Larval Behavior: Pre-settlement → Settlement

I. Some types of larval behavior
   a) = response to light (e.g., bryozoans, corals, fish)
   b) = swim up or swim down (many inverts and fish)
   c) = orient to currents (many inverts and fish)
   d) = orient to surface texture (inverts, not fish)
   e) = orient to water or surface chemistry (inverts and fish)

II. Early work on larval behavior (mostly barnacles)
    Golden age 1950-1960; received a lot of attention and great advances (e.g., Crisp, Knight Jones, Ryland (bryozoans), Barnes)
    Most of the work was motivated by field observations but generally done in lab with field collected or cultured larvae
**Example 1: Gregarious settlement — Knight Jones 1953**

**Pattern:** Barnacle aggregations on shoreline seemed to be species-specific (like settled next to like)

**Hypothesis:** Gregarious settlement response is species specific (i.e., “conspecific facilitation”)

**Test:**

<table>
<thead>
<tr>
<th>Settlement of:</th>
<th>% settlement</th>
<th>Surface with adults of:</th>
<th>Settlement of:</th>
<th>% settlement</th>
<th>Surface with adults of:</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) species #1</td>
<td>98</td>
<td>1</td>
<td>(2) species #2</td>
<td>32</td>
<td>1</td>
</tr>
<tr>
<td>(2) species #2</td>
<td>18</td>
<td>2</td>
<td>(3) species #3</td>
<td>18</td>
<td>1</td>
</tr>
<tr>
<td>(3) species #3</td>
<td>85</td>
<td>none</td>
<td></td>
<td>85</td>
<td>3</td>
</tr>
</tbody>
</table>

2 general results!

**Conclusions:** Settlement much greater in presence of inducer
Inducer is species-specific (⇒ gregarious behavior)

*Why settle gregariously?*

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**But:** what is the relationship between gregarious settlement and post-settlement growth and mortality?

**Costs of gregarious behavior:**

- Fertilization, reproductive success
- Post-settlement growth, survivorship

Distance between neighbors
Example 2: Territoriality at settlement - Crisp 1960

Species: *Balanus balanoides*

Pattern:
1) Just showed that *B. balanoides* settle gregariously
2) However, at smaller spatial scale, individuals seem to be spaced out more than expected by purely gregarious settlement.

Hypothesis: Pattern of settlement changes with spatial scale; at smaller scales, different from gregarious

Test: Sampled settlement distribution of *B. balanoides* to test for these predicted frequency distributions of distance

Conclusions: Territorial behavior at settlement - backed up w/observations of larvae settling in the lab.
Example 3: Facilitative settlement in coral reef fishes
Anderson et al. 2007 MEPS

System: blue damselfish, Chromis cyanea on coral reefs in Bahamas

Pattern: highly aggregated distribution, especially recently settled juveniles

Hypothesis: aggregations created by behavioral preference to settle with resident conspecifics

Test:

Results:

<table>
<thead>
<tr>
<th>Cumulative no. settlers/coral head</th>
<th>Present Residents</th>
<th>Absent Residents</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>10</td>
<td></td>
<td>10</td>
</tr>
<tr>
<td>15</td>
<td></td>
<td>15</td>
</tr>
<tr>
<td>20</td>
<td></td>
<td>20</td>
</tr>
</tbody>
</table>

III. The evolution of behavioral cues for settlement

Why have behavioral cues for settlement?

Why not always have cues?

Two kinds of costs... (mistakes)

1) Cue occurs in inappropriate habitats... leads to settlement in inappropriate conditions

2) Not all appropriate places have the cue... (e.g. think about coral heads without blue chromis)
Given:

- the costs of adapting to inappropriate cues,
- how many species exhibit this behavior to so many different kinds of cues,
- the implied strength of selection for these behavioral responses,
- the importance of settlement as a life-long consequence for fitness (especially for sessile species).

Can all this behavior at settlement contribute to those patterns that drove ecologists to study intertidal ecology (i.e. patterns of zonation)?

