VI) Population and Community Stability

I. Background / questions - refer back to succession

A) Do marine communities trend toward “climax states”? 
B) Is there a single “climax state”? 
C) At climax, are populations at equilibrium? 
   i.e., if perturbed, do they return to pre-perturbation levels??
D) At climax, assuming pop.s at equilibrium, is the community stable? 
   (by definition non-climax community can not be at equilibrium)

II. Working definition of stability:
A community which, when perturbed, returns to pre-perturbation 
(or a control) state (composition and relative abundance of spp.)

Community measures:

A) Return of species composition (who) and relative abundance:

B) Species diversity stabilizes:

III. Components of stability (four) for populations and communities

1) Resistance - community or population persists, 
   unaltered when exposed to a source of perturbation.

2) Resilience - community returns to equilibrium (pre-
   perturbation, control) following perturbation.

Equilibrium populations represent combined and constant effects 
of biological and physical forces on population. 
What feature of these processes bound this variation???
III. Components of stability (four)

3) Elasticity – how fast a community returns to equilibrium
   - Higher elasticity vs. Lower elasticity
   - Diagram showing perturbation over time

4) Amplitude – magnitude of perturbation that a community can return from
   - Lower moderate vs. higher amplitude
   - Diagram showing perturbation over time

IV. Assessment of stability

A) Determine if community is at a stable point
   (i.e. little variation in species composition and relative abundance over time... specifically, over several generations)

B) Apply a force - does it change?
   → see graphic definition of resistance

C) Apply a disturbance (i.e. change the community)
   Determine if community returns to pre-perturbation or control state.
   → see graphic definition of resilience

Diagrams of different states of stability

**Stable equilibrium:**
- Stable point of attraction

**Unstable equilibrium:**
- Stable only in absence of perturbation

**Multiple stable states:**
- Graph showing multiple stable states
V. Importance in theory and paradigms:

A) If communities are stable, then it is likely that processes of population and community organization are deterministic

1) Deterministic – predictable consequences from a given set of ecological processes.

2) For example, predictable effects of predation (keystone), competition (climax), mutualisms

3) In contrast, stochastic – unpredictable consequences (end points) because of varying effects and occurrence of processes. (e.g., larval supply, resource availability)

B.) Deterministic models of community organization are:

i) simpler (more predictable)

ii) likely to be more “generalizable”

V. Examples of testing ideas and occurrence of stability

VI. Examples of testing ideas and occurrence of stability

A) Benthic sessile communities

1) Coral reefs - e.g., Terry Hughes, but too long-lived!

2) “Fouling communities” communities that colonize and “foul” man-made structures (e.g., pier-pilings)
   - barnacles, algae, mussels, tunicates, hydroids, sponges, bryozoans
   - rapid colonization growth → climax quickly
   - shorter life spans → turnover
   - typically “packed” and appear stable
   - e.g., John Sutherland of “Menge and Sutherland”

B.) Example 1: Keough 1984 Ecology (patch size and isolation)

1) System: fouling communities on pilings in Australia
   - bryozoans, hydroids – rapid colonizers
     - fast growth
     - poor competitors
   - tunicates, sponges – slow colonizers
     - slow growth
     - good competitors

Ideas:

i) Patch size: smaller patches harder to colonize

ii) Patch isolation: less isolated patches more prone to intrusion

2) Approach: cleared areas of different size and isolation
VI. Examples of testing ideas and occurrence of stability

B.) Example: Keough 1984 Ecology

3.) Hypotheses:
   i) smaller patches more likely to be colonized by species with greater colonizing ability (bryozoans, hydroids)
   ii) less isolated patches more likely to experience intrusion by fast growing species (sponges, tunicates)

   Manipulated these orthogonally!!

