V) Factors affecting recruitment

B) Determinants of larval delivery

iii) Episodic events

\[ \text{storms} \quad (\text{Reed 1988 Ecology}) \]

a) Pattern: following storms there is catastrophic loss of kelpbed area, followed by quick, widespread recruitment and recovery.

b) 3 Hypotheses:

\[ H_{A1} \] whole plants carried to reef, then release spores

- but broad-scale, uniform pattern of recruitment inconsistent with pattern predicted by plant swept across reef.

\[ H_{A2} \] “seed bank” of dormant spores

- but out-plant studies by Reed suggests very short longevity (rapid loss to grazers).

\[ H_{A3} \] storms cause propagule transport to distant locations (for kelps)

- but, previous work indicated that dispersal was on the order of 1 meter.

Macrocystis sporophylls at base of plant ≤ 1m

b) 3 Hypotheses:

HA3: storms cause propagule transport to distant locations (for kelps)

- but, previous work indicated that dispersal was on the order of 1 meter.

Pterygophora

\[ \text{HA2} \] “seed bank” of dormant spores

- but out-plant studies by Reed suggests very short longevity (rapid loss to grazers).

HA1: whole plants carried to reef, then release spores

- but broad-scale, uniform pattern of recruitment inconsistent with pattern predicted by plant swept across reef.

b) 3 Hypotheses:

V) Factors affecting recruitment

B) Determinants of larval delivery

iv) Larval depletion - ecological filters

Predation

\[ \text{Gaines and Roughgarden 1987 Science} \]

a1) Pattern: from year-to-year, recruitment of \( B. \) glandula was negatively correlated with kelp abundance offshore.

b1) Hypothesis: if supply, larval abundance should be lower on inside edge of kelp bed than outside it.

\[ \text{Current} \quad \text{Sand} \]

\[ \text{Kelp} \quad \text{offshore} \quad \text{inshore} \]

No. competent larvae per hr

\[ \text{barnacle recruitment (no. / cm}^2 / \text{wk)} \]

\[ \text{kelp canopy area (m}^2 \) \]

Current

\( \text{K} \)

b) Hypothesis: if supply, larval abundance should be lower on inside edge of kelp bed than outside it.
iv) Larval depletion - ecological filters

c1) Test: sample larval concentrations with plankton pump inshore and offshore of kelp bed

d1) Results:

i) Cyprid larvae - the settlement stage for Barnacles

Confirmed: 70 times greater concentration offshore than inshore!

ii) Nauplius larvae - pre-settlement stage - released by adults

Opposite pattern!

b3) New hypothesis: predation by juvenile rockfish filters cyprids

c3) Test: looked at the relationship between abundance of juvenile rockfish (Sebastes) and Balanus glandula recruitment over a three year period.

<table>
<thead>
<tr>
<th>Year</th>
<th>rockfish density # observed / min</th>
<th>Balanus recruitment #/cm²</th>
<th>kelp bed area m²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1983</td>
<td>0.7</td>
<td>3.7</td>
<td>8,500</td>
</tr>
<tr>
<td>1984</td>
<td>7.2</td>
<td>1.4</td>
<td>33,000</td>
</tr>
<tr>
<td>1985</td>
<td>236</td>
<td>0.05</td>
<td>46,500</td>
</tr>
</tbody>
</table>

d3) Results: Rockfish hypothesis not rejected but change in kelp bed size—complicates the interpretation a bit
iv) Larval depletion - ecological filters
“recruitment shadow”  Gaines et al. 1985 Oecologia

d) Results:

cyprid concentration

<table>
<thead>
<tr>
<th>Site</th>
<th>I</th>
<th>II</th>
<th>III</th>
</tr>
</thead>
</table>

settlement rates #/cm²/day

<table>
<thead>
<tr>
<th>Site</th>
<th>I</th>
<th>II</th>
<th>III</th>
</tr>
</thead>
</table>

