 0.058          | 0.133       | 0.088        | 0.116     | 0.140     | 0.060       | 0.051        | 0.093        | 0.085        | 0.088        | 0.060        | 0.056        | 0.057        | 0.055        | 0.054        | 0.086        | 0.052        | 0.051        | 0.000        |        |       |       |        |        |         |
| TUM09        | 0.058        | 0.059          | 0.132       | 0.092        | 0.119     | 0.144     | 0.060       | 0.047        | 0.092        | 0.084        | 0.087        | 0.059        | 0.055        | 0.056        | 0.054        | 0.053        | 0.088        | 0.048        | 0.047        | 0.003        | 0.000        |        |       |       |        |        |         |
| WELLS04      | 0.154        | 0.159          | 0.035       | 0.230        | 0.191     | 0.205     | 0.073       | 0.123        | 0.019        | 0.030        | 0.028        | 0.069        | 0.068        | 0.066        | 0.069        | 0.101        | 0.123        | 0.121        | 0.115        | 0.114        | 0.000        | WHATCOM |        |       |       |        |        |         |

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Pairwise $F_{ST}$: sockeye example

**Intermediate genetic distance** – in the form of a dendrogram (Neighbor-Joining Tree)
Neutral & Adaptive Genetic Variance

(A) human chromosome 22—$48 \times 10^6$ nucleotide pairs of DNA

(B) 10% of chromosome arm ~40 genes

(C) 1% of chromosome containing 4 genes

(D) one gene of $3.4 \times 10^4$ np

regulatory DNA sequences

exon intron

gene expression

protein

& folded protein

Neutral genetic variance

- Genetic variation that has no effect on fitness
  - Genetic variation that typically occurs in non-coding regions of the genome (introns etc.), and therefore does not change proteins or expression of a gene (variation in the DNA sequence that does not translate to variation in physiological response)
  - Variation that is not under the influence of selective pressures (degree of neutral variance is not contingent on natural selection)
  - Does not violate HWE assumptions
Adaptive genetic variance

- Genetic variation that may effect individual fitness
  - Genetic variation that typically occurs in coding regions of the genome (exons etc.), and therefore can change proteins or expression of a gene (variation in the DNA sequence that translates to variation in physiological response: MHC polymorphism and immunity)
  - Variation that may be under the influence of selective pressures (degree of adaptive variance is subject to forces of evolution – natural selection)
  - Violates HWE assumptions, likely to cause deviation from HWE