Prioritizing Pacific Salmon Stocks for Conservation

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Introduction

✓ Strong homing tendency
✓ Locally-adapted development

✓ Pacific salmon populations have declined dramatically
  : Harvest, Habitat degradation, Hydropower and Hatcheries…

Steelhead
http://wdfw.wa.gov/fishing/salmon/steelhead.html

Coastal cutthroat trout

Sockeye salmon
http://www.seafoodsource.com/seafoodhandbook/finfoish/salmon-sockeye

Coho salmon
https://en.wikipedia.org/wiki/Coho_salmon

Chinook salmon
http://endlessocean.wikia.com/wiki/Chinook_Salmon
✓ Endangered species committee of American Fisheries Society

→ 214 native stocks of Pacific salmon, Steelhead and Coastal cutthroat trout

Risk of Extinction!


1) 101 stocks at High risk
2) 58 stocks at moderate risk
3) 54 stocks of special concern

Require prioritizing stocks

1) Genetic and Evolutionary consequence
2) Ecological consequence

Given & Norton, 1993. ⇒ They do have Problems.
1) Imposing an artificial linearity
2) Providing no objective means for identifying where resources
3) Difficulty in separating species that tend to rank together
4) Concealing the reasons for a particular species being threatened
5) Criteria are not equivalent and independent.

“Propose criteria for prioritizing at risk Pacific salmon stocks”
Methods

Mace & Lande, 1991. Estimate of the probability of extinction within a specific time period + Anadromous Pacific salmon

Table 1. Criteria for assessing the level of risk of extinction for Pacific salmonid stocks

<table>
<thead>
<tr>
<th>Risk of extinction criteria</th>
<th>Very high</th>
<th>High</th>
<th>Moderate</th>
<th>Special concernb</th>
</tr>
</thead>
<tbody>
<tr>
<td>Probability of extinction using population viability analysis</td>
<td>-50% within 5 years or any two of the following criteria</td>
<td>20% within 20 years or any two of the following criteria</td>
<td>5% within 100 years or any two of the following criteria</td>
<td>Historically present, b-hunted or known to still exist but no current data</td>
</tr>
<tr>
<td>Effective population size per generation</td>
<td>$N_c = 50$ or less</td>
<td>$N_c &lt; 500$</td>
<td>Not applicable</td>
<td>Build data set from which risk level can be established</td>
</tr>
<tr>
<td>Total population size per generation</td>
<td>$N = 250$ or less</td>
<td>$N &lt; 2500$</td>
<td>Not applicable</td>
<td>Run size or population strength estimate</td>
</tr>
<tr>
<td>Population decline</td>
<td>Precipitous decline</td>
<td>Chronic decline or depression</td>
<td>Decline apparent or probable</td>
<td>Demographic data such as:</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>— proportion that spawn at each age</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>— adult survival between spawnings</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Genetic data</td>
</tr>
<tr>
<td>Catastrophe, rate and effect</td>
<td>Order of magnitude decline within one generation</td>
<td>Smaller but significant decline</td>
<td>Not applicable, stocks rate at least high risk</td>
<td></td>
</tr>
</tbody>
</table>

a Based on responses to risk criteria, level of risk can be determined. For example, if a population has a probability of extinction of 50% within 5 years based on PVA, it has a very high risk of extinction. If PVA is not available, then surrogate criteria are used. For example, if $N$ is 250 or less and population decline is precipitous (the population meets two of the three surrogate criteria), the population is in the very high risk category. Example using Winchuck River fall chinook is provided in Table 2.

b Populations for which there are insufficient data to apply the risk of extinction criteria are considered of special concern. Action should be taken to obtain the necessary data, as described in this column.
# Probability of Extinction

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<td>20% within 20 years</td>
<td>5% within 100 years</td>
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<tr>
<td>- or -</td>
<td>- or -</td>
<td>- or -</td>
<td>- or -</td>
</tr>
<tr>
<td>any TWO of the following criteria</td>
<td>ONE very high risk criterion</td>
<td>- or -</td>
<td>ONE high risk criterion</td>
</tr>
<tr>
<td>- or -</td>
<td>- or -</td>
<td>- or -</td>
<td>- or -</td>
</tr>
<tr>
<td>any TWO of</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

✓ Genetic, demographic or environmental events
   → **Decline of stocks**
   ⇒ **Probability of extinction**

✓ Population viability analysis (PAV) + Time scales
   → analysis of extinction factors and their interactions
   ⇒ **ranking the level of risk according to the probability of extinction**
Effective Population Size per Generation (Ne) & Total Population Size per Generation (N)

Table 1. Criteria for assessing the level of risk of extinction for Pacific salmonid stocks

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✓ Ne: Losses of genetic variability \( \rightarrow \) decrease the ability of the stock to adapt to changing condition \( \Rightarrow \) increase the chance of extinction

✓ \( N \neq \) annual run size / \( g \cdot \) annual run size

✓ Waples, 1990. : \( Ne = g \cdot Nb \) \( \Rightarrow \) shown for pacific salmon, which die after spawning.
Population Decline & Catastrophe, rate and effect

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✔ **Category A:**
- annual run size below 500 and decline within the last 2 generation
- 90% decline in annual escapement within a single generation

✔ **Category B:** annual run size below 500 and stable
- Lesser but significant reduction

✔ **Category C:** declining at about 10 – 20% per year over the last 2 to 4 generation
Ranking Priority

✓ Focused on biological consequences for both the Species (genetic and evolutionary consequences) ecosystem (ecological consequences)

✓ Genetic and evolutionary consequences of stock extinction: proportion of adaptive genetic diversity of the species

✓ Ecological consequences of extinction: proportion of ecosystem structure and function that would be lost

⇒ Not yet possible to assess → surrogate criteria

Genetic and Evolutionary legacy + Ecological legacy ⇒ Scores

- Geographic distribution
- Morphological, Physiological variation
- Life-history variation
- Ecosystem and community organization and function

∴ Higher score indicate greater consequences of extinction
Application

Winchuck River: fall chinook salmon, winter steelhead trout and anadromous coastal cutthroat trout

**fall chinook salmon**
- Spawning populations are relatively small
- Consist almost wild fish
- Spawning survey indicate decline in adult numbers
- Depressed since about 1979

**Risk of extinction criteria:** Ne, N, population decline and Catastrophe, rate and effect

**Genetic and evolutionary legacy**
- High genetic divergence
- Unusual habitat
- Life history traits
- Unusual morphological traits
- Long isolated geographically
- Interbreed
- Avoided any severe bottleneck
- Distribution range

**Ecological legacy**
- Member of native assemblage
- Biogeographically province
- The same species and nearby stocks
- The same basin and other aquatic species
- Encouraging recovery of other imperiled population
Pacific Northwest – 20 pacific salmon stocks.

1) Stocks in the various regions 2) Stocks with various types of data 3) Various basin types 4) Species with various life histories.

Table 3. Summary of risk of extinction and biological consequences of extinction results for 20 stocks of Pacific salmon.