IV. Contribution of larval behavior to vertical zonation patterns

Processes affecting zonation → 4 possibilities

1) Larvae may be stratified in water column (behavior or hydrodynamic effects) and land at different tidal heights

Adult pattern (zonation):

 Processes affecting zonation → 4 possibilities

2) Larvae may (1) be mixed in water column, (2) exhibit settlement behavior (3) settle within appropriate zone

Adult pattern (zonation):

 Processes affecting zonation → 4 possibilities

3) Larvae may (1) be mixed in water column, (2) show no settlement behavior (3) settle randomly and (4) die back to create adult zonation pattern

Adult pattern (zonation):
Processes affecting zonation → 4 possibilities

4) Individuals may move after settlement

Adult pattern (zonation):

Example: Stratification of larvae in water column
Grosberg 1982, senior thesis!

System: Santa Cruz harbor, 2 species of barnacle on pier pilings
Balanus glandula and Balanus crenatus

Pattern:

Results:

Question: What causes vertical zonation?

General hypotheses:

H_{A1}: early post-settlement mortality limits species distribution (sensu Connell)

H_{A2}: stratification of larvae limits distribution → via behavior

Test: 10 x 10 cm plates

Sampled weekly during a period of high settlement - allows detection of 1-7 day old individuals
Conclusions:

1) settlement was same distribution as adults
2) not post-settlement processes causing adult distribution

H₀: stratification of larvae limits distribution → via behavior

Test:

Used plankton pulls to sample the water column on 3 days: new, full, half moon
sampled hourly for 24 hour periods on each day
sampled from a floating dock at 4 depths:
surface, 0.5 m, 1.5 m, and 3 m
sampling range: -4 m to +1.8 m

Results differ between species:

1) 94% of glandula larvae taken in surface waters (irrespective of tidal sequence)
2) 98% of crenatus larvae were collected < 0 m mlw, (meaning their distribution in water column changed as a function of tide!)

Conclusions:

1) Distribution of adults determined by position of larvae in water column
2) Larval distribution set by two different behaviors:

B. glandula stays in surface water, which over tidal sequences travels from about -1.2 to 1.8 m (abundances correspond to time at tidal height)

B. crenatus stays below a particular tidal level (how might it do that?)
V. Role of physical structure (e.g. kelp, seagrass, coral heads…) as a cue for settlement

Example: Carr 1994 Ecology

Pattern: among reefs and years...

Density of kelp bass settlers increases with increasing density of giant kelp... but it is not linear!

General hypothesis: kelp acts to promote recruitment of kelp bass

Specific Hypothesis: Local kelp bass recruitment should correlate to manipulated density of giant kelp

Conclusions:

Local and “regional” patterns of kelp bass recruitment are influenced by dynamics of giant kelp abundance

The relationship is not based strictly on plant density, but on biomass (shelter!). Because kelp biomass changes with plant density, recruitment relationship is asymptotic.

Giant kelp facilitates recruitment of kelp bass by providing habitat that they encounter as they pass over reefs.
Lots of examples of role of habitat structure...

In addition to *Macrocystis* and kelp bass
e.g., Carr 1994, Ecology

*Macrocystis* and kelp surperch
e.g., Anderson 1994, MEPS

Sea urchins and blue-banded goby
e.g., Hartney and Grorud 2002, Oecologia

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Sources of spatial and temporal variation in recruitment

Post-settlement:
- survival
- growth
- movement

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V. (Early) post-settlement processes as sources of variation in recruitment

“Recruitment” estimates occur at some point subsequent to settlement, so...

--Do post-settlement processes alter patterns of settlement?

--Can post-settlement processes cause density-dependent mortality that would de-couple patterns of settlement and recruitment?

--How important are competition and predation as sources of variation in recruitment AND density-dependent mortality?

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Density-independent: same probability of surviving regardless of density

Density dependence: no relationship between settler # and recruit #
Sources of spatial and temporal variation in recruitment

**Post-settlement:**
- survival
- growth
- movement
- predation
- competition

**General approach:**
1) To test for predator effects, manipulate presence and absence of predators
2) To test for density-dependence, manipulate density of settlers
3) To test for density dependence caused by predation, manipulate BOTH orthogonally

**Early post-settlement mortality: predation**

- **Steele 1997 Oecologia**
- **Johnson 2006 Ecology**
- **Anderson 2002 Ecology**

**Conclusions**

1) Post-settlement mortality is a source of variation in recruitment
2) Predation is an important source of post-settlement mortality
3) Predation is also a source of density-dependent mortality, which can decouple estimates of settlement and recruitment