Ectotherms in Changing Environments: Working in Pasteur’s Quadrant
Marc Mangel, UCSC
Ectotherms in Changing Environments: Working in Pasteur’s Quadrant
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Kate Cresswell

John Wiedenman

George Watters (NMFS)

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Santiago Salinas
Steve Munch
Working in Pasteur’s Quadrant
Working in Pasteur’s Quadrant

Quest for fundamental understanding?
Working in Pasteur’s Quadrant

Considerations of use?

Quest for fundamental understanding?
Working in Pasteur’s Quadrant

Considerations of use?

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Quest for fundamental understanding?
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Wednesday, May 1, 13
### Working in Pasteur’s Quadrant

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# Working in Pasteur’s Quadrant

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Use-Inspired Basic Research Is Central

- Improved understanding
- Improved technology

Pure basic research → Use-inspired basic research

- Existing understanding
- Purely applied research and development

Existing technology

Wednesday, May 1, 13
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Wednesday, May 1, 13
How will changing environments affect biomass of krill available for predators and what does this mean for krill fishery management?

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Will water policies designed to protect chinkook salmon lead to the loss of anadromy in steelhead?

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Considerations of use?

Yes

No

Quest for fundamental understanding?

Yes

No

Wednesday, May 1, 13
How will changing environments affect the population dynamics of parasitoids and hosts in biological control?

Considerations of use?

Yes

Quest for fundamental understanding?

Yes

No

No
Temperature Dependent Growth Curves Link These Three Disparate Species
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Atkinson et al. 2008. L&O
51:973-987
Temperature Dependent Growth Curves Link These Three Disparate Species

Atkinson et al. 2008. L&O 51:973-987

Thornton and Lessem. 1978. TAFS 107: 284-287
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Temperature Dependent Growth Curves Link These Three Disparate Species

\[ \Omega(T | g, d) = d(T - T_L)(1 - e^{g(T - T_u)}) \]

Atkinson et al. 2008. L&O 51:973-987

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Temperature Dependent Growth Curves Link These Three Disparate Species

\[ \Omega = \frac{d}{T - T_L} \left(1 - e^{g(T - T_u)}\right) \]

Changing environments
- Warming
- More frequent extreme events
- Ocean acidification

Atkinson et al. 2008. L&O 51:973-987

Thorton and Lessem. 1978. TAFS 107: 284-287


Wednesday, May 1, 13
Models Are Essential Tools
**How will changing environments affect biomass of krill available for predators and what does this mean for krill fishery management?**

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*Image of krill*
Antarctic Krill (*Euphausia superba*)

Southern Ocean Food Web

Distribution in the Southern Ocean

Atkinson et al. 2004
## Enormous biomass

<table>
<thead>
<tr>
<th>Category</th>
<th>Amount</th>
<th>Year</th>
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<tbody>
<tr>
<td>Nets</td>
<td>135-1350 million tonnes</td>
<td>(1986)</td>
</tr>
<tr>
<td>Primary production</td>
<td>100-500 millions tonnes</td>
<td>(1986-87)</td>
</tr>
<tr>
<td>Predator requirements</td>
<td>470 million tonnes</td>
<td>(1988)</td>
</tr>
<tr>
<td>Larval krill abundance</td>
<td>75 million tonnes</td>
<td>(1990)</td>
</tr>
<tr>
<td>Nets</td>
<td>38.6 million tonnes</td>
<td>(2004)</td>
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_Human biomass ~ 20 million tonnes (US) to 600 million tonnes (world)_
Enormous biomass

Nets 135-1350 million tonnes (1986)
Primary production 100-500 millions tonnes (1986-87)
Predator requirements 470 million tonnes (1988)
Larval krill abundance 75 million tonnes (1990)
Nets 38.6 million tonnes (2004)

Human biomass ~ 20 million tonnes (US) to 600 million tonnes (world)

...and patchy distribution
But biomass fluctuates and when there are few krill around predators do badly.