IV. Examples of testing ideas and occurrence of stability

C.) Example 2: John Sutherland 1974 American Naturalist

1) Approach:
   a) Put fouling plates out at different times of year

2) Results:
   Found two “stable” endpoints (climax communities)
   a) dominated by Styela – solitary tunicate
   b) dominated by Schizoporella – colonial bryozoan

3) Conclusions:
   Community trajectory and climax determined by
   a) timing of disturbance (when patches opened)
   b) larval availability (who was available, when)

B.) Example: Keough 1984 Ecology

4) Results:
   i) Less isolated patches
      - recruitment unimportant
      - vegetative growth predominates
   ii) Isolated patches
      - recruitment important in small patches (target size)
      - eventually, growth became important in large patches

5) Conclusions:
   i) size and isolation important determinant of patch fate
   ii) stability driven by predictable competitive outcomes
   iii) general lack of importance of recruitment

VII. Life History Responses

Review:

I) Manifestation of post-settlement processes
   A) Community level
      i) maintenance of diversity
      ii) patterns of stability
   B) Population level
      i) vertical patterns of zonation and abundance
      ii) horizontal patterns of species abundance
   C) Individual level responses
II) Individual level responses:

→ non-genetic or genetic-based (= life history traits)
→ Population consequences or not

A) Individual responses that may affect population and community level responses:

1) Mortality (you bet!)
2) Growth (uh huh!)
3) Fecundity (sure)
4) Morphology (hmmmm)
5) Behavior (another hmmm)

B) Individual responses that may not... need to determine effect!

1) Individual morphology
   a) response to predators (e.g. bryozoan spines - Drew Harvel)
   b) response to competitors
      - clone lines (e.g., Anthopluera elegantisima)
      - modified “warrior” polyps at border with other individual
      - barnacle hummocks: different growth form, but similar growth, survival
VII. Life History Responses

C) response to environmental variation
   (large or small scale)
   
   i) shell morphology – thickens with exposure to larger waves (Nucella - gastropod: Richard Palmer)
   
   ii) shell aspect – lower with exposure to larger waves (limpets: Keough)

Although these are not heritable morphs, the ability to change morphology is a heritable trait referred to as “plasticity”

VII. Life History Responses

D) Allocation of resources

a) Response to predators
   - If predation on smaller individuals \( \rightarrow \) shift energy to growth
   - If predation on larger individuals \( \rightarrow \) shift energy to reproduction at younger, smaller stages
   (ex. Menidia response to fishing - may have population impacts)
   (Conover and Munch 2002, Science 297:94-96)

b) response to competitors (ex. ?)

c) response to physical environment
   (ex. nudibranchs go reproductive with thermal shock)

da) sex ratio: relative abundance of females and males

Evolutionary effects of size-selective fishing on size and fishery yield

- Smaller fish harvested
- Larger fish harvested
- Average sized fish harvested


a) Response to predators
   - If predation on smaller individuals \( \rightarrow \) shift energy to growth
   - If predation on larger individuals \( \rightarrow \) shift energy to reproduction at younger, smaller stages
   (ex. Menidia response to fishing - may have population impacts)
   (Conover and Munch 2002, Science 297:94-96)

b) response to competitors (ex. ? R vs. K life histories)

c) response to physical environment
   (ex. nudibranchs go reproductive with thermal shock)

da) sex ratio: relative abundance of females and males
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e) Behavioral responses
   i) ex. Sea urchins changing their foraging behavior in response to food availability (solitary in cracks → fronts)

f) Summary
   - Biological or environmental stress may invoke individual morphological, physiological or behavioral responses that
     1) may or may not have a genetic basis (i.e. a life history trait)
     2) may or may not have population/community level consequences
     3) are easier to detect than population or community level consequences because
        - more sensitive
        - occur faster → bioassays!

VII. Life History Responses

G) Example
   morphological response to predators (Curt Lively 1986)
   a) System: intertidal of Gulf of California
      1. Chthamalus anisopoma - barnacle
      2. Acanthina angelica - predatory snail
      3. Nerita funiculata - herbivorous snail
   b) Pattern: Chthamalus has two morphs:
      - bent
      - conic
      - crevice
Looking straight down...

bent  conic

Routine conic devils

VII. Life History Responses

G) Example
- morphological response to predators (Curt Lively 1986)

VII. Life History Responses

b) Pattern: Chthamalus has two morphs:

- Acanthina & Nerita when foraging:
  - Acanthina is barnacle specialist!!!!
c) Question: What causes the distribution of the two barnacle “morphs”?