<table>
<thead>
<tr>
<th>Risk of extinction</th>
<th>Biological consequences of extinction scores (low 3, high 8)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Very high</td>
<td>Redwood Creek summer steelhead</td>
</tr>
<tr>
<td>High</td>
<td>North Umpqua spring chinook</td>
</tr>
<tr>
<td>Moderate</td>
<td>Naches spring chinook</td>
</tr>
<tr>
<td>Special concern</td>
<td>Deschutes spring chinook</td>
</tr>
</tbody>
</table>

*Italic area indicates stocks with high risk of extinction and high biological consequences of extinction scores.

Probability of extinction: current and historical run strength (dam counts, redd counts, spawning surveys and angler harvest)
Discussion

✓ Criteria by which recovery activities for at-risk stocks of Pacific anadromous salmonids

✓ Pacific salmon and other anadromous fish ⇒ relatively high priority for conservation
- unique and critical ecological role
- keystone role in maintaining biodiversity
- Indicators of environmental quality and ecological stress

✓ Ranking stocks according to risk and biological consequence of extinction
But, several weaknesses.
- Lack of sufficient information and limited or lacked (long-term)data
  → personal judgment into the analysis and limited numbers of Pacific salmon stocks
- Dominated by easily quantifiable measures

✓ Risk of extinction and biological consequences: High score → effort immediately directed toward their recovery
- Risk of extinction: High, biological consequences: Low → efforts phased in over the long term
- Biological consequences: Low → ranked from high to low probability of extinction
Thank you !
Effect of river discharge, temperature and future climate on energetic and mortality of adult migrating Fraser River Sockeye Salmon (Rand et al., 2006)

By
Cicilia S.B. Kambey
201599107
Introduction

Background
- Over past several decades, salmon fisheries has remarkable increased then lead over exploitation markedly. Nowadays salmon population decline and make into serious attention
- Management of salmon population by approaching system migration is needed for sustainable stock management
Purposes of study

1. To establish a link between energetic condition of salmon and their mortality
2. To simulate the energy usage of salmon during river migration
3. To analyzed the hydrodynamic changed that effected to adult salmon migration by modeling the hindcast (1950–2001) and forecast (from 2010–2099)
Methods

1. Study system:
   - Analyzed the distance of salmon natal tributaries (spawning ground), optimal temperature condition, their spawning season (focus on early Stuart population)

2. Energy density analysis:
   - Sampling on nine location with different seasonal salmon population between Fraser River estuary and spawning ground Stuart–Takla
Sampling Period
- July 1997 (7,500 m³/s – 15° C),
- July 1999 (9,000 m³/s – 14 °C) and
- July 2001 (5,400 m³/s – 15.5 °C)

Measured length, weight and energy density (of skin and whole body energy)

Comparing with hindcast data and estimated from modeling bioenergetic

Fig. 1 Map of Fraser River, British Columbia and migrating route
3. Overview of modeling approach

- Using Rand and Hinch (1988) migration model
- Electromyogram telemetry for calculating swimming speed
- Modified with daily discharge measurement for more realistic data
- Using Beuchamp et al. (1989) model for simulate metabolism

\[ MR = \alpha W^\beta e^{\gamma T} e^{\phi U} \] (in gram of O2 per day)

MR = Metabolic rate, W = mass of fish, T = temperature, U = swimming speed, \( \alpha = 0.0023 \) g/d O\(^2\), \( \beta = -0.109 \), \( \gamma = 0.0609 \), \( \phi = 0.012 \)
Key model assumption

1. Swimming speed was simulated stochastically using number of salmon reaching the river
2. Metabolic losses at given body mass, temperature and swim speed (at $O^2 13,560 J/g$)
3. Additional cost associated with anaerobic burst swimming (speed at 2.8 length/s)
4. Average individual migrant (population male and female)
5. Initial run-condition* with mean mass 2,626 g, mean body energy 8.4 MJ/kg, mean return time on 7 July
6. Conversion of somatic energy reserves to gonad accretion (development)
7. Transformation of somatic energy to gonadal energy
Hypothesis and future trends

1. Hypothesis

The existence of condition-depend mortality, would influence the model performance which can closely to observation data if en-route inconsequential.
Hypothesis and future trends

2. Future trends

Projection of energy use and mortality simulation during 2010–2099 based on expectation on river hydrology global climate changes based on Morrison et al. (2002). Using linear decline resulting 30% followed by increasing temperature, lowered food availability and reduce upwelling.
Hypothetical energy density

Figure 2.—Hypothetical energy density data illustrating how condition-dependent mortality might structure a spawning run of salmon. The top panel shows a theoretical normal distribution of energy densities for fish making landfall after marine residency. The bottom panel includes the theoretical normal distribution of the energy densities that would be expected assuming no en route mortality losses (dashed line) and the asymmetric distribution that would be expected if the migrant population experienced disproportionate losses to individuals with lower energy densities. The critical value for energy density, $E^*$ (thought to represent a mortality threshold), is indicated in the bottom panel.
**Result**

1997; 15°C / 7,500 m³/s

1999; 14°C / 9,000 m³/s

2001; 15.5° /5,400 m³/s

**Figure 4.**—Histogram and density profiles of energy density measured at the start and end of the migration for early Stuart sockeye salmon (Fraser River, British Columbia) collected during (a) 1997, (b) 1999, and (c) 2001. Note the truncated left tail in the distribution of energy density at the end of the migrations during 1997 and 1999. The critical value for energy density, $E^*$ (thought to represent a mortality threshold), is indicated on each plot.
Figure 3.—Metabolic rates predicted from a bioenergetics equation for adult sockeye salmon plotted against the observed metabolic rate for adult sockeye salmon confined in a water-flow-through Brett-style respirometer. The line shows a 1:1 ratio. The fit is based on a reduced-model intercept value to achieve a more conservative prediction of metabolic rate.
Result

![Graph of energy density](image)

Figure 5.—Plot of first quartile of the energy density distribution for early Stuart sockeye salmon (Fraser River, British Columbia) collected at nine stations along the spawning migration route during 1997, 1999, and 2001. Site names corresponding to the site numbers are provided in Figure 1. The critical value for energy density, $E^*$ (thought to represent a mortality threshold), is indicated on the plot with a broken line.
Figure 6.—Observed (squares) and simulated (solid lines) condition of sockeye salmon (expressed as energy density) plotted over river kilometers during (a) 1997, (b) 1999, and (c) 2001. Error bars on observations represent SDs.
Figure 7.—Actual and forecast time series of (a) mean daily July water temperature at Hell’s Gate on the Fraser River and (b) mean daily July discharge at Hope, British Columbia. The actual time series are for 1950–2001; the two lines are linear regression fits through the data. The forecast time series are from a hydrologic model and are presented as three separate stanzas during 2010–2099 (each stanza is identified by unique open or filled circles connected by a broken line).
Result