Krill have “Episodic Reproduction”
The Krill Fishery

Aquaculture feed

human food

oil
The Krill Fishery

Aquaculture feed

human food

Effects on Quality of Life

Fish oil 3g/day

NKO 1.0-1.5g/day

[chart showing percent change in various quality of life metrics]
The Krill Fishery

Aquaculture feed

“30-200 Million tonnes potential” (Mauchline 1980)

human food

Effect on Quality of Life

Wednesday, May 1, 13
**The Krill Fishery**

Aquaculture feed

human food

“30-200 Million tonnes potential” (Mauchline 1980)
Krill Fisheries are Managed by the Commission for the Conservation of Antarctic Marine Living Resources
Krill Fisheries are Managed by the Commission for the Conservation of Antarctic Marine Living Resources

Minimize by-catch
Krill Fisheries are Managed by the Commission for the Conservation of Antarctic Marine Living Resources

Minimize by-catch

Account for indirect effects on krill-dependent species
How Much Krill is Obtained from Foraging and How Does Climate Change Affect It?: A Biomass Per Recruit Model with Two Twists

Atkinson et al. 2006
How Much Krill is Obtained from Foraging and How Does Climate Change Affect It?: A Biomass Per Recruit Model with Two Twists

• Compute biomass consumed by predators, not taken by the fishery
How Much Krill is Obtained from Foraging and How Does Climate Change Affect It?: A Biomass Per Recruit Model with Two Twists

- Compute biomass consumed by predators, not taken by the fishery
- Growth is temperature dependent
How Much Krill is Obtained from Foraging and How Does Climate Change Affect It?: A Biomass Per Recruit Model with Two Twists

- Compute biomass consumed by predators, not taken by the fishery
- Growth is temperature dependent

![Graph showing growth increment vs. temperature with temperatures of -2°C to 5°C and biomass sizes of 30 mm and 50 mm.](image)

Atkinson et al. 2006
How Much Krill is Obtained from Foraging and How Does Climate Change Affect It?: A Biomass Per Recruit Model with Two Twists

- Compute biomass consumed by predators, not taken by the fishery
- Growth is temperature dependent
- A retrospective story

![Growth vs Temperature Graph](image)

Atkinson et al. 2006
Fishery Model: Biomass Per Recruit

von Bertalanffy Growth Model
Fishery Model: Biomass Per Recruit

von Bertalanffy Growth Model

\[ L(a + 1) = L_\infty (1 - e^{-k}) + L(a)e^{-k} \]
Fishery Model: Biomass Per Recruit

von Bertalanffy Growth Model

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\[ L(a + 1) = L_\infty (1 - e^{-k}) + L(a)e^{-k} = L(a) + (L_\infty - L(a))(1 - e^{-k}) \]
Fishery Model: Biomass Per Recruit

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\[ W(a) = c_1L(a)^{c_2} \]
Fishery Model: Biomass Per Recruit

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Survival Model
Fishery Model: Biomass Per Recruit

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Survival Model

\[ M(a) = m_0 + \frac{m_1}{L(a)} + m_2 L(a) \]
Fishery Model: Biomass Per Recruit

von Bertalanffy Growth Model

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\[ W(a) = c_1 L(a)^{c_2} \]

Survival Model

\[ M(a) = m_0 + \frac{m_1}{L(a)} + m_2 L(a) \]

\[ S(0) = 1 \]

\[ S(a + 1) = S(a)e^{-M(a) - \sigma_F(a)F} \]
Fishery Model: Biomass Per Recruit

\[
BPR(F \mid M, \sigma_F(a)) = \sum_{a=0}^{\infty} W(a)S(a)
\]
Fishery Model: Biomass Per Recruit

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Temperature Data from WOD (1970-2004)

Summer SST

Atkinson et al. 2008

Estimate BPR for individual cohorts from this time period for the Antarctic Peninsula and South Georgia
Temperature Data from WOD (1970-2004)

Summer SST

Estimate BPR for individual cohorts from this time period for the Antarctic Peninsula and South Georgia
Average annual temperatures experienced by krill

World Ocean Database (http://www.nodc.noaa.gov/OC5/WOD05/pr_wod05.html)
The Main Result
The Main Result

Wiedenmann et al. 2008
The Main Result

Wiedenmann et al. 2008
The Main Result

Wiedenmann et al. 2008
The Main Result

Biomass per Recruit (BPR) vs. Average Temperature (°C)

Antarctic Peninsula

Biomass per Recruit (mg)

Temperature (°C)

