Temperature
(pages 94-103 in text)

• (1) directly controls metabolic rates of ectotherms (invertebrates, fish)
  • Individual growth and development
  • Species ranges (latitude and altitude)

• (2) controls dissolved oxygen concentrations

• (3) is relatively predictable over annual cycle and can provide a basis for species adaptation.
• What determines temperature and *thermal regime* for a stream?
  – Stream thermal regime depends on environmental and landscape “setting” (Fig. 3.1 (Giller & Malmqvist 1998))
Thermal regime can be described by components or features that influence growth and development (Fig. 6.1 (Ward 1992))

- Max temp
- Min temp
- Duration above some threshold (e.g., degree-days)

Biologically-important components of the thermal regime
Thermograph

Degree-days above 0°C:
A biologically relevant way to look at temperature.
Cumulative thermal exposure

\[ 150d \times 10°C + 150d \times 20°C + 65d \times 10°C = 5,150 \text{ dd} > 0°C \]

\[ 365d \times 14°C = 5,110 \text{ dd} > 0°C \]
Stream temperatures vary with latitude (and altitude):

and position in a stream network

**Figure 5.11** Total annual degree-day accumulation (>0°C) as a function of latitude for various rivers of the eastern United States. (Reproduced from Vannote and Sweeney 1980.)

**Figure 5.12** Maximum daily temperature ranges in relation to stream order in temperate streams. (Reproduced from Vannote and Sweeney 1980.)
Streams in the same catchment:
- Can have different thermographs. Figure 5.10
- What about differences in dd >0 per year?

Note: Multiply Y-axis by 10

FIGURE 5.10 Degree-day accumulations and annual totals at six sites along White Clay Creek, Pennsylvania: (1) groundwater, (2) spring seeps, (3) first-order spring-brooks, (4) second-order streams, (5) upstream segment of third-order stream, (6) downstream segment of third-order stream. (Reproduced from Vannote and Sweeney 1980.)
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Temperature and insect life cycles

- Egg hatching
- Larval growth and development
- Adult emergence
3 Types of life cycles

[Fig. 5.2, Merritt & Cummins 1996]

Use 3 univoltine caddisfly species example:
(5 instars + pupal stage)

(1) **Slow Seasonal**
- Eggs hatch quickly, juveniles grow slowly, maturity in ~1, 2, 3 years
  - Species may have extended hatching period
  - Examples -- many univoltine stoneflies, some mayflies and caddisflies

Where adaptive?
Stable vs. unstable streams?
Perennial vs. intermittent streams?
(2) **Fast Seasonal**

- Long egg or juvenile diapause, followed by rapid growth to maturity
  - (Diapause = a state of arrested metabolism)
  - Different species emerge in Spring, Summer, or Fall

Where adaptive?

- Streams with short growing period
- Intermittent streams
- Perennial streams with competitors present
(3) **Non-seasonal**

- Many size classes present at all times
  - overlapping cohorts of multivoltine species (chironomids)
  - poorly synchronized (extended mating/egg-laying)
  - species life cycle spans > 1 yr (some stoneflies)

-Where adaptive?
  - In frequently disturbed streams with high juvenile mortality ("bet hedging" life history strategy)
  - In cold, stable streams that require more than one year to complete life cycle.
  - In warm climates where air temperatures for adults are suitable year round
Insect Eggs

• When laid, they can
  – a) all hatch immediately
  – b) hatch over time (Fig. 3.17)
  – c) hatching delayed (diapause)
• Some eggs require cold winter temperature to break diapause
  – Example: Hypolimnetic (deep) release Dam on Saskatchewan River, Canada

• Many aquatic insects in far North have winter egg diapause.

• Rising spring temps after ice-out are required to break diapause [Fig. 3.14]

• Dam warms winter water temp. to 4°C for tens of kilometers

Biotic response:
  30 genera and 12 families eliminated
  → 1 family remains!
Species have different thermal optima and tolerances

- Salmonids (trout and salmon): Geographic range determined by water temperature. (same true for insects)
- Upper thermal tolerance (Tmax) restricts trout to streams not exceeding ~20-25°C (~70°F). (“cold-water” fishes)

- Lower thermal tolerance can limit adequate growth and development in northern latitudes, or below dam outlets (~40°F or 4°C).
- An “optimal” temperature (Topt) results in greatest growth
- Higher temperatures favor other species. (Warm-water fishes)  
  Brett et al. 1969

![Growth Graph](image)
Growth rate and development:

Adult body size depends on *growth rate*, which is temperature dependent.

Different species have different thermal optima.

Strong selective pressure for larger body size. Why?
Most temperate zone aquatic species have positive growth over the winter!

- Unlike terrestrial insects (which have resting eggs or adult diapause)
- Food is available in winter!

- Some species extremely cold-adapted (Fig. 6.12 (Ward 1992)) - even under ice!