Figure 8.—Simulated time series of body energy for early Stuart sockeye salmon (Fraser River, British Columbia) at the spawning ground during 1950–2001 and 2010–2099. With respect to the first period, note the 10 years identified with open circles, of which the 5 with heavy black borders represent years of high en route mortality and the 5 with heavy gray borders represent years of low en route mortality. Three climate stanzas are shown for the second period. Simulation results from the future scenario involving a long-term decline in the body mass of sockeye salmon at the beginning of the migration are shown with a solid black line (plotted as a 5-year running average of model output).
Figure 9.—Regression of temperature-dependent metabolism (computed as $e^{\gamma T}$ in equation 1 using the mean temperature experienced by fish during the course of the migration) on migration duration for early Stuart sockeye salmon adults in the Fraser River, British Columbia. These values are model output during the period 1950–2099. This inverse relationship tends to stabilize migratory energy demands in a given year over the relatively wide range of hydrological conditions observed in the past and expected in the future.
Discussion

Energy Density

1. There several evidence were shown that energy reserved and depletion is important factor of successful salmon spawning migration
2. Rate energy depletion as functions of temperature and river discharge
3. While salmon did en-route, they suffer and high risk to mortality and found clearly asymmetry energy distribution in 1997–1999 while river condition was cold
Discussion

River discharge

1. Ocean productivity also affected to river migration mortality. High river discharge and low ocean productivity were correlated with high mortality of salmon.

2. With modeling, the hydrology event can be revealed by simulation show 1997–1999 higher water discharge and high individual mortality, 1992 and 1998 was increasing water temperature, and early 2000 was moderate water condition and low individual mortality.
Discussion

Swimming rate

1. Discharge swimming speed is the strategy of fish to survive and to reach spawning ground by delaying migration
2. Change in future climate can cause mortality due energy exhausted will not be continue to long term period because fish can reducing the transit time back to spawning ground
3. Late run of salmon had high en route stress during increasing temperature, diseases infected and low density energy
Discussion

- Model prediction weaker to open ocean upwelling in Alaska Gyre. Warmer ocean will be decreased the body size and body energy content.
- If migrant will start with lower energy densities and reach their energy threshold before reaching the spawning ground.
- Model scenario got reduced in marine growth rates that is important to elucidate linkages between life history and population problem under global climate change.
Conclusion

1. Salmon with lower condition exhibit disproportionately higher mortality during spawning run, low energetic condition and ability to reaching spawning ground.

2. The model output indicates high inter annual variability in migration energy use and marked as increased energy demands in unusually river discharge and temperature (1997–1998).
Conclusion

3. Metabolic rate increased with increased the temperature while river discharge influenced tour route

4. Some compensation of mortality have to consider such as diseases and stress

5. The model indicated the long term decline in mass adult salmon to completing their marine residency that could erode their migration ability during river migration and become alert for sustainability of salmon
Thank you
Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon

Evolutionary Aplications (2007)

Keywords:
genetic correlation, global warming, phenological change, smolt timing
Evolutionary responses to climate change

✓ Nongenetic responses might not be sufficient for the persistence of many populations

Plastic phenotype  Genotype (evolution)

to predict the effects of climate change on natural populations

✓ Salmon species have plastic life histories, but adaptation of reaction norms to local environmental conditions at a very fine spatial scale
  - Chinook (*Oncorhynchus tshawytscha*)
  - Sockeye (*Oncorhynchus nerka*)

- Complex nature of Pacific salmon life history and adaptation to diverse environments
- Expected to change due to climate warming
- Potential evolutionary responses for certain traits during particular life stage
1. Salmon life-history diversity

✓ The climate change could influence selection on multiple traits in multiple phases of the life cycle.
✓ Reflect: combination phenotypic plasticity in response to variable environmental conditions local adaptation, the suite of life history, morphological, physiological, behavioral traits.
2. Expected climate change

- **Climate change in the Pacific Northwest**
  - **Surface warming**: +1 to +6°C (global average)
  - **Winter precipitation**: on average, ~10%
  - **Summer precipitation**: no consistent pattern

- **Changes in salmon habitat**
  - rising upper ocean temperatures that increase the *stratification* of the upper ocean
  - wind patterns, potentially changing the timing and intensity of the *upwelling of nutrient-rich*
  - increasing *ocean acidification* changing *plankton community composition* with effects cascading through marine food webs

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**The evolutionary implications of climate change trends**

- describe how climate change might alter the selective regime
- review the trait’s genetic variation and heritability
- assess the likelihood and relative speed of potential evolutionary responses
3. Potential evolutionary pressures and responses

1) Heat tolerance
2) Disease resistance
3) Upstream migration
4) Spawning date, emergence date, and development rates
5) Juvenile rearing
6) Downstream migration timing and early ocean stages
7) Ocean residence
1) Heat tolerance

- Fitness in warm water is reduced at lethal temperatures, and various impacts
  - increased susceptibility to warm-water diseases
  - inhibition: behavior, growth and development - smoltification, maturation, egg development
  - energetic costs

✓ heritability for heat tolerance: cooler (0.27) > warmer (0.00)
✓ upper thermal limit: behaviors that reduce exposure to the highest temperatures
2) Disease resistance

- Parasitic and bacterial diseases become more virulent with increasing temperature
  - lower host resistance when the fish were thermally stressed
  - higher pathogen population growth rates, due to shorter generation time
    - selection should favor increased resistance to these diseases

- The Columbia River
  - increased temperature, lower flows, slower juvenile migration
  - increased exposure and susceptibility to certain diseases

- Resistance responds: depend on heritability for resistance
  - population have been exposed to particular diseases; tend to have higher resistance
  - heritability for resistance to common diseases range from very low to moderate
    - limit the pace of future adaptation
3) Upstream migration

- Successful spawning
  i) stay in the ocean long enough to acquire adequate energy stores
  ii) use energy efficiently during migration
  iii) avoid migration when conditions are especially difficult (e.g. high temperatures, very low flow)
  iv) arrive prior to the appropriate spawning date
3) Upstream migration

- The future evolution of migration time will be constrained
  - if salmon migrate earlier in the summer but spawn at the same date in fall will need
    - more energy to sustain themselves for the longer period of fasting
    - more stored energy might be in conflict
    - to leave the ocean earlier in the summer, missing some of the best growing conditions

Water temperature has risen

Plastic or Genetic? Unclear!
4) Spawning date, emergence date, and development rates

Emergence timing
- too early, before food is seasonally available
- too late to capitalize on crucial growth opportunities

<table>
<thead>
<tr>
<th>Spawning date</th>
<th>Temperature-specific developments</th>
</tr>
</thead>
<tbody>
<tr>
<td>linked to water temperature nearby spawning locations; habitat inaccessibility at a particular time; energetic demands on adults</td>
<td></td>
</tr>
</tbody>
</table>

- High heritability
- Low heritability
- transplanted to New Zealand; diverged several weeks in maturation date
- transplanted to New Zealand; was not accompanied

Warmer winters
- accelerate development
- earlier emergence
- optimal food conditions might not
5) Juvenile rearing

- Body size & Growth rate
  - the contributions of body size and growth rate to survival do appear to vary

