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Residualization and Maturation versus Smolting Factors for *O. mykiss* Parr

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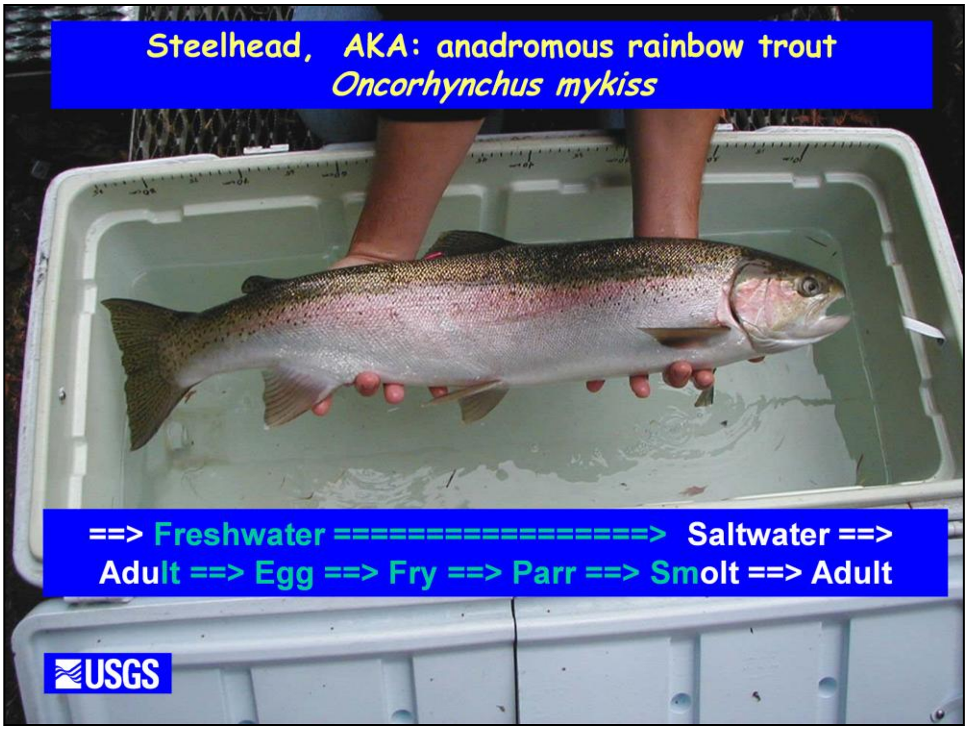
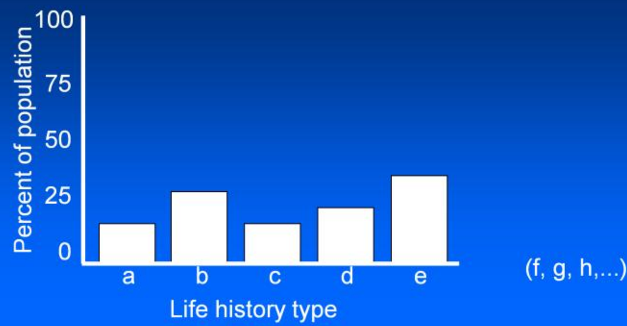


•The star of the show in the Wind River is the steelhead, AKA anadromous rainbow trout.

•It was listed as “Threatened” in 1998, and remains so today.

•For those new to steelhead biology, I put some of the common-use words we use to describe the life history stages of this critter, with the developmental stages from egg to fry to parr taking place in freshwater, when they then undergo a huge physiological change or “smolting” associated with preparing for 1 to several years in saltwater.



N = 32 (Thorpe 2007)

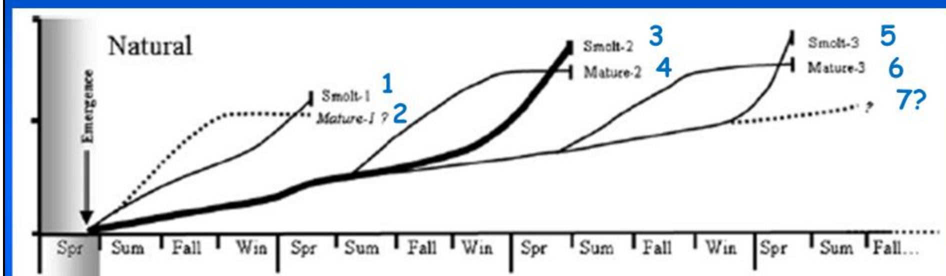
Some *O. mykiss*: Life history types

a = Resident, never smolt
b = Rear in natal area until smolting
c = Rear in natal area for 2 yrs, emigrate
d = Rear in natal area for 1 yr, emigrate
e = Rear in natal area less than one year

… Like Chinook on steroids!

Typical juvenile life history trajectories in the Pacific Northwest

Showing *n* = 6+ trajectories



n = 3 maturation ages + (3 smolt ages x 3 salt years per smolt age) = 27

N = 32 (Thorpe 2007)

Modified graph from: Berejikian et al. (2011)