Why are females larger than males?
The optimal thermal regime for species is one that maximizes

- Larval body size (and thus adult fecundity)
- Larval metabolic efficiency of energy use

→ Results in more, larger individuals and thus greater local population abundance
Metabolic efficiency and body size

- High temp → **high metabolism** so **high cellular respiration losses** (metabolic heat) which is not available for growth → small adult
- Low Temp → **slow metabolism** and **low growth potential**, available energy allocated to adult tissue rather than growth → small adult

- For every species, there is an **optimal** temperature that **maximizes** larval/adult body size
  - Established experimentally for several insect species by Vannote and Sweeney (1980)
  - Consider an insect species that must complete development in a **fixed time** (e.g., univoltine or synchronously emerging species)
Metabolic efficiency and body size

- High temp $\rightarrow$ high metabolism so high cellular respiration losses (metabolic heat) which is not available for growth $\rightarrow$ small adult
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For every species, there is an optimal temperature that maximizes larval/adult body size
- Established experimentally for several insect species by Vannote and Sweeney (1980)
- Consider an insect species that must complete development in a fixed time (e.g., univoltine or synchronously emerging species)
Where in a species’ geographic range would you expect to see largest individuals? Largest populations sizes, and why?

- What environmental or landscape factors might be complicate this expectation?
Adult emergence:
- Juveniles develop adequately to become sexually mature
- If temperature too cold, then what?
  - 1) failure to develop and local population cannot persist
  - 2) some species are able to delay maturation, e.g., go from univoltine to semi-voltine (recall example from earlier lecture)

Two thermal cues for timing of emergence:
- 1) cumulative degree-days > 0°C
- 2) fixed temperature of emergence

[Fig. 7.13 Sweeney et al. 1992]

Ischnura elegans (damselfly)
- 43°N trivoltine
- 53°N univoltine
- 57°N semivoltine

What is Advantage? (Hint: cue)

**Figure 7.13.** Date of first adult emergence (triangles) for various geographic populations of *Ephemera septentrionalis* superimposed on isothermal lines showing the date that a given temperature is reached in streams throughout its geographic range. Isothermal lines are smoothed temporally and latitudinally from daily temperature records for 50 sites.
• **Photoperiod** can also be a trigger in temperate streams
  - Why?
    • good predictor of air temperature for adult

• **2 Types of emergence:**
  - **Synchronous**, i.e., all adults appear within a few days
    • Mayflies - Adults don’t feed
    • Evolutionary reason for synchronous emergence?
      – swamp predators
      – find mate
  - **Asynchronous**, i.e., adults emerge over time
    • Often variation in size of adult
      – Later emergers usually smaller (Fig. 10 (Vannote & Sweeney 1980))
• In cold weather (e.g., February) you can find small aerial aquatic insects along Poudre R. (midges, Chironomidae)
• How do they survive?
• Which *life cycle* type would you put them in?
• What kind of *voltinism* would they exhibit?
• What *emergence cue* would they use?
Aquatic Insect Life Cycles – variable responses to multiple selective forces

**Eggs can hatch:**
- Immediately → single juvenile cohort
- Delayed, then all at once
- Continuously → multiple cohorts

**Adults can emerge:**
- Synchronously (all at once)
- Asynchronously (spread over time)

**Females can lay eggs all at once** (short-lived) **or multiple times** (longer-lived)

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Aquatic

Egg → Juvenile instars → (Pupa) →
GROWTH & DEVELOPMENT

Terrestrial

Adult
EMERGENCE

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**Time**

Temperature

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Autumn  |  Winter  |  Spring  |  Summer
EVOLUTION
– maximizes individual fitness
\[ \rightarrow \text{maximize growth (g) and minimize mortality risk (µ)} \]

Why maximize $g$?

How to maximize $g$?

Avoid competition?
(Similar species often develop at different times and thus avoid larval overlap). This pattern reflects evolutionary strategy.

Larger female size $\rightarrow$ more eggs

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FIGURE 5.14 Larval growth period for five species of riffle-inhabiting ephemeralid mayflies in White Clay Creek, Pennsylvania. (●) Ephemera simulata; (▲) E. dorothea; (□) Seratella deficiens; (■) S. serrata; (inverted open triangle) Eurypleusa verisimilis. (Reproduced from Sweeney and Vannote 1981.)
**How minimize $\mu$?**

**What are sources of mortality risk?**

<table>
<thead>
<tr>
<th></th>
<th>Biotic</th>
<th>Abiotic</th>
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</thead>
<tbody>
<tr>
<td>Juvenile (aquatic)</td>
<td>Predation (invertebrates, fish)</td>
<td>Disturbance (frequency and intensity)</td>
</tr>
<tr>
<td>Adult (terrestrial)</td>
<td>Predation (insects, spiders, birds)</td>
<td>Air temperature (limited aerial season?)</td>
</tr>
</tbody>
</table>

*The relative strength of these sources of mortality factors can vary a lot in different streams and regions!*
Upshot:

Over evolutionary time species have “balanced” the interacting selective factors that influence growth and mortality of both juveniles and adults in an attempt to maximize fitness. This results in a very wide range of life cycle strategies, including:
- number of generations per year
- egg development time and synchrony of hatching
- timing and synchrony of adult emergence

Some of these strategies are “fixed” by evolution; others are more plastic and can vary within a species among streams and regions, reflecting the local environmental selection forces that affect the balance of growth and mortality in the juvenile and adult life stages.