- Climate-induced changes in growth rate are likely to be primarily plastic
  i) heritability of growth rate can be relatively low (0.04 – 0.3)
  ii) difficult to predict; many other selection such as egg size, behavior, age and size at smolting, age and size at maturity
  iii) adaptation; strongest at low temperatures, rather than high
  iv) have not found strong selection on growth rate or body size
6) Downstream migration timing and early ocean stages

- Climate changes to impose contradictory selection on migration timing
  - in river survival: favors earlier migration
  - early ocean survival: favors later migration

```
Climate Changes

<table>
<thead>
<tr>
<th>Warm</th>
<th>earlier snowmelt rising summer temp.</th>
<th>unfavorable river in earlier summer</th>
<th>earlier migration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Increase intensity and delay of upwelling</td>
<td>improve late-entry smolts</td>
<td>later ocean entry slower migration</td>
<td>increase in-river mortality</td>
</tr>
</tbody>
</table>
```

Downstream migration & Ocean entry

“Migration Timing“
- Time for growth before migration
- Hazard of river, ocean conditions
7) Ocean residence

- Growth rate respond to climate change
  - alterations in metabolic costs of foraging in a warmer ocean
  - shifts in prey abundance, composition, distribution

- Genetic variability in the migration patterns of salmon represents
  - adaptation of migration routes toward regions favorable for growth and survival

- poorly understood that it is difficult to speculate
  - how rapidly adaptation might occur
  - how it would interact with proximate responses to currents, temperature, food availability
4. Integrating across the complexity

- The timing of five major life-history events

<table>
<thead>
<tr>
<th>Date</th>
<th>Adaptive equilibrium</th>
<th>Climate change scenario</th>
<th>Plastic response</th>
<th>Potential selection pressure</th>
</tr>
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<tbody>
<tr>
<td>upstream migration</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>spawn</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>emerge</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>ocean entry</td>
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<td></td>
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</table>
4. Integrating across the complexity

✓ Salmon populations are **locally adapted** before climate change

![Diagram showing adaptive equilibrium and timing of events](image)

✓ the mean timing of each event approximates the optimal timing
4. Integrating across the complexity

- How fitness functions might shift under potential climate change scenario

Earlier onset of stressful temperature (warming)

- Optimal spawning date will shift later
- Optimal spawning date will shift later

- Earlier timing of upstream migration
- Hasten egg development
- Fry to emerge too early
- Earlier adult migration but later spawning

- Longer stay in freshwater & energetic coasts and higher risk of predation and thermal stress

- Emergence timing should be earlier

- Advance the optimal timing of smolt migration

- Delays optimal ocean entry

- Food available

- Delayed upwelling
4. Integrating across the complexity

- The expected plastic response of each life-history event to climate change

**Migration & spawning** largely unchanged
- low plasticity

**Earlier downstream migration**
- earlier warming

**Earlier emergence timing**
- warmer incubation temp.

**Earlier ocean entry**
- Migration speeds accelerate
4. Integrating across the complexity

- Potential natural selection on the timing of each life-history

Mismatch the new optimum and the phenotype distribution
Thank you for your attention!
The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes

-Sayre Hodgson and Thomas P. Quinn

201692132 김혜광
Introduction

- Migration is an **energetically demanding part** of the life cycle, and animals tend to evolve physiological and behavioral traits that **suit the environmental conditions** they experience during migration (Dingle 1996).

- The **timing** of upstream migration is presumed to be an **adaptation to the long-term average conditions experienced by migrating adults**, including water temperature, flow regime, and other abiotic factors, and the optimal spawning date (Gilhousen 1990).

- Although salmon migrate from the ocean to fresh water to breed and little or no feeding takes place prior to spawning, the **time elapsed between upstream migration and spawning varies** among species and populations.

- Hypothesize that The timing of migration reflects constraints on adult survival and energetics prior to spawning.
Introduction

• The **objective** of this study was to develop a comprehensive explanation of the **timing patterns** of adult North American sockeye salmon.

• **Differences in timing** among populations were **hypothesized** to relate to **temperature conditions** along the migration route.

• **Populations in warmer, southern rivers** were **hypothesized to return early**, when outlet temperatures are lower, and presumably hold below the thermocline in lakes, avoiding the higher outlet temperatures that occur later in the season.

1) The mean delay between migration and spawning is longer among populations from rivers that exceeded the critical temperature.

2) The variance in delay between migration and spawning is higher among populations from rivers that exceeded the critical temperature.
Results & Discussion

- Migration date increased linearly with spawning date, excluding the outliers.
- Later spawning dates were associated with higher peak temperatures.
Results & Discussion

- Examples of timing of populations with short and long delay patterns.

Water temperatures
Average dates of migration
Average dates of spawning

(a) Wood River Lakes

(b) Lake Washington

Results & Discussion

- Long delays between migration and spawning were more common in populations with short (<100 km) migrations.
- Delays were longer among coastal than among interior populations in areas with both high and moderate temperatures.
Results & Discussion

- Delay were generally greater at high temperatures, but effect was only significant for coastal populations.
**Results & Discussion**

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**Fig. 6.** Relationship between the peak average water temperature and the average temperature experienced by coastal and interior sockeye salmon populations on the date of peak upriver migration. The time of peak migration was classified as after, on, or before the date of peak average temperature.

- The average peak migration temperature generally increased with the peak average temperature.
- No populations’ peak migration date coincided with times of average temperatures >19°C
Results & Discussion

- Spawning timing

  - Populations experiencing lower incubation temperatures generally spawn earlier than populations experiencing higher temperatures (Brannon 1987, Webb and McLay 1996).
  
  - Spawning tends to occur earlier in populations which spawn at higher latitudes and in areas with lower peak water temperatures.
Results & Discussion

- Migratory timing strategies
  
  (migrate through areas with peak average temperatures $\geq 19^\circ C$)

1. If the thermal regime during incubation dictates early spawning

- The fish return early, before summer temperatures peak, and spawn with little delay.
- This is the prevalent pattern in populations spawning in interior locations
- This pattern occurred in two of the populations.
Results & Discussion

2. Thermal regime during incubation is mild, dictating late spawning
   • The fish may return late in the season, after temperatures peak, and spawning with little delay.
   • This pattern was seen in some coastal populations.
   • This pattern occurred in 10 of the populations.

3. Populations spawning late may migrate to fresh water early (before temperatures peak) and experience a long delay in the lake before spawning.
   • This pattern occurred in 11 of the populations.

The mean and variance of delay among populations from warm areas would be greater than those for populations from cold areas.
Results & Discussion

- Delay

  - In sockeye salmon populations that experience moderate temperatures, migration generally occurs about 30-40 days (mean = 36 days) before spawning.

  - Among coastal populations, delays averaged 54 days longer for populations with higher peak water temperatures than for those from cooler areas, reflecting patterns 2. and 3. above.

  - Interior populations tended to have shorter delays between migration and spawning than coastal populations, regardless of differences in peak water temperatures.
Thank you
The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes

Sayre Hodgson and Thomas P. Quinn

Introduction & Methods

The timing of adult sockeye salmon migration into fresh water is an adaptation by populations to prevailing thermal regimes. This adaptation is critical for the successful migration of sockeye salmon. The study was conducted by Sayre Hodgson and Thomas P. Quinn.