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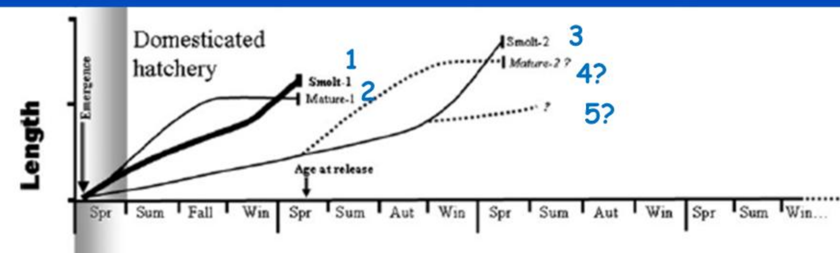
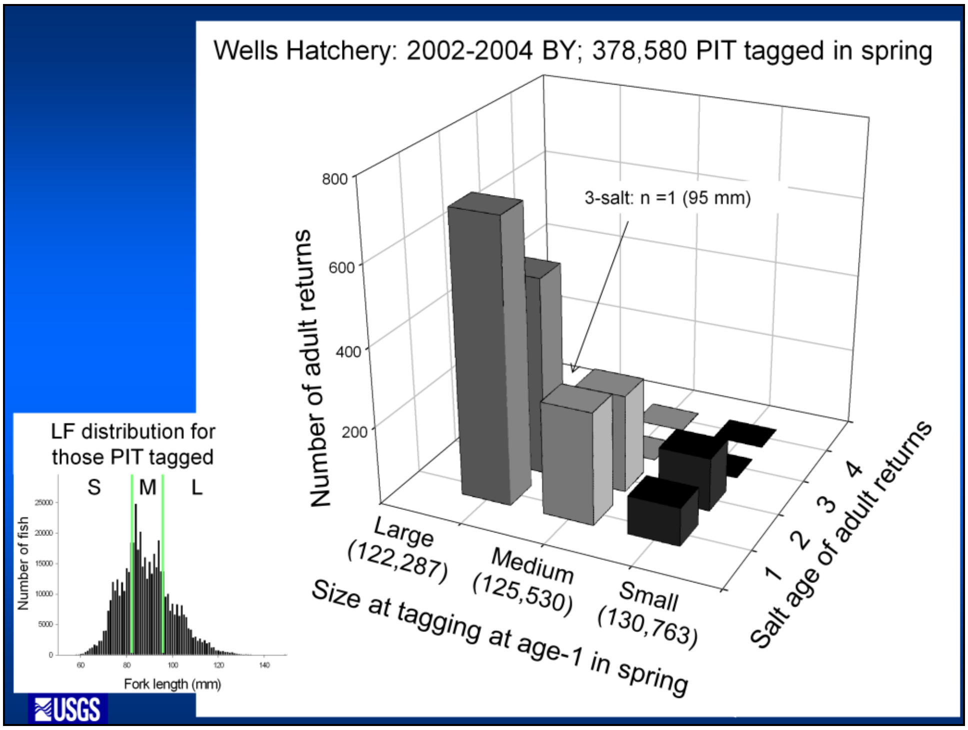
Typical juvenile life history trajectories in a hatchery



Modified graph from: Berejikian et al. (2011)



Wells Hatchery: 2002-2004 BY; 378,580 PIT tagged in spring
3-salt: n =1 (95 mm)
Number of adult returns
800
600
400
200
Large (122,287)
Medium (125,530)
Small (130,763)
Size at tagging at age-1 in spring
1 2 3 4
Salt age of adult returns
LF distribution for those PIT tagged
S M L
Number of fish
Fork length (mm)
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A Case of Differential Mortality, with Larger Smolts Surviving Better?

Or is it a Function of Growth, Developmental Switches, and the Energy Budget?

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Effects of Fish Size, Temperature, and Limited Food on Lipid Stores of Age-0 Steelhead

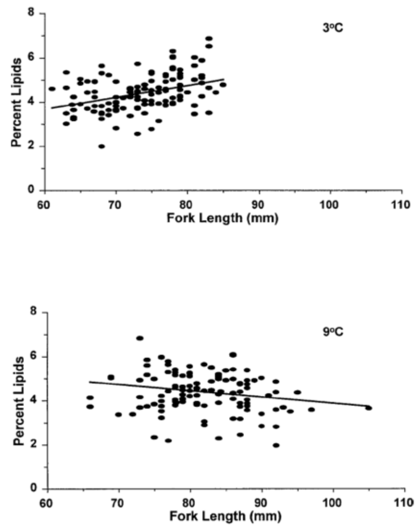
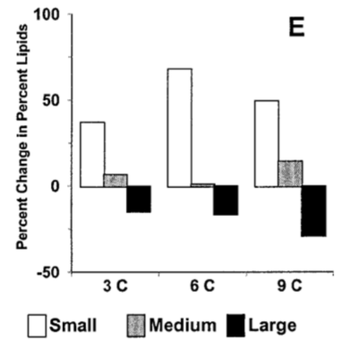


FIGURE 2.—Relationship between percent lipid content (based on wet weight) and fork length for juvenile steelhead (three size-classes combined) held at water temperatures of 3°C ($N = 122$; upper panel) and 9°C ($N = 115$; lower panel) over a 111-d period. Lines are linear regressions for each treatment (3°C: slope = 0.053, y-intercept = 0.522, $r^2 = 0.135$, $P < 0.001$; 9°C: slope = −0.029, y-intercept = 6.747, $r^2 = 0.046$, $P = 0.021$).

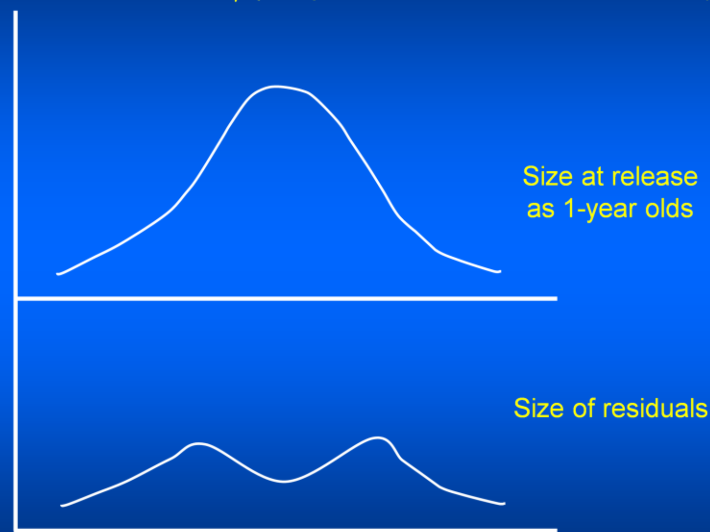
Which fish are more ready for the rigors of their first winter?



