Evolutionary Ecology of Life Span: Lessons from the Rockfish

Marc Mangel
University of California
Santa Cruz, Ca 95064
Longevity in fish

• Long life  15-50 years

• Extremely long life  >50 years
And there are Methusaleh fish

¥ Spur dogfish (*Squalus acanthias*), an elasmobranch, lives to 60 years at a size of 1 m.

¥ Beluga sturgeon (*Husa Husa*) up to 118 years, 5 m length

¥ White sturgeon (*Acipenser transmontanus*) to 100 years

¥ Icelandic-Norwegian herring (*Clupea harengus*) lives to 30 years, rarely exceeding 35 cm. Tropical clupeids live 3-5 years.
The Rockfish are an Remarkable for their Longevity

Maximum Longevity in 46 species of fishes in the family Scorpaenidae
The Rockfish are "Overage" for their length

Fig. 2. Maximum recorded length and maximum recorded age for Sebastes spp., in comparison with other northeast Pacific fishes.
Organisms are complex adaptive systems: a genetic program responding to environmental cues.

The tools for the analysis of such systems are

- Non-linear dynamics
- Stochastic processes
- Optimization
“Just what the hell is a Lagrange multiplier anyway?”

Anonymous comment found above a urinal in a bar in Faro, Portugal during the April 1979 NATO Advanced Research Workshop on Search Theory
Working hypothesis

Life span cannot be divorced from environment because the environment sets the selective forces acting on life span

Approaches

Ultimate perspective

Proximate perspective
Reproductive Life Span and Variation in Spawning Success

Living a Long Life in the North East Pacific Ocean
is not easy….Short-lived fish have a tough time of it
Characterizing the Life History of Fish

Von Bertalanffy Growth

\[ L(t) = L_4 \left( 1 - \exp\left( -k(t - t_0) \right) \right) \]

Parameters are

- Asymptotic size
- Growth rate
- Size at age 0
Additional parameters

Maximum life span $A_{\text{max}}$

Mortality rate $M$ (constant over age)

“Life history invariants”

$k \ A_{\text{max}} \sim 3.5$ (CV 28%)

$M \sim 1.14 \ k$ (CV 42%)
Temperature or Food?

¥Feeding has a powerful effect on

Asymptotic size

Size at maturity

¥Temperature has a powerful effect on

Rate of growth

Rate of living

Age at maturity
Temperature dependence of asymptotic length and growth rate in desert pupfish (Cyprinodon macularias)

(Kinne, O. 1960. Physiological Zoology 33:288)
Walleye asymptotic size and size at maturity as a function of temperature
Population Growth in an Environment with Decadal Long Regimes

- Environment in one of two states (good/bad)

\[ \Pr\{E(t+1) = j \mid E(t) = i\} = p_{ij} \]

- Asymptotic size determined by the environment

\[ L(t + 1) = L(t) \exp(-k) + L_4(E(t))(1 - \exp(-k)) \]
• “Gonadal accumulation” hypothesis: fish accumulate resources for reproduction when the environment allows it.

• Reproduction occurs when accumulated gonadal tissues exceeds a threshold value, which could be 0.

\[
G(t + 1) = G(t) + 0.03A(L(t))^B(1 - \varepsilon \frac{k}{k_{max}})
\]
Population Dynamics Model

\[ N(t+1,a+1) = N(t,a) \exp(-M) \]

\[ N(t,0) = s_e(E(t)) \sum_{a=1}^{3} \frac{G(t,a)}{w_0} \left(1 - \frac{G_{thr}}{G(t,a)}\right) N(t,a) \]

Fitness measure: Geometric Mean Growth Rate
(\(= \exp(a)\))
Persistence is not Possible with Short Life Span
Proximate Perspective: Trade-offs in Behavioral Ecology

- Predation risk-starvation risk


- Rapid growth and
  Mature function
  Somatic development
  Immune function
  Resistance to physiological stressors

We've got to go after aging itself — Jay Ohlshansky (14 May 01)

**Working Hypothesis**

There is a trade-off between metabolic rate (rapid growth) and internal damage due to oxidative processes.

This trade-off shapes life span.
The Sources and Cellular Response to Reactive Oxygen Species

“Metabolic Choice” and Life Span

Dissecting von Bertalanffy Growth

Weight and Length Allometrically Related

\[ W(t) = L(t)^3 \]

Change in Weight is a Balance of Anabolic and Catabolic Factors

\[ W(t+1) - W(t) = aY[O_2]L(t)^2 - ma[O_2]L(t)^3 \]

So Length Dynamics Become

\[ L(t+1) = \left\{ L(t)^3 + aY[O_2]L(t)^2 - ma[O_2]L(t)^3 \right\}^{1/3} \]
Structural Assumption about Maturity

• Mature once size is 60% of asymptotic size (another Beverton data mining result)

• Reproduction allometrically related to size once the threshold size is passed
Additional State Variable

\[ D(t) = \text{Oxidative damage accumulated to age } t \]

Dynamics of Damage: Juvenile Fish

\[ D(t + 1) = D(t) + \kappa ma[O_2]L(t)^3 \]

Dynamics of Damage: Adult Fish

\[ D(t + 1) = D(t) + \kappa ma[O_2]l^3 + \kappa r Al^B \]

Oxygen consumption rates

46.7 \( W^{.75} \) ml \( O_2/hr \) non-gestating fish

62.4 \( W^{.90} \) ml \( O_2/hr \) gestating fish
Survival depends upon both size \((l)\) and damage \((d)\)

\[
\text{Prob\{survive to age } t+1\} = s(l,d) = \exp\{-\mu/l\} \exp\{- (d/d_c)\}^2
\]

Bigger size is better  
Slower growth is better
Lifespan Determined by the One in Ten Million Fish

- "Predation dominates damage"
- "Neither dominant"
- "Damage dominates predation"
What Pattern of Oxygen Use Maximizes the Long-Term Number of Descendants?

\[ F_J(l,d,t) = \text{Maximum long-term number of descendants given } L(t) = l < L_{rep} \text{ and } D(t) = d \]

\[ F_A(l,d,t) = \text{Maximum long-term number of descendants, given } L(t) = l > L_{rep} \text{ and } D(t) = d \]

These are evaluated by the method of stochastic dynamic programming (of which classic life history theory and Euler-Lotka equations are a special case).

For juveniles if next size is less than \( L_{\text{rep}} \):

\[
F_J(l,d,t) = \max_a s(l,d) F_J(l'(a),d'(a),t+1)
\]

If next size is larger than \( L_{\text{rep}} \)

\[
F_J(l,d,t) = \max_a s(l,d) F_A(l'(a),d'(a),t+1)
\]

For adults

\[
F_A(l,d,t) = \max_a \{ R(l) + s(l,d)F_A(l'(a),d'(a),t+1) \}
\]
Predicted Pattern of Metabolic Choice
Associated Size and Survival Curves

Life span of the 1 in 10 million fish is 57 years
Some Comments

• “Theoretical” rather than “Calculational” Models

  Temperature, food and oxygen profiles

• Density dependent growth

Red Grouper in the Gulf of Mexico

<table>
<thead>
<tr>
<th></th>
<th>$L_{inf}$</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979-81</td>
<td>78.9 cm</td>
<td>0.18</td>
</tr>
<tr>
<td>1991-92</td>
<td>92.6 cm</td>
<td>0.16</td>
</tr>
</tbody>
</table>

• Offspring quality explicitly