Results

The results of the study showed that the timing of migration is influenced by the thermal regime. The delay and variance in migration timing were found to be influenced by the prevailing thermal regimes.

Discussion

The discussion section highlights the importance of thermal regimes in determining the timing of migration. It was found that the delay and variance in migration timing are influenced by the thermal regime.

Introduction

**HOMING**

Female salmon lay eggs in a nest in the stream bed and are fertilized by the males. Adult males and females die shortly afterward.

Alevins, newly-hatched salmon, live off of an attached food source and stay in the nest and grow.

When the food run is used up, the salmon fry leave the nest to find food for the first time. As it grows, it becomes stream-rolled with poor marks and is called a parr.

When a young salmon becomes silver-colored, it is called a smolt. After growing for a while, smolts swim downstream to the ocean. When they reach the ocean, they spend time where the river meets the ocean as their bodies change to allow them to live in salt water.

Salmon return to the stream they were born in to reproduce. No one knows how they recognize their natal stream. They stop feeding once they return to fresh water.

Salmon grow to maturity in the ocean. This can take 5-7 years depending on the species. Some salmon migrate thousands of miles in the ocean. Most salmon maintain a silvery color while in the ocean.

Source: [http://www.enchantedlearning.com/subjects/fish/printouts/Salmon.html](http://www.enchantedlearning.com/subjects/fish/printouts/Salmon.html)
Introduction

**Migration**

**Mature**

**Homing**

**Spawning**
Introduction

- For many species and populations, these migrations pose extraordinary **bioenergetic and navigational challenges**
  - Thousands of kilometers
  - Distinct sets of orientation clues
  - Distinct challenges for orientation
- Despite these challenges, **homing is generally precise**
Introduction

• In this paper, we briefly review the mechanisms underlying homing at all stages of the Pacific salmon (*Oncorhynchus* spp.) migration but emphasize the final, freshwater phase.

• In this review, we discuss olfactory imprinting and homing by wild salmon.
Ocean migrations

- **Salmon** converge on their river of origin with remarkable spatial and temporal precision despite initiating homeward migration from widely distributed feeding areas.
- These observations are consistent with the hypothesis that **homing salmon** are guided by a map and compass system on the open ocean.
Ocean migrations

- Juvenile salmon are able (1) to orient to the sun’s position, (2) to polarized light patterns and (3) to the earth’s magnetic field
River migrations

- Oceanic orientation mechanisms → Riverine migration mechanisms

  ✓ Olfactory discrimination of home stream water
  ✓ Other sensory systems (e.g. compass mechanisms)
River migrations

• The olfactory imprinting hypothesis for salmon homing (Hasler and Wisby 1951) based on behavioral experiments demonstrating that fish can discriminate between the waters of different streams on the basis of odors:
  ✓ Streams differ in chemical characteristics that are stable over time
  ✓ Salmon can distinguish these differences
  ✓ Salmon learn the chemical characteristics of their natal stream prior to or during their seaward migration

• The process of olfactory learning and homing is intimately linked to hormone levels at different life stages

• Juvenile coho salmon learn the odors of their home stream during a sensitive period termed the parr-smolt transformation (PST)

• Kokanee (the non-anadromous form of sockeye salmon), which normally migrate from their natal site soon after emergence from the gravel, are able to imprint on artificial odorants as alevins and emergent fry as well as at the smolt stage
Olfactory imprinting and thyroxine levels

- Many of the changes that occur during the parr-smolt transformation are associated with surges in the plasma levels of the hormone thyroxine.

- Thyroid hormone surges may influence neural development in the salmon olfactory system and facilitate olfactory imprinting.
Olfactory imprinting by wild salmon

Hatchery
- Single water source
- Under stable conditions
- Single salmonid species

Wild
- Constantly changing environmental conditions
- A variety of water sources
- Various salmonid species
Olfactory imprinting by wild salmon

Hatchery

- Sensitive period for olfactory imprinting is during the PST

Wild

- Sensitive period for olfactory imprinting may differ between species
- Wild salmon must imprint prior to the PST (i.e. coho salmon)
Olfactory imprinting by wild salmon

• Juvenile salmon learn a **series of olfactory waypoints** as they migrate through fresh water and later retrace this odor sequence as adults
• **Thyroid activity** changes during freshwater residence in response to changing **developmental status** and **environmental conditions**
Ecological and evolutionary aspects of homing

• Homing to natal sites has led salmon to evolve population-specific adaptations to the physical and biotic characteristics of these sites.

• The sockeye salmon
  ✓ Egg size: fine substratum < coarser substratum
  ✓ Male body size and shape: shallow streams $\rightarrow$ small and shallow-bodied

• Ecological factors (e.g. complex combination of homing, habitat quality, intrasexual competition and availability of mates) culminate in the variation in reproductive success.
Prioritizing Pacific Salmon Stocks for Conservation

태평양 연안에는 pacific salmon, steelhead, 그리고 coastal cutthroat trout 등이 존재하며, 이 중 pacific salmon은 강한 귀소 경향과 지역적 적응을 통해 발달한다. 하지만 어획, 서식지 악화, 수력 발전 그리고 부화장 등으로 인하여 개체수가 급격하게 감소하고 있다. 미국 수산학회의 멸종 위기 종 위원회에서는 pacific salmon, steelhead, 그리고 coastal cutthroat trout을 포함하여 214개의 stocks의 캘리포니아, 오리건, 그리고 아이다호에서 멸종위기이며, 1973년 미국 멸종 위기 종 보호법에 101개 stocks는 높은 멸종 위기, 58개의 stocks는 중간 위험의 멸종 위기 그리고 54개의 stocks는 특별 관심을 두어야 한다고 명시하였다. 이에 따라 멸종의 위기 stocks에 대한 우선순위가 요구되어지기 때문에, 우선순위를 정하는 기준을 제시하고, 우선순위를 추정해보았다.

멸종의 위험과 특정 시간 구도를 적용하여 3가지 레벨로 구분하였다. 개체군 실용성 분석을 이용한 멸종 가능성, 세대 당 효과적인 개체군 크기 (Ne), 세대 당 총 개체군 크기 (N), 개체군 감소와 참사율과 영향에 따라 카테고리 A, B, 그리고 C로 분류하였다. 이 때, A 기준 두 개를 만족하면, 카테고리 A, A 기준이 1개 만족하거나 B 기준 두 개를 만족하면 카테고리 B, B 기준 1개를 만족하면 카테고리 C로 나눈다.

유전적, 진화론적 결과는 종의 적응하는 유전적 다양성의 비율이며, 생태계 구조와 기능에서 손실될 수 있는 비율은 생태학적 결과이다. 하지만 이를 통해 직접적으로 평가하는 것이 어렵기 때문에 다른 기준을 이용하게 되고, 지리학적 분포, 형태학적, 생리학적 변화 그리고 생활사의 변화 같은 유전적, 진화론적 유물과 생태계와 군집 조직과 기능의 생태학적 유물에 따라 스코어를 매기는 데 높은 스코어일 경우, 멸종의 결과가 커진다.