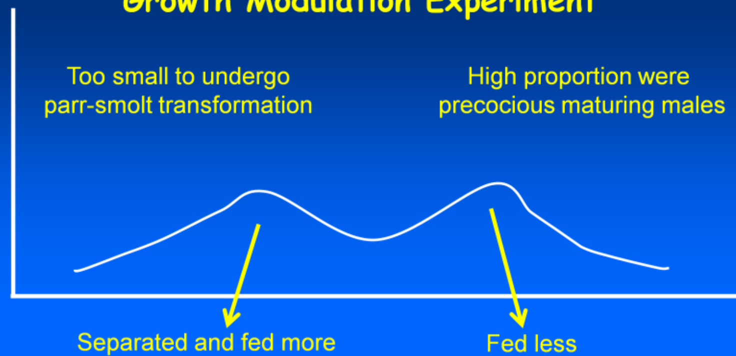
From: Connolly and Petersen (2003)

Size at Release and Residualism

O. mykiss in Kalama Falls Hatchery (Sharpe et al. 2007; NAJFM 27:1355-1368)



Growth Modulation Experiment



Reduced residualism; Increased smoling

No change in residualism

Caveat: "Additional study is needed to determine whether earlier, more protracted rearing on a restricted diet would decrease residualism among large fish."

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Continued: Sharpe et al. (2007)

Developmental Switches in Atlantic Salmon

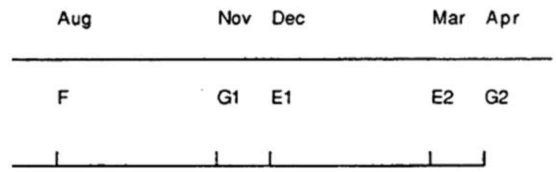

Table 4. The developmental switches in the model of Atlantic salmon

Developmental Switch	Date	Description
F	1 August	Whether to feed ($F = 1$) or to become anorexic ($F = 0$) during the winter months
$G1$	1 November	Whether to continue gonad ($G1 = 1$) growth or to switch it off ($G1 = 0$)
$E1$	1 December	Whether to initiate developments for emigration ($E1 = 1$) the next spring or not ($E1 = 0$)
$E2$	1 March	Whether to continue developments for emigration ($E2 = 1$) or to abort preparations ($E2 = 0$)
$G2$	1 April	Whether to continue advanced gonad growth ($G2 = 1$) or to abort ($G2=0$)

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Modified from: Mangel (1994)

Developmental Switches in Steelhead (California)

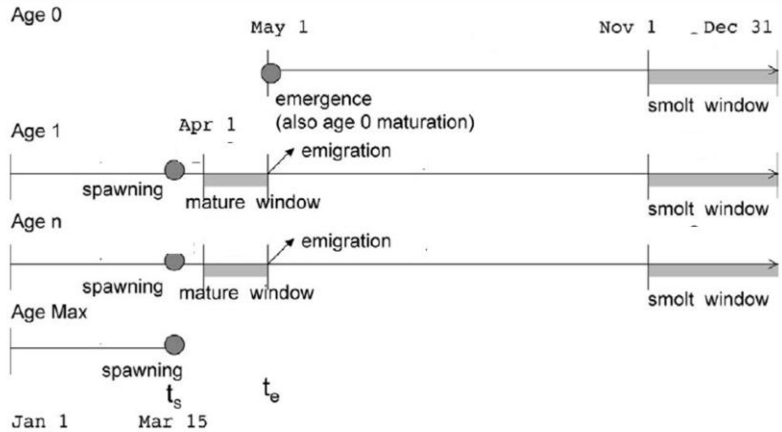

FIGURE 1.—Timeline of the model of steelhead life history. The intervals are designated according to their corresponding survival rates (s_p), as described in the appendix.

Modified figure from: Satterthwaite et al. (2009)

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The Energy Budget:

Growth = Consumption - Respiration – Waste

Consumption = Cmax · *p* · *f* (T)

$Cmax = CA \cdot Weight^{CB}$

p = proportion of maximum consumption

T = temperature

$f(T) = K_A \cdot K_B$

$K_A = (CK1 \cdot L1) / (1 + CK1 \cdot (L1 - 1))$

$L1 = e^{(G1 \cdot (T - CQ)}$

$$G1 = \frac{1}{(CTO - CQ)} \cdot \ln\frac{(0.98 \cdot (1 - CK1))}{(CK1 \cdot 0.02)}$$

$K_B = (CK4 \cdot L2) / (1 + CK4 \cdot (L2 - 1)$

$L2 = e^{(G2 \cdot (CTL - T))}$

$$G2 = \frac{1}{(CTL - CTM)} \cdot \ln\frac{(0.98 \cdot (1 - CK4))}{(CK4 \cdot 0.02)}$$

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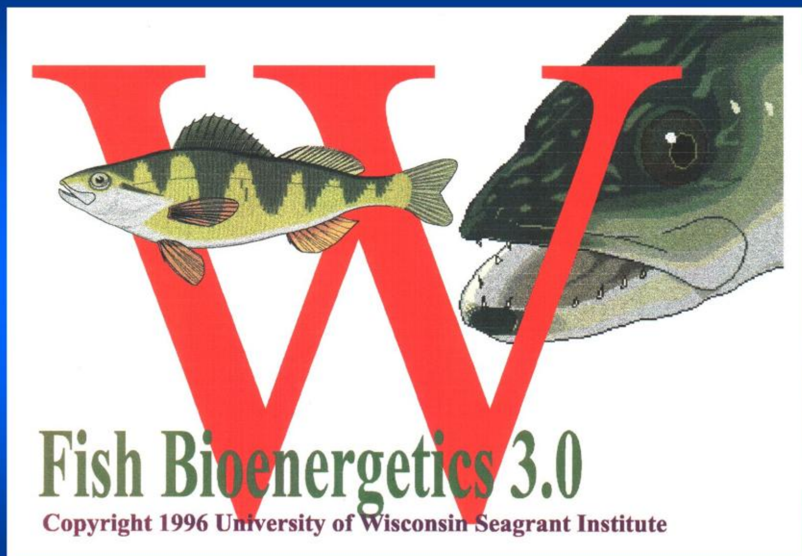
The Energy Budget