Results were consistent with “larval depletion hypothesis”, but other hypotheses not rejected (assumption that change in cyprid # = depletion)

Particularly likely alternative:
hydrodynamic -- difference in cyprid # caused by hydrodynamic reasons (e.g., greater water movement/exchange at site 1 → more water → more cyprids → more settlement)

Processes affecting larval supply

1. Variable production
   i) species traits
   ii) environmental variation (in productivity)

2. Physical oceanographic processes
   i) biogeographic scale
   ii) intermediate scale processes
      a) internal waves
      b) upwelling

3. Episodic events - storms

4. Mortality and Depletion
   i) rockfish predation
   ii) hydrodynamic influence of kelp
   iii) larval depletion

Larval dispersal, mortality

Temporal scales

1 min 1 hour 1 day 1 week 1 month 1 year 1 decade 100 years

Lin. spatial scales

1 cm 100 km 1000 km

Source of spatial and temporal variation in recruitment
V) Factors affecting recruitment

C) Processes affecting settlement

1) Physical processes (e.g., turbulence, current speed)

2) Larval behavior

I) types

II) history of larval behavior studies - barnacles

III) conditions for evolution of behavioral cues (settlement)

IV) contribution to vertical zonation

Larval Behavior → Pre-settlement → Settlement

I. Some types of larval behavior

a) Phototaxis — response to light (e.g., bryozoans, corals, fish)

b) Geotaxis — swim up or swim down (many inverts and fish)

c) Rheotaxis — currents (many inverts and fish)

d) Rugotaxis — surface texture (inverts, not fish)

e) Chemotaxis — water or surface chemistry (inverts and fish)

II. Early work on larval behavior (mostly barnacles)

Golden age 1950-1960 when 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

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

System: 3 species of barnacles in the rocky “you know where”...

Example 1: Gregarious settlement — Knight Jones 1953

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

c) Test: In laboratory aquaria, presented cyprids (barnacle larvae) with choice of settling on surfaces with either:

1) adults of own species, or

2) another species, or

3) no barnacles
d) Results: 2 general results!

1) Strong conspecific attraction
2) No settlement in absence of barnacles
   i.e. no settlement without some sort of cue (inducer)!

Settlement of:
(1) *B. balanoides*  (2) *B. crenatus*  (3) *E. modestus*

% settlement

100

Surface with adults of:

1  2  0  0
1  2  0  0
1  3  0  0

1) Settlement much greater in presence of inducer
2) Inducer is species specific (⇒ gregarious)

e) Conclusions:

Why settle gregariously? **Benefits:**

1) Indicates good habitat
2) Benefit in numbers (e.g., swamp predators)
3) Higher likelihood of finding mates

But, what is the relationship between gregarious settlement and post-settlement growth and mortality?
(what does gregarious behavior do ⇒ minimize distance to nearest neighbor)

Example 2: Territoriality at settlement - Crisp 1960

a) Species: *Balanus balanoides*
b) 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.
c) Hypothesis: pattern of settlement at smaller spatial scale different from gregarious

3 types of distributions are possible...

generated by 3 behavioral mechanisms:

- Dispersion: clumped, random, uniform
- Mechanism: gregariousness, no behavior, territoriality
d) Test: sampled settlement distribution of *B. balanoides* to test for these predicted frequency distributions of distance

![Graph showing clumped, random, and uniform frequency distributions.]

e) Results: normally distributed frequency distribution... uniform

f) 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. 2005 MEPS

a) System Blue damselfish, *Chromis cyanea* on coral reefs in Bahamas

b) Pattern: highly aggregated distribution, especially recently settled juveniles

c) Hypothesis: aggregations created by facilitative settlement: behavioral preference to settle with resident conspecifics

d) Test: establish different densities of resident species and determine if settlement rate increases with resident density level

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e) Results:

1) No settlement in absence of resident adults or recruits

2) Strong positive relationship between settlement rate and number of residents

f) Conclusion:

Conspecific residents facilitate settlement