Growth Increment (%)

Wiedenmann et al. 2008

Wednesday, May 1, 13
The Main Result

Average Temperature (°C)

Biomass per Recruit (BPR)

Wiedenmann et al. 2008

Growth Increment (%)

Temperature (°C)

Biomass per Recruit (mg)

Temperature (°C)

Antarctic Peninsula

South Georgia

Wednesday, May 1, 13
Biomass for Predators per Recruited Krill

- South Georgia (constant starting length)
- South Georgia (fluctuating starting length)
- Antarctic Peninsula

Cohort year

Biomass per recruit (mg)
Temperature Fluctuations Require An Adaptive Fishery Policy

Biomass per recruit (mg) vs Fishing mortality (F)

1974, 1996, 1985

Year of cohort birth

Fishing mortality (F)

F = 0.15, 0.35, 0.48

Wednesday, May 1, 13
**Will water policies designed to protect chinkook salmon lead to the loss of anadromy in steelhead?**

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Wednesday, May 1, 13
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Steelhead are an Iteroparous Oncorhynchus

Egg → Parr → mature in freshwater

smolt → Resident / Rainbow

Steelhead (return to spawn in freshwater)

emigrate to ocean
THE SALMON FAMILY TREE

STEELHEAD

PACIFIC SALMON
20 MILLION YEARS AGO
ANCESTRAL SALMON

EXTINCT

SAFER TOOTH

PINK

SOCKEYE

RED

CHINOOK

KING

COHO

SILVER

ATLANTIC SALMON

CUTTHROAT

WESTERN TROUT

MASU

HUMPY
A Tool For Water Management in A Changing Climate

A Tool For Water Management in A Changing Climate


• Release cold water for steelhead in the summer and early fall.
A Tool For Water Management in A Changing Climate


• Release cold water for steelhead in the summer and early fall.

• Release cool water in the late fall for Chinook salmon (*O. tshawytscha*) holding and spawning.

- Release cold water for steelhead in the summer and early fall.

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- Plan: Minimize the amount of the cold water released in summer and early fall, so that more cool water is available for Chinook.

• Release cold water for steelhead in the summer and early fall.

• Release cool water in the late fall for Chinook salmon (*O. tshawytscha*) holding and spawning.

• Plan: Minimize the amount of the cold water released in summer and early fall, so that more cool water is available for Chinook.

• Concern: *Releasing too much cool water in fall may lead to the loss of anadromy in steelhead*
Previous work on the life-history of Atlantic salmon

John Thorpe                       Neil Metcalfe
Felicity Huntingford

Wednesday, May 1, 13
Previous work on the life-history of Atlantic salmon

In juvenile development, maturation in the stream as a resident parr and smolting are mutually exclusive.

The fastest-growing juveniles in a cohort mature as resident parr, the next fastest become smolts, while the slowest remain immature parr in stream for another year.

A decision window occurs in the fall preceding smolting, during which the juvenile salmon decides which pathway to follow.
FRESH WATER:

November: Fertilization
Initiate Maturation

April: Birth
Is state sufficiently
great to complete maturation?

- Yes
  - Continue maturation
    Reproduce in November

- No
  - Inhibit maturation

Mature parr

July
Is state sufficiently great
to survive smolt migration

- Yes
  - Feed over the winter
    Migrate the following May

- No
  - Lose appetite over Winter
    Delay migration

S1 smolt

S2, S3 smolt
We Combine More Complicated Models of Individual Growth To Link Behavior and Growth

Growth Rate = Anabolism - Catabolism
We Combine More Complicated Models of Individual Growth To Link Behavior and Growth

Growth Rate = Anabolism - Catabolism

\[
\frac{dW}{dt} = \Omega(T(t)) fW(t)^c \frac{a(t)}{a(t) + \kappa(t)} - (1 + a(t)) \alpha e^{\beta T(t)} W(t)
\]
We Combine More Complicated Models of Individual Growth To Link Behavior and Growth

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\frac{dW}{dt} = \left( \Omega(T(t)) fW(t)^c \right) \frac{a(t)}{a(t) + \kappa(t)} - (1 + a(t)) \alpha e^{B_T(t)} W(t)
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Growth Rate = Anabolism - Catabolism

\[ \frac{dW}{dt} = \Omega(T(t))fW(t)^c \frac{a(t)}{a(t) + \kappa(t)} - (1 + a(t))\alpha e^{BT(t)} W(t) \]
State Dependent Life History Theory: Patch Selection
State Dependent Life History Theory: Patch Selection

