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

**Larvae**
- survive, grow, develop, disperse

**Pelagic Environment**
- reproduce

**Benthic Environment**
- settlement

**Adult**
- survive, grow, mature

**Juvenile**
- settle

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In the beginning... when ecologists first wandered into the intertidal...

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

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**Rocky Intertidal Zonation**

- mussels
- gooseneck barnacles
- acorn barnacles, tunicates, sponges, anemones
- pink coralline algae
- ‘keystone’ predator *Pisaster*
In the beginning... when ecologists first wandered into the intertidal...

i) zonation exhibited across a very short distance
   - Implies very strong determinants of distribution and abundance
   - wonderful opportunity to examine causes of zonation

II) Almost all of the early ecological studies designed to explain zonation concentrated on processes affecting individuals after settlement (i.e. juv.s and adults in benthic habitat)

Reasons:
   i) those were the organisms (life stages) of which patterns were described (zonation)
   ii) logistically easier to work on questions involving benthic stages than larvae (in the field)
   iii) benthic populations thought to be replenished by a limitless pool of larvae (i.e. benthic interactions more important determinants of benthic populations
II) 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 physical factors

[[rapid shift in environmental conditions and successful species]]

iii) what was the most likely physical factor that could cause zonation in intertidal areas? ---Tides

Sun and moon have different gravitational strengths (previous slide) 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

http://tbone.biol.sc.edu/tide/

Tide lags each day throughout month because moon rotates around earth

When moon is same side as sun (new moon), or opposite sun (full moon), tides are strong (spring tide)

When moon is 90° to sun and moon, tides are weak (neap tide)
II) Tides as a determinant of zonation patterns in intertidal

a) *Tides are sinusoidal.* Appearance of the sine wave tidal function might lead one to believe that the relationship between *immersion time* (time underwater) and tidal height decreases smoothly (and linearly or gently curvilinear) with increasing tidal height:

![Mean no. hr of immersion](image)

Does this correspond intuitively to sharp breaks in zonation patterns?


i) Pattern: sampled distributions of species of macroalgae along CA and Oregon coasts and found (at all sites):

<table>
<thead>
<tr>
<th>Tidal Level</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>CC, En, Eg, Eg, fr</td>
</tr>
<tr>
<td>High</td>
<td>CC, En, Eg, Eg, fr</td>
</tr>
</tbody>
</table>

ii) General hypothesis: tidal fluctuation 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”)

Nonetheless, an early example exploring this hypothesis...

**c) Questions / observations:**

i) Should upper and lower limits both be set by physical factors?

ii) Critical tidal levels were less good at explaining animal distributions; particularly mobile animals - does this cause rejection or modification of the general hypothesis?

iii) Alternative hypotheses?

- Upper limits
  - a) radiation (UV)
  - b) desiccation
  - c) thermal stress
  - d) freshwater
  - e) lack of settlement - larval supply
  - f) food availability
  - g) biotic interactions

- Lower limits
  - a) submersion
  - b) lack of settlement - larval supply
  - c) biotic interactions

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

![Literally cut and weighed tide tables!](image)

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
c) Questions / observations:

iv) How best to distinguish among these alternative hypotheses?

v) What processes or mechanisms are responsible for each alternative?

III) Connell and the experimental revolution

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

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

b) System:

- Two species of barnacles and a carnivorous gastropod in the rocky intertidal:
  i) *Semibalanus balanoidies* (S) - a large barnacle
  ii) *Chthamalus stellatus* (C) - a small barnacle
  iii) *Thais lapillus* (T) - predatory snail
III) Connell and the experimental revolution

c) 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 Ctham and Semi overlap extensively as recruits but little as adults

3) Thais only found in adult distribution of Semi

III) Connell and the experimental revolution

d) Hypotheses (and circumstantial evidence)

1) Upper limits - propose some for both species
   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)

c) Heat stress / desiccation - data and observations were consistent with this hypothesis (mechanism untested)

   i) settlement above adult distribution for both species (rejects settlement hypothesis)
   ii) much greater mortality for juveniles above adult distribution
d) Hypotheses (and circumstantial evidence)

2) Lower limits - consider each species separately
   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

2-a) Lower limit of *Semibalanus* set by predation?

ii) Prediction:

   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
III) Connell and the experimental revolution

d) Hypotheses (and circumstantial evidence)

2) Lower limit of Semibalanus set by predation?

iii) Results:

<table>
<thead>
<tr>
<th>Tidal Height</th>
<th>Low</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean size of Semibalanus (mm)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

- Lower limit not set by predation, but size distribution changed (important later)

3) Other Biological Interactions? eg. competition with algae (untested)

4) Physical factors? — immersion— untested — why?

III) Connell and the experimental revolution

d) Hypotheses (and circumstantial evidence)

2) Lower limits - consider each species separately

b) Chthamalus

iii) Predation/Competition — Tested both at once (allows for test of multiple causality and interaction among factors)

- attached rocks with juvenile Chthamalus and Semibalanus at several tidal heights
- remove Semibalanus from ½ of each rock
- half of rocks at each tidal height were enclosed in cages (to exclude predators)

i) Physical processes — immersion

- placed rocks with Chthamalus juveniles in tidepools (of same tidal height)
- 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) Connell and the experimental revolution

d) Hypotheses (and circumstantial evidence)

2-b-iii) Lower limits of Chthamalus set by predation and/or competition?

- Chthamalus percent cover

![Graph showing predictions and conclusions]

Conclusions:
- Only predation important
- Only competition important
- Both C and P important (additive effects)
- C and P interact (multiplicative effects)

ii) Predictions:

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

- Only predation important
- Only competition important
- Both C and P important (additive effects)
- C and P interact (multiplicative effects)

iii) Connell and the experimental revolution

2) 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

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

- 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
III) Connell and the experimental revolution

2) Other examples (David Wethey, 1984)
   e) Design:
      - unmanipulated “control” treatment level to compare manipulations with (why???)
      - manipulations designed to test for artifacts of main manipulation

1) Unmanipulated control - predators, no shading
2) 2-sided cage, with screen “roof” - no shade but physical effect of a roof
3) Full cage with screen “roof” - exclude confounding effects of predators, no shade
4) 2-sided cage, with clear plastic roof - “cage effects” and no shading
5) Full cage, with clear plastic roof - exclude predators, no shading
6) 2-sided cage, with opaque (shading) plastic roof - cage effects, shading
7) Full cage, with opaque (shading) plastic roof - exclude predators, with shading

(7) vs. (5) both exclude predators and differ only in the degree of shading
All others get at artifacts of predator exclusion and materials for manipulating shading

III) Connell and the experimental revolution

2) Other examples (David Wethey 1984)

f) Results:
   i) No cage or roof material effects
   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.