The role of reproductive timing as a driver of genetic differentiation in populations of Pacific herring

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Reproductive timing and geography influence genetic differentiation of Pacific herring

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Some important aspects of diversity

- Spatial distribution of populations
  - Especially when dispersal is limited
  - Demographic processes
Some important aspects of diversity

- Spatial distribution of populations
- Life history traits
- Contribute to stable productivity of wild populations (Siple and Francis, 2015)
Reproductive phenology is an important life history trait that mediates ecological interactions:

- Predation
- Example: Scoters co-occur with spawning herring, eat eggs

Figure from Armstrong, et al. 2016; Data from Lok et al. 2012
Reproductive phenology is important life history trait

- Evolution:
  - Gene flow is limited between populations/individuals that reproduce at different times
  - “Isolation by time”
    - Example: Sockeye from Cedar River (Hendry et al. 2005)

Photo by Jonny Armstrong
Reproductive timing in Pacific herring

• Salish Sea herring exhibit a wide diversity of spawn times:
  • Some populations start reproducing as early as January
  • Reproductive activity in the region continues through May
Research Questions

• Do differences in spawn timing limit gene flow between populations?

• Is gene flow limited by geographic distance?
Sampling Locations

- Late spawners
- Coastal vs. inlet spawners
- Puget Sound spawners
Summary of methods used

Decontamination

DNA extraction

RAD Sequencing

Video by Mary Fisher
Summary of methods used

Filter for good-quality sequences

Sort sequences

Filter for missing data and minor allele frequency

~ 1-5 million sequences per herring

~ 29,000 DNA markers

~ 8,106 variable DNA markers
Population structure across the coast

Discriminant analysis of principal components: 36% of variation

~ 8,000 DNA markers
Population structure across the coast

- Late-spawning populations are isolated (Small et al. 2005; Mitchell 2006; Beacham et al. 2008)

Discriminant analysis of principal components: 36% of variation
• Late-spawning populations are isolated (Small et al. 2005; Mitchell 2006; Beacham et al. 2008)

• Large-scale patterns of geographic differentiation
Late spawners: isolation by distance

Dispersal distances are limited between late-spawning populations

Adjusted R-squared = 0.37; p-value: 0.0004
Inlet populations are isolated (Beacham et al. 2008)
March & April spawners: isolation by distance

- Dispersal distances are limited by geographic distance separating populations
- Even at modest spatial scales (~200 km)

Adjusted R-squared = 0.50; p-value: $10^{-09}$
Spawn timing drives genetic differentiation in the Salish Sea

- Early and diverse spawning
- Spawn timing limits dispersal between populations in Salish Sea

Adjusted R-squared = 0.31; p-value: 0.001
What more can we learn from RAD sequencing?

Thyroid-stimulating hormone (TSHb)

- “Master regulator of seasonal reproduction”
- Triggers photoperiod-induced reproduction in mammals, birds, fish
- Spring & autumn Atlantic herring: different alleles for TSH receptor**

Nuclear envelope protein (SYNE2)

- Influences development of photoreceptors in retina
- Spring & autumn Atlantic herring: different alleles of SYNE2**

* Barrio et al. 2016
** Lamichhaney, Fuentes-Pardo, et al. 2017
Summary

- Dispersal distance is:
  - Limited over moderate geographic scales (100s of km)
  - Limited by temporal differences in spawn timing
    - Even among primary spawners
Implications for conservation and management

- Conserve:
  - Populations with diverse spawn timing
  - Spatial diversity of spawning populations across the coast
  - If local extinction occurs -> neighboring populations recolonize

Photo by Grant Callegari
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Collaborators

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Questions?
What can we learn from temporal replicates?

- Allele frequencies stable over time
- Homing behavior in terms of spawning season
IBT and IBD all pops
IBD in Salish Sea?

- Small spatial scale
- Dispersal is limited (FST ≠ 0)
  
BUT

- Not correlated to geographic distance separating populations
BC primary spawners: isolation by distance

- Dispersal is limited by geographic distance
- Even at modest spatial scales!

adjusted R-squared = 0.71, p-value = 9 e-07
Key notes about IBD

- When dispersal is restricted, we expect to observe increase in genetic diff with increasing geo distance.
- IBD should develop most quickly in 1-d systems and short distances.
- At migration-drift equilibrium, no variation in IBD slope should be observed across the spp range (Hutchinson & Templeton 1999)
- IBD slope depends on geographic scale considered (Bradbury and Bentzen 2007)
Abstract

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There is growing recognition that maintaining diversity in life history traits contributes to the sustainable management of wild populations. One important life history characteristic is reproductive phenology, and it has been shown that differences in the timing of reproduction can act as a barrier to gene flow between populations. If the difference in reproductive timing determines the level of connectivity, one would expect that genetic differentiation between populations would increase as a function of difference in reproductive date. This pattern, known as “isolation by time” (IBT), has been observed in wild populations of salmonids containing early and late runs. Pacific herring in the Salish Sea also exhibit a wide diversity of spawn times; some populations start reproducing as early as January and reproductive activity in the region continues through May. Here, we test whether these temporal differences in reproduction influence the genetic population structure of herring. We collected adult herring from seven different locations in the Salish Sea during active spawning events (N = 48 per site). Samples were sequenced using a restriction site-associated (RAD) approach and approximately 3,000 polymorphic loci were genotyped in each sample. We found a positive correlation between genetic differentiation and difference in spawn date, with evidence of migration between populations with similar spawn timing. Several loci exhibited exceptionally steep gradients in allele frequencies, including one locus linked to the photoperiodic regulation of reproduction. Our discovery of IBT in Pacific herring support the adaptive significance of spawn timing and underscore the importance of conserving spawning time diversity in Puget Sound herring.