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Growth = Consumption - Respiration – Waste

Bioenergetics modeling—Primary inputs:

Temperature (constant or variable)

Diet (caloric value)

Food acquisition (% of maximum)

Activity (e.g., swim needs for position and food)

Metabolic rate (effects food demand)

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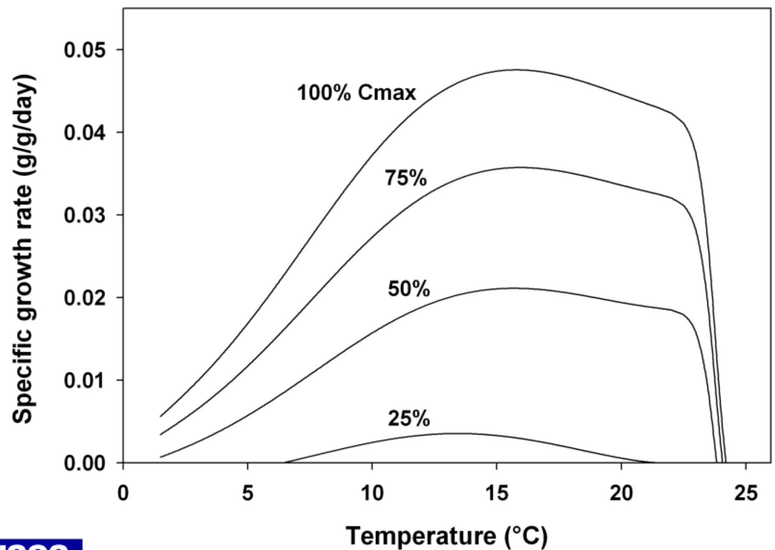
Bioenergetics Parameter values for *O. mykiss*

Species	Steelhead	
Latin name	*Oncorhynchus mykiss*	
age	Adult	Age-1
Source	Rand et al. 1993	Railsback and Rose 1999
CONSUMPTION		
Equation	3	3
CA	0.628	0.628
CB	-0.3	-0.3
CQ	5	3.5
CTO	20	25.0
CTM	20	22.5
CTL	24	24.3
CK1	0.33	0.2
CK4	0.2	0.2
RESPIRATION		
Equation	1	2
RA	0.00264	0.013
RB	-0.217	-0.217
RQ	0.06818	2.2
RTO	0.0234	22.0
RTM	0	26.0
RTL	25	0
RK1	1	0
RK4	0.13	
ACT	9.7	1.3
BACT	0.0405	0.0405
SDA	0.172	0.172
EGESTION/EXCRETION		
Equation	3	3
FA	0.212	0.212
FB	-0.222	-0.222
FG	0.631	0.631
UA	0.0314	0.0314
UB	0.58	0.58
UG	-0.299	-0.299
PREDATOR ENERGY DENSITY		
Equation	2	2
Energy density	*	*
Alpha 1	5764	5764
Beta 1	0.9862	0.9862
Cutoff	4000	4000
Alpha 2	7602	7602
Beta 2	0.5266	0.5266

Effects of Feeding Success (% Cmax) and Temperature on Growth Rate of Age-1 Steelhead



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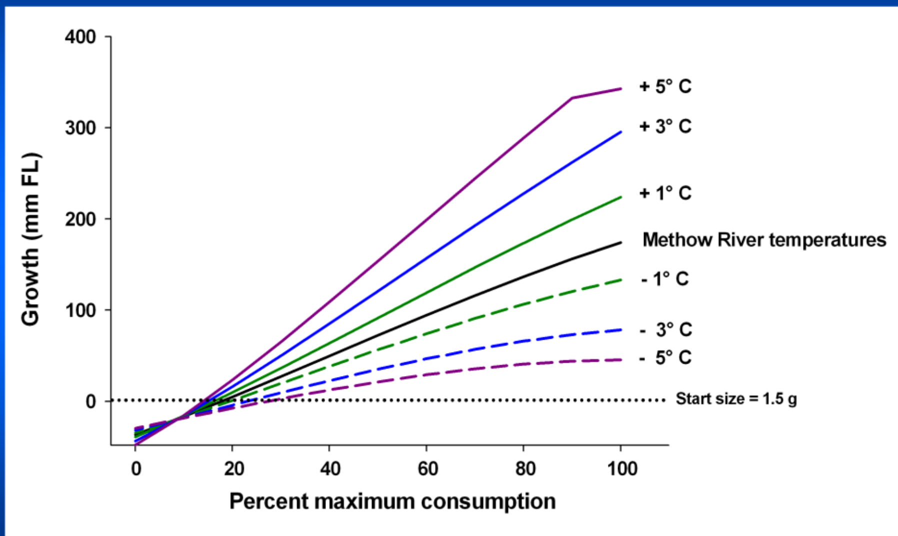
Effects of Feeding Success (% Cmax) and Water Temperature on First-Year Growth of Age-0 Steelhead



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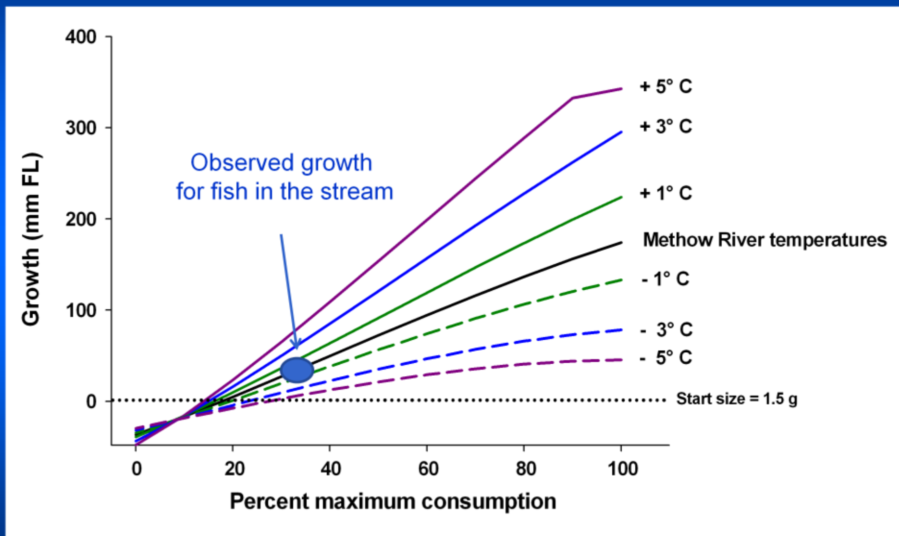
Effects of Feeding Success (% Cmax) and Water Temperature on First-Year Growth of Age-0 Steelhead