• A central place forager that has a single state: energy reserves
  \[ X(t) = x \]
State Dependent Life History Theory: Patch Selection

• A central place forager that has a single state: energy reserves
  \( X(t) = x \)

• Foraging during a period of length \( T \)
State Dependent Life History Theory: Patch Selection

• A central place forager that has a single state: energy reserves $X(t) = x$

• Foraging during a period of length $T$

• Can visit one of 3 patches
State Dependent Life History Theory: Patch Selection

• A central place forager that has a single state: energy reserves $X(t) = x$

• Foraging during a period of length $T$

• Can visit one of 3 patches

• $F(x,t)$ = maximum expected fitness from time $t$ to $T$, given an organism has $X(t) = x$ reserves
State Dependent Life History Theory: Patch Selection

$\beta_i =$ probability of dying in patch $i$

$\lambda_i =$ probability of finding food in patch $i$

$\alpha_i =$ energetic cost of visiting patch $i$

$G_i =$ energy gain in patch $i$
Terminal fitness function, $\phi(x)$

\[ F(x,T) = \phi(x) = \text{expected future survival or reproduction} \]
The Equation of Stochastic Dynamic Programming
The Equation of Stochastic Dynamic Programming

\[ F(x, t) = \max_i E \{ \phi(X(T)) \mid X(t) = x \} \]
The Equation of Stochastic Dynamic Programming

\[ F(x,t) = \max_i E\{\phi(X(T)) \mid X(t) = x\} \]

At the terminal time

\[ F(x,T) = \phi(x) \]
The Equation of Stochastic Dynamic Programming

\[ F(x,t) = \max_i E \{ \phi(X(T)) \mid X(t) = x \} \]

At the terminal time

\[ F(x,T) = \phi(x) \]

And for previous times

\[ F(x,t - 1) = \max_i (1 - \beta_i) \left[ \lambda_i F(x - \alpha_i + G_i,t) + (1 - \lambda_i) F(x - \alpha_i,t) \right] \]
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The Equation of Stochastic Dynamic Programming

\[ F(x, t) = \max_{i} E \{ \phi(X(T)) \mid X(t) = x \} \]

**At the terminal time**

\[ F(x, T) = \phi(x) \]

**And for previous times**

\[ F(x, t - 1) = \max_{i} (1 - \beta_i) \left[ \lambda_i F(x - \alpha_i + G_i, t) + (1 - \lambda_i) F(x - \alpha_i, t) \right] \]
Optimal patch choice, $i^*(x,t)$

$$F(x,t - 1) = \max_i (1 - \beta_i) \left[ \lambda_i F(x - \alpha_i + G_i, t) + (1 - \lambda_i) F(x - \alpha_i, t) \right]$$
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- Gray: No Risk or Gain
- Yellow: Moderate Risk and Gain
- Blue: High Risk and Gain

Terminal Fitness ($\phi(x)$) vs. Energy Reserves ($x$)

Energy Reserves ($x$) vs. Energy Reserves ($x$)
Laboratory And Field Studies with Populations from Central Coast and Central Valley -- Contrasting Environmental Regimes

• When does the decision window for emigration occur?

• How does the timing of the decision window vary among populations?

• How does the variability in winter temperatures modify the emigration decision?

• Is early maturation of parr controlled by a similar decision window?
American River Sites
- Sunrise
- Gristmill
- Watt Avenue
  - Barrier: Nimbus Dam

Mokelumne River Sites
- Day-Use Area
- Mackville Rd.
  - Barrier: Camanche Dam

Wednesday, May 1, 13
The Growth Models Allow Us To Infer Food Density From Foraging Behavior

\[
\frac{dW}{dt} = \Omega(T(t))fW(t)\frac{a(t)}{a(t) + \kappa(t)} - (1 + a(t))\alpha e^{\beta T(t)}W(t)
\]
And Predict Growth in the Field

