Population and Community Stability in Marine Systems

Do marine communities trend toward “climax states”?
Is there a single “climax state”?
At climax, are populations at equilibrium?
I.e., if perturbed, do they return to pre-perturbation levels???

At climax, assuming pop.s at equilibrium, is the community stable?
(what about non-climax community?)

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) Species composition and relative abundance return to pre-disturbance levels:
B) Species diversity stabilizes:

Population measures:
A) Fairly constant (i.e. bounded) dynamics at equilibrium
Equilibrium populations represent COMBINED and CONSTANT effects of multiple biological and physical forces on population...
What feature of these processes bound this variation???

4 Components of stability...
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.
3) Elasticity - how fast a community returns to equilibrium

4) Amplitude - magnitude of perturbation that a community can return from

How do we assess stability?

1) Determine if community is at a stable point
   (i.e. little variation in species composition and relative abundance over time)

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

3) 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:**

Multiple stable points are shown, indicating the possibility of different stable states within the system.
Importance in theory and community paradigms:

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

**Deterministic** - predictable consequences from a given set of ecological processes.

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

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

2) Deterministic models of community organization are:
   a) simpler (more predictable)
   b) likely to be more "generalizable"

Examples of testing ideas and occurrence of stability

**1) Benthic sessile communities**
   a.) Coral reefs - e.g., Terry Hughes, but too long-lived!
   b.) “Fouling communities” communities that colonize and “foul” man-made structures (e.g., pier-pilings)
      - barnacles, algae, mussels, tunicates, hydroids, sponges, bryozoans
      - rapid colonization growth → reach climax community quickly
      - shorter life spans → rapid turnover
      - typically "packed" and "appear" stable

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

**System:** fouling communities on pilings in Australia

- bryozoans, hydroids - rapid colonizers
  - slow growth
  - poor competitors
- tunicates, sponges - slow colonizers
  - fast growth
  - good competitors

**Approach:** cleared areas of different size and isolation

Ideas:
1) smaller patches harder to colonize
2) less isolated patches more prone to intrusion

Examples of testing ideas and occurrence of stability
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)

Results:

Less isolated patches?
- recruitment unimportant
- vegetative growth predominates

Isolated patches?
- recruitment important in small patches (target size)
- eventually, growth became important in large patches

Conclusions:

1) size and isolation important determinant of patch fate
2) stability driven by predictable competitive outcomes
3) general lack of importance of recruitment

Example 2: John Sutherland 1974 American Naturalist

Approach:
- Put fouling plates out at different times of year

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

Conclusions:
- Community trajectory and climax determined by
  1) timing of disturbance (when patches opened)
  2) larval availability (who was available, when)

Life History Responses

Review:

I) Manifestation of post-settlement processes
   A) Community level
      1) maintenance of diversity
      2) patterns of stability
   B) Population level
      1) vertical patterns of zonation and abundance
      2) horizontal patterns of species abundance
   C) Individual level responses
Individual level → Life history responses

Individual responses that may affect population and community level responses...

1) Individual morphology

a) response to predators (e.g. bryozoan spines - Drew Harvel)

b) response to competitors

  e.g. clone lines (e.g. Anthoplueria elegantisima)

  modified “warrior” polyps at border with other individual

  low density

  high density

  e.g. barnacle hummocks: different growth, but similar “performance” form

2) Change allocation of resources

a) Response to predators

  - If predation on smaller individuals → shift energy to growth

  - If predation on larger individuals → 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)

d) sex ratio: relative abundance of females and males

C) response to environmental variation (large or small scale)

  e.g. shell morphology – thickens with exposure to larger waves (Nucella - gastropod: Richard Palmer)

  e.g. shell aspect – lower with exposure to larger waves (limpets: Keough)

protected shores  exposed shores
3) Behavioral responses
   e.g. Sea urchins changing their foraging behavior in response to food availability (solitary in cracks → fronts)

Summary:
   Biological or environmental stress may invoke morphological, physiological, behavioral responses that...
   1) may or may not have population/community level consequences
   2) are easier to detect than population or community level consequences (why?)

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

System: intertidal of Gulf of California
1. Chthamalus anisopoma - barnacle
2. Acanthina anjelica - predatory snail
3. Nerita funiculata - herbivorous snail

Pattern: Chthamalus has two morphs:

Pattern (continued): Chthamalus has two morphs:

Acanthina & Nerita when foraging:

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

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

Result:
**Question:** What causes the distribution of the two barnacle “morphs”?

2) **H₂:** *Acanthina* causes distribution because of limited foraging distribution from cracks and the differential vulnerability of bents and conics. Conics more vulnerable to *Acanthina* predation.

**Test:** compare survival of the two morphs in the presence and absence of *Acanthina*

**Result:**

<table>
<thead>
<tr>
<th>Survival after 5 days</th>
<th>present</th>
<th>absent</th>
</tr>
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<tbody>
<tr>
<td><strong>Conclusions:</strong></td>
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</table>

*Acanthina* much better at attacking conics - uses spine

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2) **H₂ continued:** *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* influences distribution of morphs.

**Test:**

- Crevices
- Near
- Far

Cages (P-)
Control (P+)

- cleared both cages & controls of barnacle at onset

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**Results:**

<table>
<thead>
<tr>
<th>% cover</th>
<th>Time</th>
<th>Near-cages</th>
<th>conic</th>
<th>bent</th>
</tr>
</thead>
<tbody>
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**Conclusions:**

1) In absence of *Acanthina*, conics generally do better than bents.
2) Far from cracks, conics do better than bents.

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

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**New observation → new question.**

**Question:** what causes the change in morphology conic→bent?

**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)

**Test:** see if snails could induce bent morph

- plots cleared and caged, then added:
  - *Acanthina*, *Nerita*, both, neither
**Hypothesis:** Acanthina or Nerita induce the bent morphology near cracks

**Result:**

<table>
<thead>
<tr>
<th></th>
<th>% bent morph</th>
</tr>
</thead>
<tbody>
<tr>
<td>control</td>
<td>0</td>
</tr>
<tr>
<td>Acanthina</td>
<td>10</td>
</tr>
<tr>
<td>Nerita</td>
<td>10</td>
</tr>
<tr>
<td>both</td>
<td>20</td>
</tr>
</tbody>
</table>

**Conclusions:**

Another new question: Why not always be bent?

**Question:** Is there a cost to the bent morph?

**Hypothesis 1:** Bent morph is competitively inferior to the conic morph

**Test:** compared survivorship of combined (crowded) bent and conics with solitary bents and conics.

**Result:**

<table>
<thead>
<tr>
<th></th>
<th>% survivorship to 10 mo</th>
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<tbody>
<tr>
<td>bents</td>
<td>20</td>
</tr>
<tr>
<td>conics</td>
<td>20</td>
</tr>
<tr>
<td>solitary</td>
<td>0</td>
</tr>
<tr>
<td>crowded</td>
<td>0</td>
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</table>

**Conclusion:**
Question: Is there a cost to the bent morph?

Hypothesis 2: Structural geometry of bent morph
- reduced growth → delayed onset of reproduction
- reduced lifetime fecundity → reduced reproductive success

Test 1: compare growth rates (bent vs. conic)
Test 2: compare onset of reproduction (bent vs. conic)
Test 3: compare fecundity (bent vs. conic)

Result 1:

Result 2:
% individuals with eggs

Result 3:
Number of eggs

Body length of barnacle
**Conclusions**: (overall)

Bent morph:

Conic morph:

***Both morphs advantageous (reproductive success) in different conditions***