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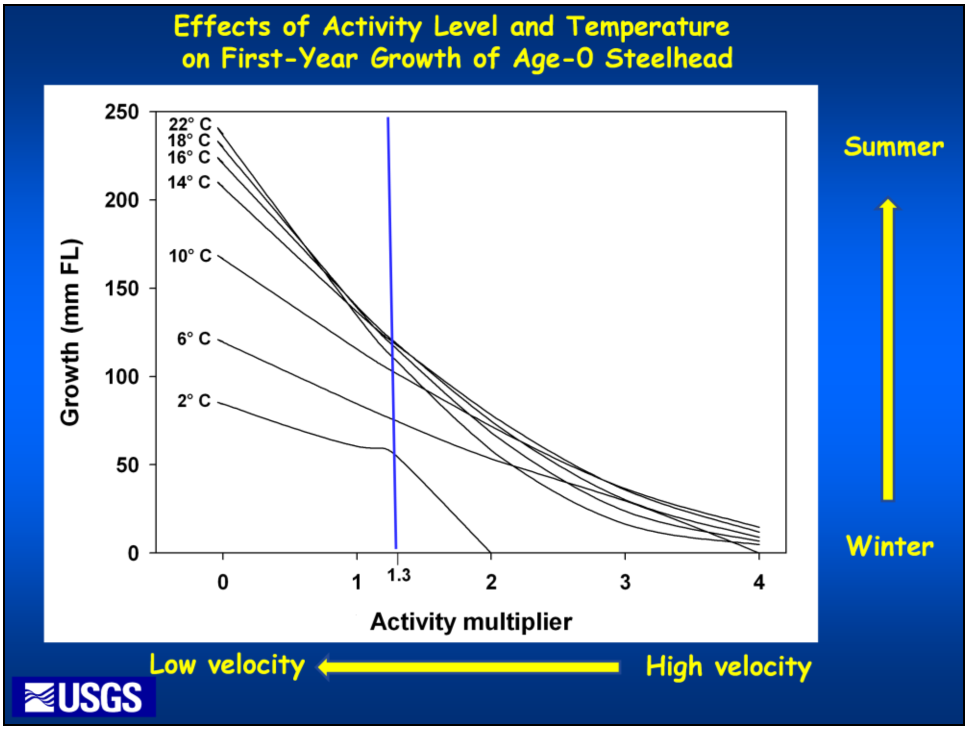

Effects of Activity Level and Temperature on First-Year Growth of Age-0 Steelhead
Growth (mm FL)
250
200
150
100
50
0
22° C
18° C
16° C
14° C
10° C
6° C
2° C
0
1
1.3
2
3
4
Activity multiplier
Summer
Winter
Low velocity
High velocity
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Concept: Smolting as a stream's failure to meet a fish's trophic and reproductive requirements

Benefit of migration (vertical axis):
- ↑ growth
- ↑ survival
- ↑ fecundity

Cost of migration (horizontal axis):
- ↓ survival
- ↑ age at maturity

Benefit \ Cost	Low	High
High	Steelhead (when not met)	??
Low	??	Non-anadromous rainbow trout (when met)

Derived from: Thorpe 1994; Hendry et al. 2004

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Conclusion about the difficulty of a hatchery manager's plight to amplify the steelhead life history

To be successful, a hatchery must negotiate through a complex web of variation in fish response to rearing conditions in hopes of limiting life history expression to a limited array of combinations of fresh-water and salt-water age.

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Integration of Bioenergetic Components

Thorpe 2007 (Marine Ecology Progress Series 335:285-288):
"… fish will mature if the rate of acquisition of surplus energy during a critical period exceeds a genetically determined threshold."

Mangel and Satterthwiate 2008 (Bulletin of Marine Science 83:107-130):
"… water flows-which affect metabolic gains through the availability of drift and metabolic costs through the temperature dependence of catabolic processes-will be important determinants of growth (and thus survival) and of whether or not fish smolt after 1, 2, or 3 yrs…"

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Timing of Life History "Decisions"

Beakes et al. 2010 (TAFS 139:1263-1275):
"We speculate that not only are steelhead adopting a life history pathway in the fall, the condition of fish soon after emergence can significantly affect which pathway is adopted…"

Metcalfe et al. 1995 (Animal Behaviour 49:431-436):
"Higher metabolic rates presumably cause a greater proportion of the yolk reserves to be utilized in respiration over a set amount of time, so leading to an earlier requirement for exogenous food."

Suggests that individual variation in metabolic rate, mediated by environmental conditions affecting growth (such as food availability, food acquisition, temperature, and velocity), has much to do with decisions about smolting and residualism.