A) American River

B) Mokelumne River
We Couple This to A Behavioral Model

- Size advantage of anadromy
- Fecundity advantage of size
- Survival penalty of small emigrants
- Mortality risk of waiting to mature

Length-Based Marine Survival

![Graph showing % Survival vs FL at emigration (mm)]
State variables
State variables

$l$ – fork length (mm)
State variables

$l$ – fork length (mm)

$g$ – sexual maturity indicator variable (1=mature, 0=immature)
State variables

\( l \) – fork length (mm)

\( g \) – sexual maturity indicator variable (1=mature, 0=immature)

\( e \) – smolting indicator variable (1=smolt, 0 = parr)

Smolting and maturing sexually are mutually exclusive
State variables

\[ l \] – fork length (mm)

\[ g \] – sexual maturity indicator variable (1=mature, 0=immature)

\[ e \] – smolting indicator variable (1=smolt, 0 = parr)

Smolting and maturing sexually are mutually exclusive

Fitness

\[ F(l, g, e, t) = \text{Maximum expected lifetime egg production given length, maturation indicator, and smolting indicator at time } t \]
The Timeline for Stochastic Dynamic Programming

Age 0
- Emergence
- (also age 0 maturation)
- Smolt window

Age 1
- Spawning
- Mature window
- Emigration

Age n
- Spawning
- Mature window

Age Max
- Spawning
- Ts
- Te

Jan 1  Feb 1

Nov 1  Sb  Dec 31

S0  S5

Smolt window
Smolt thresholds

Mokelume R.

American R.

Growth (mm) over course of window

Length (mm) at end of decision window

Observed fish

Evol Apps 3:221-243
We Have Many Other Predictions and Comparison with Data

• We can reproduce geographic patterns
• Older anadromous fish on Scott Creek (TAFS 138:532), mix of life histories on Mokelumne (Evol App 3:221), young anadromous fish on American (Evol App 3:221)
• Larger size threshold valley vs. coast (TAFS 139:1263)
• Individual life histories for Scott Creek (TAFS 141:781)
Will Anadromy Be Lost for Steelhead on the American River?

• Scenario 1: Extend the easy food availability into the fall, reduce modeled temperatures by 3°C for October and November:
Will Anadromy Be Lost for Steelhead on the American River?

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  - For 5 out of 6 cases for which we predicted all anadromy under baseline conditions, we still predict anadromy under altered growth conditions
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• Scenario 1: Extend the easy food availability into the fall, reduce modeled temperatures by 3°C for October and November:

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  - In one case we predict that the slowest growing parr might now wait and smolt at an older age
Will Anadromy Be Lost for Steelhead on the American River?

- Scenario 1: Extend the easy food availability into the fall, reduce modeled temperatures by 3°C for October and November:
  - For 5 out of 6 cases for which we predicted all anadromy under baseline conditions, we still predict anadromy under altered growth conditions
  - In one case we predict that the slowest growing parr might now wait and smolt at an older age
  - Only if freshwater survival is low and parr could mature as YOY do we predict a shift to the resident life history
Will Anadromy Be Lost for Steelhead on the American River?

• Scenario 2: Reduce temperatures June 21 – September 21 and increase net survival over the summer by 30%.
Will Anadromy Be Lost for Steelhead on the American River?

- Scenario 2: Reduce temperatures June 21 – September 21 and increase net survival over the summer by 30%.

- We never predict freshwater maturity for any scenario examined, although if freshwater survival were high to begin with some of the slowest growing parr might wait and smolt at older ages.

Intrigue With Temperature Dependent Growth
\[ \Omega(T \mid g, d) = d(T - T_L)(1 - e^{g(T - T_u)}) \]
Intrigue With Temperature Dependent Growth

\[ \Omega(T \mid g, d) = d(T - T_L)(1 - e^{g(T - T_u)}) \]

The shape and limits of the curves depend on the availability of food

(Crozier et al. 2010, JAE 79:342-349)
**Intrigue With Temperature Dependent Growth**

\[
\Omega(T \mid \theta, d) = d(T - T_L)(1 - e^{g(T - T_u)})
\]

*The shape and limits of the curves depend on the availability of food*

(Crozier et al. 2010. JAE 79:342-349)

*Across species lower and upper lethal temperatures are correlated*

Rosso et al. 1993. JTB 162:447-463
Intrigue With Temperature Dependent Growth

\[ \Omega(T \mid g, d) = d(T - T_L)(1 - e^{g(T-T_u)}) \]

But within species there is a tradeoff between performance at low temperature and that at high temperature.