이런 기준에 따라 winchuck river의 fall chinook salmon을 적용한 결과, 멸종의 위험에 따라 보통 위험, 카테고리 C로, 유전적, 진화론적 유물에서 2점, 생태학적 유물에서 2점을 받았다. 그리고 태평양 북서쪽의 20개의 stocks에도 적용하여, table 4를 결과로 제시하였다.

우선순위를 선정함에 있어서 자료와 정보가 부족하여 분석에 개인의 판단, 주관성이 들어갈 수 있으며, 사용할 수 있는 stock의 수가 제한되어 있다. 그리고 쉽게 정량화할 수 있는 측정을 주로 한다는 단점이 있다. 하지만 이런 우선순위에 따라 보존과 회복에 대한 계획을 세울 수 있는데, 멸종의 위험과 생물학적 결과가 높은 점수일 때 회복을 위한 즉각적이고 적절적인 노력을, 멸종의 위험은 높지만, 생물학적 결과가 낮으면 장기간에 걸쳐 단계적 노력을 그리고 생물학적 결과가 낮으면 멸종의 낮은 가능성이어서 높은 가능성을까지 세 번째 순위로 고려되어야 한다.
Abstract: Effect river discharge, temperature and future climate on energetic and mortality of adult migrating Fraser River Sockeye Salmon

We evaluated the effects of past and future trends in temperature and discharge in Fraser River on the migratory performance of the early Stuart population of sockeye salmon *Oncorhynchus nerka*. Fish of lower condition exhibited disproportionately higher mortality during the spawning run, elucidating a critical link between energetic condition and a fish's ability to reach spawning grounds. We simulated spawning migration by accounting for energetic demands for an average individual in population from the time of entry into Fraser River estuary to arrival at spawning grounds (about 1.200 km upstream) and estimated energy expenditures for the averages migrant during 1950-2001. The model output indicates relatively high interannual variability in migration energy use and a marked increase in energy demands in recent years related to unusually high discharges (e.g. 1997) and warmer than average water temperature (e.g. 1998).

We examined how global climate change might effect discharge, water temperature and energy used by sockeye salmon during their spawning migration. Expected future reductions in peak flows during freshets markedly reduce transit time to spawning ground, representing a substantial energy saving that compensated for the effect of the increased metabolic rate resulting from exposure to warmer river temperatures. We suggest that such watershed-scale compensatory mechanism may be critical to long term sustainability of Pacific Salmon, given expected changes in climate. However such compensation will probably only be applicable to some stock and maybe limited under extremely high temperatures where non-energetic factors such as diseases and stress may play more dominant in defining mortality.

Our result further indicate that a long-term decline in the mean mass of adult sockeye salmon completing their marine residency could erode their migration fitness during the river migration and hence jeopardize the sustainability of sockeye salmon and the fishery that targets them.
Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon

Crozier et al, 2007 (Evolutionary Applications)

기후변화는 서식지를 변화시키지만, 서식지의 범위와 표현형(phenotype)의 변화와 같은 nongenetic 반응이 개체군의 지속력을 설명하기에 불충분하기 때문에 기후변화에 따른 진화적 반응에 대한 연구는 중요하다. 서식지 변화에 따른 생리학적, 행동학적 변동은 지역적인 반응을 잘 반영한다. 유전 메커니즘과 가소성(plasticity)은 자연개체군에 대한 기후변화의 영향을 예측하고 구분하는데 있어 중요하다. 연어는 다양한 생활사를 가지며 미세공간 규모에서 지역적인 환경 조건에 적응한다. 따라서 서식지의 천이에 대한 적절한 타이밍이 중요하며, 각각의 생활상단계에서의 요구조건들에 대하여 고려해야 한다. Pacific Northwest의 연어(Sockeye 연어, Sockeye 연어)는 공동적인 생활사를 가지고 있으며, 이들에 대한 생활사 단계의 복잡한 환경, 온난화와 관련한 예상되는 변화, 지역적인 적응, 다양한 생활사 단계에서 여러 특성간의 진화적 변화, 변화 가능한 반응들에 대하여 알아보고자 한다.

Salmon life-history diversity 가을철 담수에서 산란을 하고, 배아는 겨울동안 자갈 내에서 배양된다. 봄에 부화하면 몇달~몇년동안 자라게 되고, 강의 하류나 연안으로 이주한 후 바다로 나간다. 다시 담수로 돌아와서 산란하기까지 몇달~7년정도 바다에서 지내게 된다. 환경과 행동이 각 단계에서 다양하기 때문에 기후변화에 대한 영향을 받을 수 있게 된다. 연어의 생활사 다양성은 다양한 환경 조건에 따라 phenotypic plasticity과 특정 지역에 대한 적응을 잘 반영한다.

Expected climate change 북극 태평양은 온난화 되고 있으며 겨울의 강수가 증가하고 여름의 강수는 폐턴이 다양하게 나타난다. 온난한 겨울은 강수를 증가시키고 snow melting을 앞당기게 된다. 대기의 따뜻해지며 수증기가 증가하게 되면 여름의 가뭄이 더해진다. 이에 따라 성층화, upwelling의 시기와 세기, 해양 산성화로 인한 억제가 들어맞고 다. 이러한 환경 변화에 의해 생활사 단계에서 어떤 선택적 변화가 나타나는지, 특정에 대한 유전적 변동과 유전율은 어떠한지, 잠재적인 진화 반응의 속도는 어떠한지 평가하고자 한다.

Potential evolutionary pressures and responses (1) Heat tolerance 따뜻한 물은 생존과 발달을 증가시키지만, 스트레스를 준다. 절영에 대한 민감성을 증가시키고, 정상적 행위를 억제하며, 온화, 동연변이, 난자 개발과 같은 성장과 발달에 영향을 주며, 애너지 손실을 증가시킨다. 각 온도에 대한 생존율이 다양하게 나타나는 것도에 대한 내용이 진화할 수 있음을 나타낸다. chinook 연어는 낮은 온도에서 산란과 부화가 낮으며, 열에 대한 저항성이 늘어나는 하지만 유전되지 않는다. 최고 23°C까지의 서식지를 가지지만 그 이상의 온도에서는 살 수 없으며, 높은 온도에 있는 개체군들은 차가운 환경을 찾아가게 된다. 만약, 모든 개체군이 따뜻한 물을 피해하는 행동을 가지면, 기후변화에 대한 영향에 대하여 개선할 수 있지만, 그렇지 않다면 특정 온신처의 이용은 적절한 행동의 진화에 달려 있다. 하지만 이에 대한 적응력은 알려져 있지 않다.

(2) Disease resistance 온도가 증가할수록 병원균의 성장은 빨라지고, 기생성, 세균성 질병 감염이 증가하고 저항력은 약화된다. 수온이 증가하고, 유속이 감소하며, 특정 질병에 대한 노출과 민감성이 증가되며 방어 체계가 반응한다. 저항력은 유전율(heritability)에 달려 있으며, 병에 오래 노출된 개체군에서는 유전율이 낮게 나타난다.