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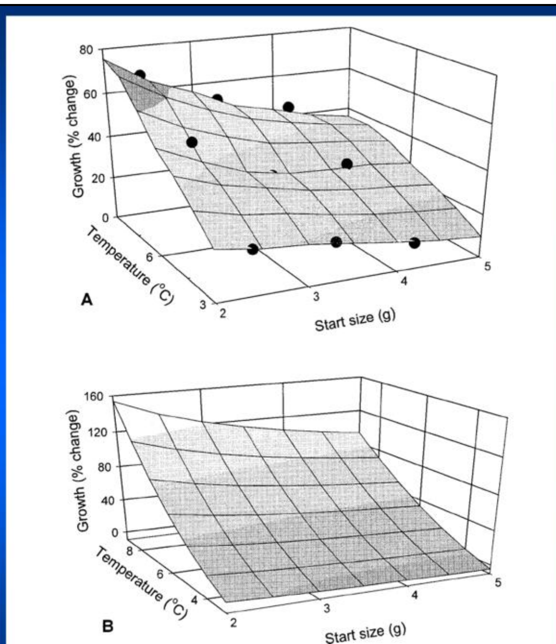


FIGURE 3.—Growth of juvenile steelhead predicted by bioenergetics simulations based on (A) *P*-values fit to laboratory experiments (black circles indicate laboratory results) and (B) *P*-values held constant at 0.170.

From: Connolly and Petersen, 2003

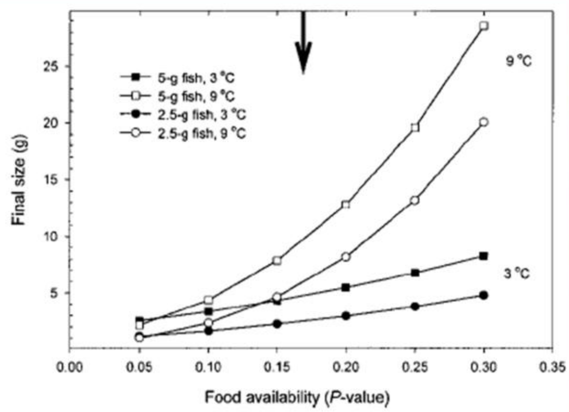


FIGURE 4.—Size predicted at the end of a winter period for small (2.5-g initial size) and large (5-g initial size) juvenile steelhead as a function of food availability (*P*-value) and temperature. Size was predicted with a bioenergetics model simulating fish growth over a 111-d period and was configured to match our laboratory experiments (see text). The vertical arrow is the average *P*-value for laboratory experiments.

From: Connolly and Petersen, 2003

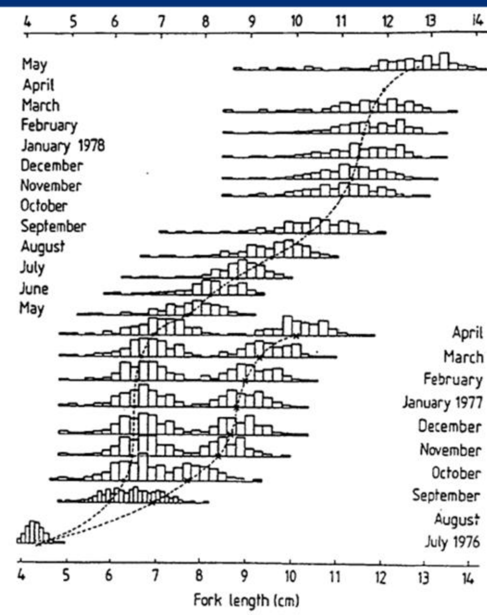
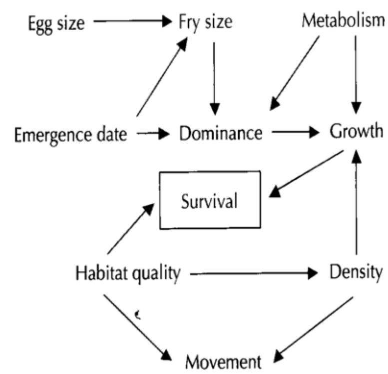


Fig. 1. The development of a bimodal size distribution from a unimodal size distribution of Atlantic salmon siblings. From THORPE *et al.* (1992).

From: Mangel (1994)

Complex and Dependent Interactions

FIGURE 11-9. Diagrammatic representation of some of the factors influencing movement, growth, and survival of juvenile salmonids in streams.



From Quinn 2005

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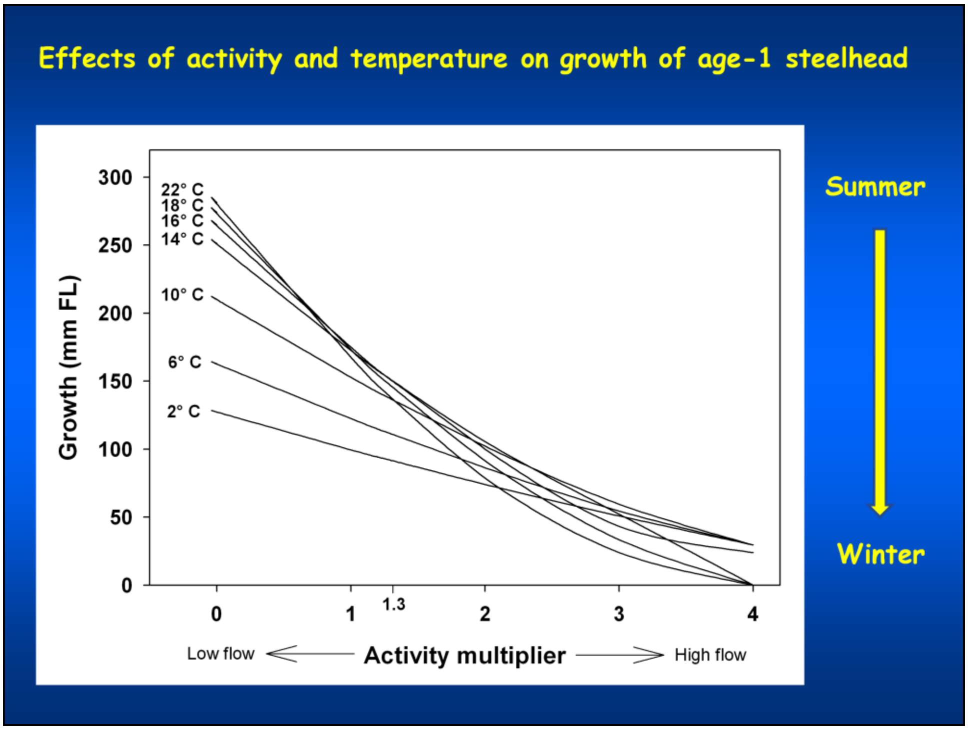