1) $H_{A1}$: Desiccation
   Bent morph is more resistant to desiccation and more desiccation stress near cracks

c1) Test: transplanted both types to clearings along gradient and followed survivorship

$\text{low exposure}$

$\text{high exposure}$

$\text{crevice}$

$\text{survivorship}$

$d1)$ Result: -no difference

2) $H_{A2}$: $Acanthina$ causes distribution because of limited foraging distribution from cracks and the differential vulnerability of bents and conics. Conics more vulnerable to $Acanthina$ predation.

c2) Test: compare survival of the two morphs in the presence and absence of $Acanthina$

$\text{Survival after 5 days}$

$\text{present}$

$\text{absent}$

$\text{bent}$

$\text{conic}$

$d2)$ Result: $Acanthina$ much better at attacking conics - uses spine

e2) Conclusion:
2) **H\textsubscript{A2}**: Acanthina causes distribution because of limited foraging distribution from cracks and the differential vulnerability of bents and conics. Conics more vulnerable to Acanthina predation.

- foraging distribution of Acanthina \(\rightarrow\) and distribution of morphs

\textbf{c\textsubscript{3}}) **Test:** Crevice Near Far

- cleared both cages & controls of barnacle at onset

\textbf{d\textsubscript{3}}) **Results:**

\begin{table}[h!]
\begin{tabular}{|c|c|c|}
\hline
& Near-cages & Far-cages \\
\hline
\% cover & & \\
\hline
Conic & \text{\textbullet} & \text{\textbullet} \\
Bent & \text{\textbullet} & \text{\textbullet} \\
\hline
\end{tabular}
\end{table}

\textbf{e\textsubscript{3}}) **Conclusions:**

i) Acanthina disproportionately eats conics, but the effect is limited to its foraging distribution near cracks.

ii) In absence of Acanthina, conics generally do better than bents.

3) **Hypothesis:** Acanthina or Nerita induce the bent morphology near cracks

(recall that bents are only near cracks and only where Acanthina or Nerita have been foraging)

\textbf{c\textsubscript{4}}) **Test:** to see if snails could induce bent morph

- plots cleared and caged, then added: Acanthina, Nerita, both, neither

\textbf{d\textsubscript{4}}) **Result:**

\begin{table}[h!]
\begin{tabular}{|c|c|}
\hline
& \% bent morph \\
\hline
Control & 0 \\
Acanthina & 30 \\
Nerita & 30 \\
both & 30 \\
\hline
\end{tabular}
\end{table}
e) Conclusions:
1) Acanthina, and only Acanthina, can induce bent morph.
2) This is a "plastic" trait, not a genetic polymorphism, that is triggered in any barnacle by the slime of Acanthina.
3) Bent morph restricted to near-crevice, because that's the only place where Acanthina slime is found.

D) Another new question: Why not always be bent?
(Obviously an advantage with respect to predation!)

Life History Theory - Trait will be fixed in population unless there is a cost associated with it.

Question: Is there a cost to the bent morph?
1) Hypothesis 1: Bent morph is competitively inferior to the conic morph
   a) Test: compared survivorship of combined (crowded) bent and conics with solitary bents and conics.
   b) Result: no evidence of competitive disadvantage
   c) Conclusion: no evidence of competitive disadvantage

2) Hypothesis 2: Structural geometry of bent morph
   → reduced growth    → delayed onset of reproduction
   → reduced lifetime fecundity    → reduced reproductive success
   i) Test₁: compare growth rates (bent vs. conic)
   ii) Test₂: compare onset of reproduction (bent vs. conic)
   iii) Test₃: compare fecundity (bent vs. conic)
Question: Is there a cost to the bent morph?

2) Hypothesis 2: Structural geometry of bent morph
   i) Test₁: compare growth rates (bent vs. conic)
      ii) Result₁:

![Graph showing conic growth > bent growth](image)

Question: Is there a cost to the bent morph?

2) Hypothesis 2: Structural geometry of bent morph
   i) Test₂: compare onset of reproduction (bent vs. conic)
      ii) Result₂:

![Graph showing no difference](image)

Question: Is there a cost to the bent morph?

2) Hypothesis 2: Structural geometry of bent morph
   i) Test₃: compare fecundity (bent vs. conic)
      ii) Result₃:

![Graph showing 50% more eggs in conics](image)

iii) Conclusions: (overall)

1) Bents more resistant to predation
2) Bents occur near crevice
3) Conics grow faster and produce more babies
4) So both morphs advantageous (reproductive success) in different conditions