“Bipartite” life cycle of benthic marine organisms with pelagic larvae

Larvae
- survive, grow, develop, disperse
- Pelagic Environment
- settlement

Juvenile
- survive, grow, mature
- Benthic Environment
- Adult

Rocky Intertidal Pattern: species distributed in discrete zones relative to elevation and tidal height.

Rocky Intertidal Zonation

mussels
- gooseneck barnacles
- acorn barnacles, tunicates, sponges, anemones
- pink coralline algae
- ‘keystone’ predator *Pisaster*

Almost all of the early ecological studies designed to explain zonation concentrated on processes affecting individuals after settlement onto the rock.

Why?

i) those were the life stages of which zonation patterns were described

ii) logistically easier to work on questions involving benthic stages than larvae

iii) benthic populations thought to be replenished by a limitless pool of larvae (i.e. benthic interactions more important determinants of benthic populations)

Rocky Intertidal Zonation exhibited across a very short distance

- Implies very strong determinants of distribution and abundance
- Wonderful opportunity to examine causes of zonation

Tides as a determinant of zonation patterns in intertidal

i) Intertidal zone is an (ecotone), the interface of two distinct habitats; terrestrial, and marine (higher, more terrestrial tolerant; lower more marine tolerant)

ii) what could cause such sharp boundaries in species distributions? It seemed clear that such boundaries had to be the result of rapid shifts in environmental conditions

iii) what was the most likely physical factor that could cause zonation in intertidal areas? **Tides**
Sun and moon have different gravitational strengths and topography of ocean basin modifies tidal current so that high (and low) tides are not same height. This is referred to as **mixed** semi-diurnal tides.

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**Diurnal (twice daily) tides**

- **SUN**
- **MOON**
- **Tide Level**

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**Tides as a determinant of zonation patterns in intertidal**

- Mean number of hours submerged
- height in intertidal

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**An early example exploring this hypothesis...**

**Doty (1946, Ecology 27:315-328)**

- **i)** Pattern: sampled distributions of species of macroalgae along CA and Oregon coasts and found (at all sites):
  - Six distinct zones: crustose coraline reds (cc), Gigartina (G), Endocladia (En), Egregia (Eg), fleshy reds (fr), Laminaria - kelp (L)

- **ii)** General hypothesis: tidal fluctuations and differential tolerance to immersion causes zonation of species in intertidal

- **iii)** Specific hypothesis: species zones will correlate with discrete zones of immersion ("critical tide levels")

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**Example Doty (1946, Ecology 27:315-328)**

- iv) Test: Calculated the actual immersion times over the tidal range:

  - Mean no. hr of immersion (= submergence)

- v) Results: dramatic non-linear steps in immersion that correlated with algal zonation!

- vi) Conclusion: physical factors - immersion - control species distribution and determine zonation of species in intertidal
Questions / observations:
Should upper and lower limits both be set by physical factors?

→ Where do intertidal species come from?
→ Would physical factors determine lower limit?

“Mobile animal distributions not well explained by tidal levels”
does this cause rejection or modification of the general hypothesis?

Alternative hypotheses?

<table>
<thead>
<tr>
<th>Upper limits</th>
<th>Lower limits</th>
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<tbody>
<tr>
<td>a) radiation (UV)</td>
<td>a) submersion</td>
</tr>
<tr>
<td>b) desiccation</td>
<td>b) lack of settlement - larval supply</td>
</tr>
<tr>
<td>c) thermal stress</td>
<td>c) biotic interactions</td>
</tr>
<tr>
<td>d) freshwater</td>
<td></td>
</tr>
<tr>
<td>e) lack of settlement - larval supply</td>
<td></td>
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<tr>
<td>f) food availability</td>
<td></td>
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<tr>
<td>g) biotic interactions</td>
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</tbody>
</table>

How best to distinguish among these alternative hypotheses?
What processes or mechanisms are responsible for each alternative?