Effects of activity and temperature on growth of age-1 steelhead
Summer
Winter
Growth (mm FL)
300
250
200
150
100
50
0
22° C
18° C
16° C
14° C
10° C
6° C
2° C
0
1
1.3
2
3
4
Low flow
Activity multiplier
High flow

Differences in Expression of Life History in *O. mykiss* in Near-by Watersheds

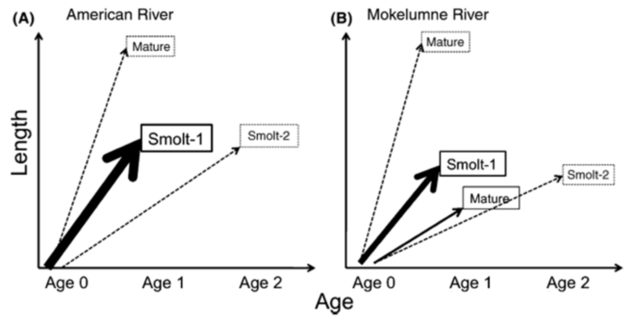

Figure 8 Predicted life histories as a function of size at age on the American (A) and Mokelumne (B) Rivers. Solid lines represent growth trajectories (with within year variability smoothed out) observed in the field, broken lines are outside the range of currently observed variability. The thicknesses of solid lines correspond to the proportion of fish following each trajectory. Smolt ages are at time of emigration.

From: Satterthwaite et al. (2009)