(3) Upstream migration 성공적인 산란을 위해서는 애너지의 모으기 물을 충분히 바다에서 지내야하고, 회유동안 효율적으로 애너지를 이용해야 하며, 온도가 높고 흔히 뜨거운 환경을 피해야 하고 적절한 산란지에서 도착해야한다. Columbia River에서 4~5월에 강으로의 회유가 나타나며, Snake River Chinook 연어는 8월 중하순에, sockeye 연어는 9~10월에 알을 낳는다. 이주가 늦어지게 되면 온도에 대한 온신처를 찾는 것이 늦어져 사망률이 높다. 7월의 따뜻한 수온은 회유시기를 1달 이상 앞당긴다. 즉, 여름철 온도에 대한 스트레스를 피하기 위해 봄의 이른시기에 회유하는 것을 선택한다. 하지만 이런 선택이 유전적인지 일시적인지 알 수 없으며, 표층수 온이 회유 타이밍에 영향을 줄 수는 있지만 이런 경향성은 약하다. 그래도 변화된 상태에서 진화적으로 적응한다.
(4) Spawning date, emergence date, and development rates 늦은 여름에 산란하고, 겨울동안 배아가 발달하며, 이 른 봄에 치어들이 부화하게 된다. 치어의 부화시기그는 너무 이르면 먹이가 부족하여 생존률이 낮아지고, 너무 늦으면 성장기회를 놓치게 된다. 산란 장소에 따른 수온의 차이는 산란시기에 영향을 줄 수 있다. 산란시기는 부화 시기의 선택보다는 성체가 요구하는 에너지 공급이나, 온도에 따라 달라지게 된다. 즉, 부화율, 배아의 발달률은 부화 당시의 수온과 관계가 있지만, 특정 시간대에 서식지에 도달했는가와 성체에게 에너지 공급이 원활한 곳인 가가 중요하다. 겨울이 빨라지면 배아의 발달을 가속화 시키고 부화를 앞당긴다고 되지만 최적의 먹이조건도 같은 비율로 앞당겨지지 않는다. 따라서 산란시기와 발달률에 대한 보충적인 변화가 필요하게 된다. 산란시기는 높은 수온을 지니며, 뉴질랜드로 이적했을 때, 성주식시기가 몇 주 앞당겨졌지만 산란이 늦음이 나타났다. 발달률은 온난화에 따라 증가하는지에 대한 확신이 없으며, 산란시기보다 수온원을 늦게 낮을 수 있다. 발달률이 부화시기 에 맞추어 적응하는 것처럼 보이더라도 산란시기의 확장이 발달률의 확장을 수반하지는 않았다. 하지만 산란시기 가 부화시기에 영향을 주지 못한다면, 발달률이 부화시기에 적응하는 메커니즘으로 남게 될 것이다.

(5) Juvenile rearing 청년기의 연어는 담수에서 서식하게 되는데, 이 기간동안 빨라하고 흐름이 느린 환경에 있다면 멸종 위험이 증가하게 된다. 가을에 흐름이 감소하고 여름에 온도가 높을 때, 포식과 성장에 영향을 준다. 성장에 대한 현지의 적응이 나타나지만 이는 진화된 것으로 보기는 어렵다. 성장률의 수온은 상대적으로 낮으며, 알의 크기, 행동, smolting 나이와 크기, 성체의 나이와 크기 등에 대한 여러가지 선택이 가능하기 때문에 예측하기 어렵다. 낮은 온도에서 적응을 강하게 나타내며, 기후변화를 경험한 연어들 중에서도 성장률과 크기에 대한 변화가 나타나지 않기도 한다.

(6) Downstream migration timing and early ocean stages 회유 전의 성장 시기, 강과 바다의 상태 사이의 trade-off에 따라 회유 타이밍이 결정된다. 강 하류로의 회유 동안, 온도가 높으면 성장률이 낮아지고 흐름이 빨라 성장률이 증가한다. 높이 빨리 늦게 되면 이른 여름동안 강에서 부적절한 환경을 만나게 되고 회유가 빨라지게 된다. 하지만 바다로의 회유는 청년기의 연어가 바다에 도달했을 때의 상태에 따라 다르며, 기후변화에 따라 upwelling이 늦어지게 되면 바다로의 회유가 늦어지는 대신 강에서의 사망률이 증가하게 된다. 즉, 강에서는 이른 회유가 선호되며 초기 바다에서는 늦은 회유가 선호되는 경향을 보인다.

(7) Ocean residence 연어는 바다에서 1~4년정도 머무며, 기후변화에 의해 먹이를 찾는 비용의 변화, 먹이의 양과 구성의 변화를 겪게 된다. 이주경로의 변화는 성장과 생존을 반영하며 해류, 수온, 먹이 이용도에 대한 적응을 나타낸다.

Integrating across the complexity 계절적 변화는 진화적이거나 표현적 가소적 두가지 반응 모두 일 수 있으며, 한 단계에서의 변화는 다른 단계의 변화를 이끈다. 1) phenotype의 분포는 예상되는 환경과 잘 맞으며, 연어는 기후변화에 앞서 지역적으로 적응중심을 알 수 있다. 2) 잠재적으로 기후가 온난화하게 되면, 강으로의 회유가 빨라지고 산란이 늦어지게 된다. 먹이공급 때문에 부화시키는 빨라지게 되고 바다로의 회유는 늦어지게 된다. 3) 강으로의 회유 시기와 산란시기의 늦은 plasticity 때문에 크게 변하지 않는다. 부화시키기와 강으로의 회유는 온난화에 따라 빨라진다. 4) 기후변화에 따라 잠재적으로 이른 강으로의 회유와 늦은 산란이 예상되며, 바다로의 회유는 점점 늦어질 것이다.
The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes

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Introduction & Methods

회유를 하는 동안 동물은 그 동안 겪은 환경조건에 맞추어 생리적이고 행동적인 특성을 발달시킨다. 이 논문에서는 개체군간 timing의 차이가 회유하는 동안의 온도에 달려있으며, 남쪽 강의 개체군은 빨리 되돌아오며 높은 하구 온도를 피해 호수의 수온약층 아래에 머물 것이라고 가정하였다. 따라서 이 실험은 어느 정도의 온도를 넘는 강의 개체군에서 회유와 산란 사이의 기간인 delay가 더 길고 variance가 더 높을 것이라는 가설을 세웠다. 실험은 회유 날짜와 산란일, 이 두 날짜의 차이인 delay를 수온과 회유 거리, 위치에 비교하여 실험하였다.

Results

이 연구에서 회유 날짜는 6월 중순부터 11월이었으며, 산란일은 7월 중순부터 12월 말이었다. 산란일이 늦은수록 회유 날짜도 늦은편이었으며, 평균 수온이 높았다. 긴 delay는 회유거리가 짧을때, 연안의 개체군보다는 내륙의 개체군에서 나타났다. 평균 수온이 높을수록 연어가 회유하는 동안 겪은 수온도 높았으나 19도 이상에서 회유하는 개체군은 없었다.