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(Crozier et al. 2010. JAE 79:342-349)
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The shape and limits of the curves depend on the availability of food.

(Crozier et al. 2010. JAE 79:342-349)
RESULTS

Growth rate differed among juvenile Atlantic salmon experiencing differences in incubation temperature (Fig. 2). Judged from group differences between residuals from a common growth model, there were overall significant differences in growth among the incubation temperature treatments (ANOVA, $F_{2,323} = 15.35, p < 0.001$). Juvenile salmon experiencing heated temperatures during the whole incubation period grew faster overall than the 2 other treatment groups (Table 1), whereas there were only marginal differences in overall growth rate between the natural and mixed incubation temperature treatments. The thermal scaling of growth did not differ significantly between the treatment groups (Table 2). The estimated lower thermal limit for growth ($T_L$) was 6.82, 7.70 and 6.76°C for natural, mixed and heated incubation temperatures, respectively. The estimated upper thermal limit for growth was 24.80, 24.43 and 25.15°C for natural, mixed and heated incubation temperatures, respectively. As judged from confidence intervals of the estimated coefficients, there was no significant difference in the thermal scaling of growth between treatment groups.

The maximum growth rate (height of the growth curve, $c$) was significantly higher in the heated compared to the natural and mixed incubation temperature treatments, as judged from the coefficients and bootstrapped confidence intervals (Table 2, Fig. 2). However, there were no differences in the maximum growth rates of fish reared in the natural and mixed incubation temperature treatment (Table 2). As a result, the heated incubation temperature group grew faster from temperatures of approximately 17°C upwards, reaching an optimal temperature for growth ($T_M$) at 19.73°C. This was slightly higher than those of the natural and mixed temperature treatments (17.90 and 19.20°C, respectively) and, as judged from the overlap in confidence intervals, not significant (Table 2). Also, when considering uncertainties in the estimated coefficients, there were only minor differences in growth along the tested temperature gradient for natural and mixed incubation temperature treatments (Fig. 2d).

**Table 1.** Tukey multiple comparisons of means for analysis of variance (ANOVA) with residuals from common growth model fitted for fish from all incubation temperature treatment groups as the response and treatment (natural, mixed and heated water temperatures) as the factor.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Mean difference</th>
<th>95% CI</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mixed vs. natural</td>
<td>−0.31</td>
<td>−0.61, −0.01</td>
<td>0.044</td>
</tr>
<tr>
<td>Heated vs. natural</td>
<td>0.40</td>
<td>0.09, 0.70</td>
<td>0.005</td>
</tr>
<tr>
<td>Heated vs. mixed</td>
<td>0.71</td>
<td>0.40, 1.01</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

**Fig. 2.** Salmo salar. Temperature scaling of body size standardized growth ($\Omega$, %) for juvenile Atlantic salmon kept at (a) natural, (b) mixed and (c) heated incubation temperatures (°C, cf. Fig. 1). Lines are fitted thermal growth models (Eq. 2, see Table 2 for parameter values); dots indicate individuals. (d) Estimated growth models from natural (---), mixed (•••) and heated (—) incubation temperatures are superimposed on each other and given with 95% confidence intervals (grey shading). Horizontal line indicates zero growth.
A Tradeoff Between Performance at Low Temperature and at High Temperature

\[ \Omega(T \mid g, d) = d(T - T_L)(1 - e^{g(T - T_u)}) \]

\[ y = 0.55685 - 0.97095x \quad R = 0.99825 \]
Salinas and Munch
(Ecology Letters. 2012. 15:159-163)

21-22°C
Salinas and Munch
(Ecology Letters. 2012. 15:159-163)
Salinas and Munch
(Ecology Letters. 2012. 15:159-163)
Offspring Growth Curves Shift According to Mom’s Experience
Offspring Growth Curves Shift According to Mom’s Experience
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Offspring Growth Curves Shift According to Mom’s Experience
Conclusions and Looking Forward
Conclusions and Looking Forward

• The natural world is a variable and complicated place
Conclusions and Looking Forward

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How do increasing temperature and ocean acidification interact?
Conclusions and Looking Forward

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How do increasing temperature and ocean acidification interact?