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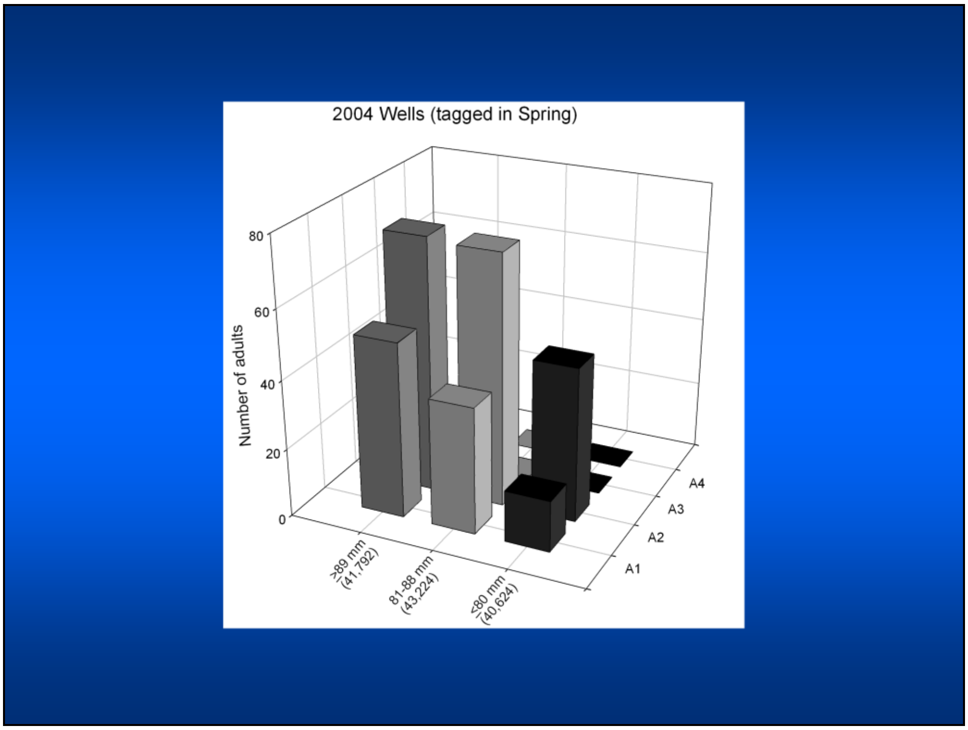
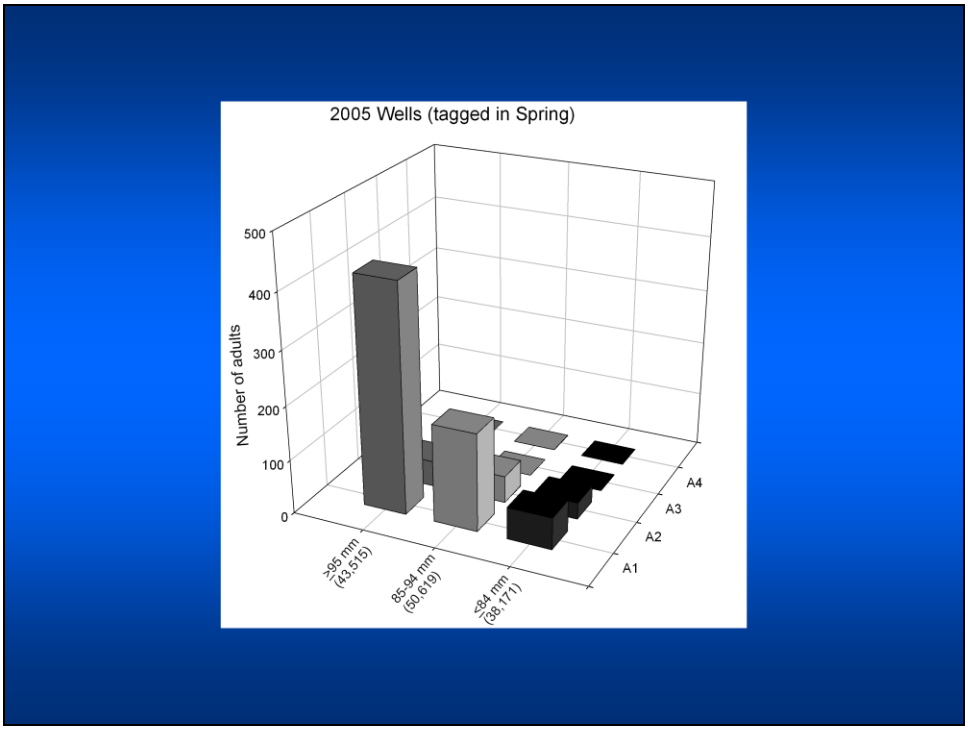
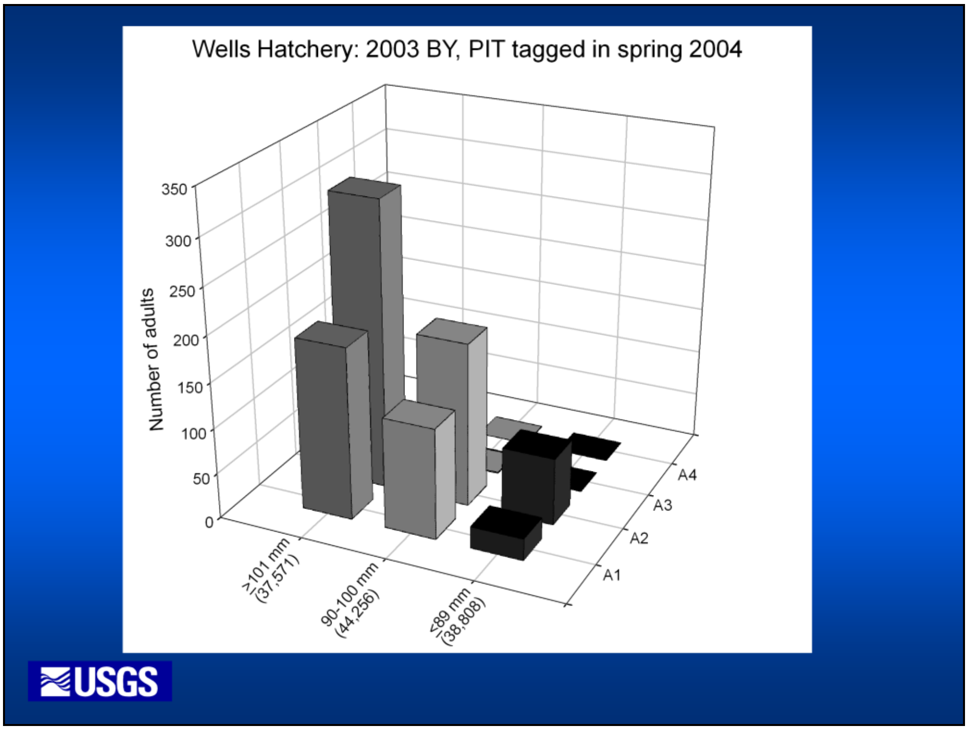
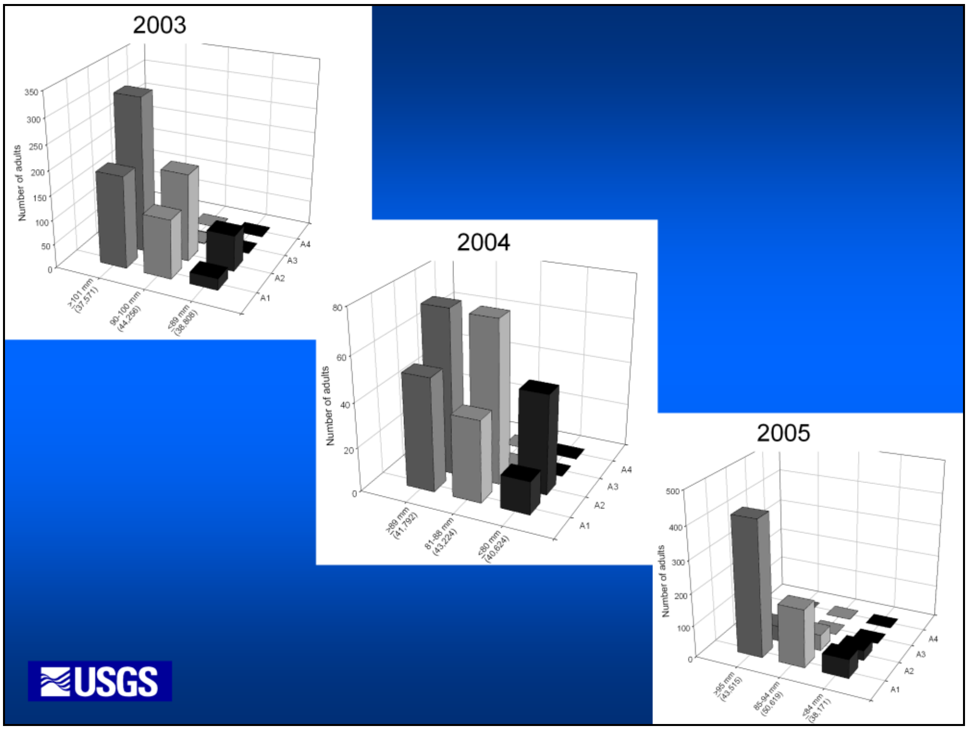

2004 Wells (tagged in Spring)
Number of adults
80
60
40
20
0
>89 mm
(41,792)
81-88 mm
(43,224)
<80 mm
(40,624)
A1
A2
A3
A4


2005 Wells (tagged in Spring)
Number of adults
500
400
300
200
100
0
≥95 mm (43,515)
85-94 mm (50,619)
≤84 mm (38,171)
A1
A2
A3
A4



Wells Hatchery: 2003 BY, PIT tagged in spring 2004
Number of adults
350
300
250
200
150
100
50
0
>101 mm
(37,571)
90-100 mm
(44,256)
<89 mm
(38,808)
A1
A2
A3
A4
USGS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