Discussion

온도가 낮은 편인 높은 위치와 수온이 낮은 곳에서 산란하는 개체군이 일찍 산란하는 경향을 가진다. 회유를 하는 동안 19도가 넘는 높은 수온을 겪는다면, 연어는 3가지 전략을 취한다.

• 첫 번째, 부화하는 동안의 온도가 이른 시기에 산란하도록 영향을 준다면, 그 연어는 여름 온도가 정점에 오르기 전에 일찍 돌아와 약간의 delay를 거쳐 산란한다. 이 패턴은 내륙지역에서 산란하는 개체군에서 보여졌으며, 23개의 개체군 중 2개의 개체군에서 일어났다.

• 두 번째, 부화하는 동안의 온도가 온화하여 늦은 시기에 산란을 하게 한다면, 그 연어는 온도정점이 지나 높은 시기에 돌아와 약간의 delay를 거친후 산란한다. 이 패턴은 연안의 개체군에서 보여졌으며, 23개의 개체군 중 10개의 개체군에서 일어났다.

• 세 번째, 산란을 늦게 하는 개체군이 회유는 일찍 시작하지만, 긴 delay를 거친 후 늦게 산란하는 것이다. 이 패턴은 23개의 개체군 중 11개의 개체군에서 나타났다.

이러한 결과를 종합해보면, delay의 평균과 variance는 따뜻한 지역의 개체군이 차가운 지역의 개체군보다 더 크다는 것을 알 수 있다. 이와는 다르게 적절한 온도를 겪은 연어 개체군들은 회유하는 데 약 30일에서 40일 정도가 걸렸다.

연안 개체군과 내륙의 개체군을 비교해보면, 연안의 개체군은 수온이 높은 지역이 수온이 낮은 지역보다 delay가 54일 더 길게 나타났으며 3가지 전략 중 2변과 3변을 보여주었다. 내륙의 개체군들은 온도와는 상관없이 연안의 개체군보다 더 짧은 delay를 가지는 경향을 보였다.
Homing in Pacific Salmon: Mechanisms and Ecological Basis

연어과에 속하는 어류의 가장 큰 특징은 알을 낳기 위해 자신이 태어난 곳으로 돌아오는 회유(homing)를 한다는 것이다. 연어는 자신이 태어난 곳에서 0-3년(종이나 개체군에 따라 달라짐) 정도를 머물며 성장을 하고, 그 이후에 바다로 나가게 된다. 그곳에서 연어는 알을 낳을 수 있는 성적인 성숙과정(약 1-3년)을 보낸 후, 자신이 태어났던 강으로 돌아와(homing) 산란을 한다. 이 homing의 과정에서 연어는 많은 방해요소를 겪게 된다. 그것은 (1) 수천 킬로미터에 달하는 이동거리와 (2) homing을 방해하는 복잡한 단서들, (3) 이러한 단서들로 인한 homing 방향의 혼란이 있다. 하지만 연어들은 이러한 방해요소에도 불구하고 정확한 homing을 이루어 낸다. 연어의 homing은 ocean migration과 river migration의 두 가지로 크게 구분된다. 이 중 ocean migration에 관한 연구자료는 많이 부족한 상황이다. 간접적인 결과들로부터 연어는 폭 넓고 다양한 섭이장에서 다양한 homing timing에도 불구하고 놀라운 공간적 시간적 정확성을 가지고 모인다는 것을 알 수 있다. 이를 통해 연어가 어떠한 방향 시스템(compass system)을 통해 homing을 한다는 것을 알 수 있다. 현재 이 방향 시스템으로 알려진 것은 (1) 태양의 위치, (2) 편광의 패턴, (3) 지구의 자기장이지만, 이들의 정확한 이용방법에 대한 연구는 부족한 상황이다.

연어가 강으로 들어오면 ocean migration에서 river migration으로 메커니즘을 전환하며, 이 때 중요한 방법이 olfactory discrimination(후각적 구분)이다. 후각적 각인(olfactory imprinting)을 통한 homing을 처음으로 주장한 것은 Hasler와 Wisby (1951)였으며, 이들의 주장에는 주요한 3가지 가정이 있었으며, 그것은 다음과 같다: (1) 여러 stream의 화학적 특징은 다르며, 그것은 일정 시간 동안 안정을 유지한다. (2) 연어는 이런 차이를 구분할 수 있다. (3) 바다로 migration하는 동안이나 그 이전에 이런 화학적 차이를 배운다. 후각적 각인에 있어서 중요한 역할을 하는 것은 호르몬의 작용이므로, 연어가 2년생 연어가 바다로 나가는 단계 - 동안 후각적 각인을 하며 이때 다양한 화학적 차이를 인식하는 것이 연구를 통해 밝혀졌는데, 최근 일부 종(Kokanee, non-anadromous한 형태 중 하나)의 경우 PST 이전에 후각적 각인이 일어나기도 한다고 보고 되었다. 이 후각적 화학적 차이를 인식하는 역할은 특히 갑상선 호르몬 중 하나인 티록신으로 발현된다. 부화장의 실험을 통해 신우와 같은 중요한 사실을 알게 되었지만, 실제 야생 생물의 연어에 이와 같은 문제가 존재한다. 그 문제는 다음과 같다: (1) 실제 환경은 지속적으로 변화하며, (2) 다양한 water source가 있고, (3) 연어의 종의 다양하다. 실험을 통해 같은 종인 coho salmon에서 이런 차이로 발견되는데, 부화장에서 길러진 coho salmon은 PST 기간동안 후각적 각인이 일어난 반면, 야생의 coho salmon은 PST기간 이전에 후각적 각인이 일어났다. 또한 최근의 연어는 단일의 후각적 각인이 아닌 series 형태로 후각적 각인을 하기 때문에, 상황에 따라 homing의 장소(태어난 곳, 자란 곳)를 변경하기도 한다. 모델에 후각적 각인
과 갑상선 호르몬과의 관계를 적용하여 살펴본 결과 야생 연어의 호르몬 변화는 불규칙적으로 나타났으며, 태어난 지 얼마 안된 시기에도 후각적 각인이 일어날 만큼의 충분한 갑상선 호르몬이 분비되는 것을 볼 수 있었다. 이러한 변화는 야생에 존재하는 다양한 환경적 요인(다양한 물의 흐름, 수온, 화학적 조성 등)이 이런 호르몬의 분비를 촉진했기 때문으로 생각된다.

Homing은 연어의 진화적인 측면에도 영향을 준다. 그 예로 같은 종의 sockeye salmon의 알의 크기가 알을 낳는 기층이 모래와 같이 가는 잎자의 경우 자갈과 같은 거친 잎자의 기층에 비해 그 크기가 작은 것을 관찰할 수 있다. 또한 homing과정의 복합적 작용과 서식지의 상태, 생식을 위한 잎의 수, 성내의 경쟁 등이 생태학적으로 연어의 생식의 성공을 변동시키게 된다.