• But much of that complexity and variability can be understood if we bring the right tools and right approaches to bear on the problem
Conclusions and Looking Forward

• The natural world is a variable and complicated place.

How do increasing temperature and ocean acidification interact?

• But much of that complexity and variability can be understood if we bring the right tools and right approaches to bear on the problem.

What role does the rearing facility on the Carmel River play in persistence?

What is the best way to release the small amount of water available?
Conclusions and Looking Forward

- It is likely unreasonable to expect identical responses to changing environments across wide swaths of biogeographic range; rather we should expect more subtlety to what happens
Conclusions and Looking Forward

• It is likely unreasonable to expect identical responses to changing environments across wide swaths of biogeographic range; rather we should expect more subtlety to what happens

How do we capture implications of environmental change for successful biological control?
Conclusions and Looking Forward

- It is likely unreasonable to expect identical responses to changing environments across wide swaths of biogeographic range; rather we should expect more subtlety to what happens.

How do we capture implications of environmental change for successful biological control?

How temperature and habitat quality affect parasitoid lifetime reproductive success—A simulation study

Damien Denis\textsuperscript{a}, Jean-Sébastien Pierre\textsuperscript{a}, Joan van Baaren\textsuperscript{a}, Jacques J.M. van Alphen\textsuperscript{a,b}

\textsuperscript{a} UMR 6553 ECORIO, Université de Rennes 1, Campus de Beaulieu, Avenue du Général Leclerc, 35 042 Rennes Cedex, France
\textsuperscript{b} IBED, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands
Conclusions and Looking Forward

We really do not understand how temperature dependent growth rates are generated and need to do so.
**Conclusions and Looking Forward**

We really do not understand how temperature dependent growth rates are generated and need to do so.

*The First Law of Biology*: All entities and processes of life are obedient to the laws of physics and chemistry.
Conclusions and Looking Forward

We really do not understand how temperature dependent growth rates are generated and need to do so.

*The First Law of Biology*: All entities and processes of life are obedient to the laws of physics and chemistry

*The Second of Biology*: All entities and processes of life were created by evolution through natural selection

There is much to be done in Pasteur’s Quadrant
There is much to be done in Pasteur’s Quadrant and not a moment to be lost.

(Russell Crowe as Jack Aubrey)
How will changing environments affect the population dynamics of parasitoids and hosts in biological control?

<table>
<thead>
<tr>
<th>Quest for fundamental understanding?</th>
<th>Considerations of use?</th>
</tr>
</thead>
<tbody>
<tr>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td>No</td>
<td></td>
</tr>
</tbody>
</table>
The Classification of Insect Life Histories

**a)** Generations per Year:
- Multivoltine: >1
- Univoltine: 1

**c)** Egg Production After Emergence:
- Pro-ovigenic: >0
- Synovigenic: ⩾0

**b)** Eggs per Host:
- Solitary: 1
- Gregarious: >1

**d)** Combining the characteristics:
- Multivoltine
- Univoltine
- Solitary
- Gregarious
- Pro-ovigenic
- Synovigenic
The Pro-ovogenic Parasitoid in a Changing Climate
The Pro-ovogenic Parasitoid in a Changing Climate

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journal homepage: www.elsevier.com/locate/ecolmodel

How temperature and habitat quality affect parasitoid lifetime reproductive success—A simulation study

Damien Denis\textsuperscript{a,\,*}, Jean-Sébastien Pierre\textsuperscript{a}, Joan van Baaren\textsuperscript{a}, Jacques J.M. van Alphen\textsuperscript{a,b}

\textsuperscript{a} UMR 6553 ECOBIO, Université de Rennes I, Campus de Beaulieu, Avenue du Général Leclerc, 35 042 Rennes Cedex, France
\textsuperscript{b} IBED, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

Given a level of lipids at pupation and that eggs cannot be resorbed, what allocation to survival and reproduction maximizes lifetime expected reproductive success?
The Pro-ovogenic Parasitoid in a Changing Climate

![Graph showing activity rate ($A_r$) and metabolic rate ($M_r$) vs. temperature (°C). The graph illustrates how parasitoid activity and metabolic rate change with temperature.](image)
The Pro-ovogenic Parasitoid in a Changing Climate

![3D diagram showing the relationship between optimal initial egg load, temperature (Temp, °C), and lipid cost of patch exploitation/t (vp).]