Connell and the experimental revolution

Most ecological field studies prior to study we are to examine were purely descriptive (like Doty’s)

Connell, J. H.:
PhD in Milport, England

Connell and the experimental revolution

System: two species of barnacles and a carnivorous gastropod in the rocky intertidal:

i) Balanus (Semibalanus) balanoides (S) - a large barnacle
ii) Chthamalus stellatus (C) - a small barnacle
iii) Thais (Nucella) lapillus (T) - predatory snail

Connell and the experimental revolution

Pattern: disjunct vertical distribution of adults of the two barnacle species in intertidal zone

1) Adult distributions more restricted than recruit distribution:
   - at upper limits for both species
   - at lower limits for Chthamalus

2) Distribution of Chtham and Semi overlap extensively as larvae but little as adults

3) Thais only found in adult distribution of Semi

Connell and the experimental revolution

Hypotheses (and circumstantial evidence)

1) Upper limits -
   a) set by settlement distribution?
      - inconsistent with observation that settlement occurs higher than adult distribution
   b) species interactions? (untested by Connell)
      Why untested?
      i) Chthamalus - few organisms above it (including predators)
      ii) Semibalanus - no evidence from other work that Chtham negatively affects Semi
Hypotheses (and circumstantial evidence)

1) Upper limits - propose some for both species
c) Heat stress / desiccation - data and observations were consistent with this hypothesis
i) settlement above adult distribution for both species (rejects settlement hypothesis)
ii) much greater mortality for juveniles above adult distribution

Connell and the experimental revolution

Hypotheses

2) Lower limits -
   a) *Semibalanus*
      i) set by settlement distribution? Perhaps, because lower limits of both recruits and adults are similar
      ii) set by predation by *Thais*
         - Connell tested by experiments with cages
         - paired replicates at different tidal heights within and below range of *Semi*

Connell and the experimental revolution

Lower limit of *Semibalanus* set by predation?

i) Experimental design:

Caged plots to exclude predators
Un-caged plots with predators

ii) Prediction:

<table>
<thead>
<tr>
<th>Tidal Height</th>
<th>Density (no./m²⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>High</td>
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</tbody>
</table>

iii) Results:

a) predation more intense at lower limits, but
b) *Semi* were not completely excluded at any tidal height
c) in absence of predators, tidal ht unimportant to *Semi* abundance

Connell and the experimental revolution

Lower limits

*Chthamalus*

i) Physical processes — immersion
   - placed rocks with *Chtham* juveniles in tidepools (of same tidal ht)
   - compared survivorship to those not in tidepools
   - no difference in survivorship
   - conclusion: immersion not important

ii) Settlement distribution — unlikely
   - settlement distribution much lower than adult distribution
   - indicates post-settlement mortality

iii) Predation/Competition — Tested both at once (allows for test of interaction among factors)
   - attached rocks with juvenile *Chtham* and *Semi* at several tidal heights
   - remove *Semi* from ½ of each rock
   - half of rocks at each tidal ht were enclosed in cages (to exclude predators)

<table>
<thead>
<tr>
<th><em>Semi</em></th>
<th><em>Thais</em></th>
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<tr>
<td>+</td>
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<td>+</td>
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</table>
Connell and the experimental revolution

**Lower limits of *Chthamalus* set by predation and/or competition?**

**Results:**

<table>
<thead>
<tr>
<th>Chtham. percent cover</th>
<th>+ Semi</th>
<th>- Semi</th>
<th>+ Thais</th>
<th>- Thais</th>
</tr>
</thead>
</table>

- *Semi* limits Chth distribution and abundance (competition)
- Thais does not control Chth by itself
- *Semi* and *Thais* jointly limit Chth distribution and abundance
- Thais eats *Semi*, enhancing Chth distribution and abundance

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Connell and the experimental revolution

**Other examples (the “take off” of field experiments)**

David Wethey (1984, Biological Bulletin)

- **System** - same as Connell’s (*Semibalanus* and *Chthamalus*), But in New England on east coast of US
- **Pattern** - same as Connell’s (*Semibalanus* and *Chthamalus*), But focus greater focus on explaining upper limits

**c) General hypotheses:**
- i) Solar exposure affects *Semi* (more than Chth) restricting its upper limit
- ii) Competition with *Semi* restricts Chth lower limit

**d) Specific hypotheses:**
- Shading areas above *Semi* upper limit of *Semi* will:
  1) allow *Semi* to extend higher (test of (i) above)
  2) cause decrease in Chth because of increase in *Semi* (iii) above

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Connell and the experimental revolution

**Other examples (David Wethey 1984)**

**Results:**

<table>
<thead>
<tr>
<th>Semi</th>
<th>Chth</th>
</tr>
</thead>
</table>

- ii) Survivorship of *Semi* above normal adult distribution:
- iii) Survivorship of *Chth* above normal adult distribution:
- iv) Decreased survivorship of *Chth* in shade because of increased abundance of *Semi*:

**Conclusions:**
- i) Upper limit of *Semi* set by “solar exposure”
- ii) Lower limit of *Chth* set by competition with *Semi*.
- iii) Support for Connell’s Rule!