Temperature (Temp, °C)  Lipid cost of patch exploitation/t (vp)
The Pro-ovogenic Parasitoid in a Changing Climate

![3D graph showing the relationship between mean LRS, temperature (Temp, °C), and lipid cost of patch exploitation per unit time (yp).]
Are Parasitoids Smart Enough to Recognize Changing Environments?
Are Parasitoids Smart Enough to Recognize Changing Environments?

Only one egg at a time but two kinds of hosts: previously unparasitized (fitness increment $f_u$) or previously parasitized (fitness increment $f_p$)

$$f_u > f_p$$
Only one egg at a time but two kinds of hosts: previously unparasitized (fitness increment $f_u$) or previously parasitized (fitness increment $f_p$)

$$f_u > f_p$$

No host encountered

$$F(x,t) = (1 - \lambda_u - \lambda_p)e^{-m}F(x,t + 1) + \lambda_u \{f_u + e^{-m_{ov}}F(x - 1,t + \tau)\}$$

$$+ \lambda_p \max\{e^{-m}F(x,t + 1), f_p + e^{-m_{ov}}F(x - 1,t + \tau)\}$$
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Unparasitized host encountered

$$+\lambda_p \max\{e^{-m} F(x,t+1), f_p + e^{-m_{ov}} F(x-1,t+\tau)\}$$
Are Parasitoids Smart Enough to Recognize Changing Environments?

Only one egg at a time but two kinds of hosts: previously unparasitized (fitness increment $f_u$) or previously parasitized (fitness increment $f_p$)

\[ f_u > f_p \]

\[
F(x,t) = (1 - \lambda_u - \lambda_p)e^{-m}F(x,t + 1) + \lambda_u \left\{ f_u + e^{-m_{ov}} F(x - 1, t + \tau) \right\}
\]

No host encountered (Previously parasitized host encountered)

\[ + \lambda_p \max \{e^{-m}F(x,t + 1), f_p + e^{-m_{ov}} F(x - 1, t + \tau)\} \]
First Period Fitness Provides a Measure of Selection
The Likelihood of Superparasitism Depends Upon Time and State

The graph shows the egg complement boundary over time. The x-axis represents time, labeled as $t$, ranging from 0 to 40. The y-axis represents the egg complement boundary, ranging from 0 to 8.

At point A, the line indicates a decision to reject an inferior host, while at point B, the decision is to accept an inferior host.

Wednesday, May 1, 13
The Prediction of Superparasitism Depends Upon Mortality

Time to start superparasitism

Mortality during search
The Prediction of Superparasitism

Time to start superparasitism

Mortality during search

Mortality cue manipulation
A Result So Strong that One Didn’t Even Need Statistics

![Graph showing bar chart with environment categories and superparasitism counts](image)

- Steady, Good
- Steady, Bad
- Dropping, Good
- Dropping, Bad

Environment (barometric pressure and encounter rate)
A View of Things to Come

(Mangel and Roitberg (TPB.1992 42:308-321))
A View of Things to Come

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• Standard Nicholson-Bailey dynamics
A View of Things to Come

(Mangel and Roitberg (TPB. 1992 42:308-321))

• Standard Nicholson-Bailey dynamics

• Two host types (e.g. better hosts that grew in warmer places poorer hosts that grew in the shade) with density dependent production of host phenotypes (fewer hosts ==> higher fraction of them are better quality)
A View of Things to Come
(Mangel and Roitberg (TPB.1992 42:308-321))

• Standard Nicholson-Bailey dynamics

• Two host types (e.g. better hosts that grew in warmer places poorer hosts that grew in the shade) with density dependent production of host phenotypes (fewer hosts ==> higher fraction of them are better quality)

• Parasitoid behavior selected to choose the time at which to start attacking the poorer host type
Things can be ‘normal’
Things can be ‘normal’

But also pretty strange

Parasites

Hosts

Parasites

Hosts

Parasites

Hosts