I. Types of Density Dependence

1. Density Independent

2. Density Dependent
   A. Direct (Negative) Density Dependence
   B. Inverse (Positive) Density Dependence

Direct (negative) density dependence

Population (N)
Per capita growth rate (r)

b, birth rate
d, death rate

Inverse (positive) density dependence

Inverse density dependence -- The Allee Effect
(W.C. Allee 1931. Animal Aggregations: A study in General Sociology)

Inverse (positive) density dependence

Does not regulate populations
- makes them more...
  - susceptible to extinction
  - prone to explosion

Inverse density dependence
Rate
Population (N)
Time

Population
0 20 40 60 80 100
0 20 40 60 80 100

Inverse density dependence -- The Allee Effect

Example: white abalone (*Haliotis sorgeneni*)
- first marine invertebrate to be listed as an endangered species
- male and female need to be within ~ 1 m to reproduce
- current densities in good habitat ~ 1 hectare (100 x 100 m)

II. Population Structure -- Closed vs. Open

"Closed" Populations
- Little or no exchange among populations
- Supply
- Production

"Open" Populations
- Significant exchange among populations
- Supply
- Production

Most benthic marine organisms live in open populations because...
- adult habitat is patchy
- adults are relatively sedentary
- there is dispersal of planktonic larvae

"Bipartite" life cycle of benthic marine organisms with pelagic larvae
- Larvae
  - survive, grow, develop, disperse
  - reproduce
  - Pelagic Environment
  - settlement
  - Benthic Environment
  - Adult
  - Juvenile
  - survive, grow, mature

"Bipartite" life cycle of benthic marine fishes with pelagic larvae

Spatial structure of populations can affect gene flow, genetic diversity, population dynamics, and population persistence

Closed populations: self-replenishing
- Limited dispersal: stepping-stone
- Open populations
- Single source
- Multiple sources: larval pool
- Larval pool
III. Metapopulation Dynamics

**Metapopulation**: a collection of open subpopulations
- i.e., a population composed of spatially isolated subpopulations that are connected by dispersal among them
- the metapopulation is a closed population
- at a large enough spatial scale, all populations are closed

<table>
<thead>
<tr>
<th>Subpopulation density</th>
<th># immigrants (settlers)</th>
<th>per-capita rate of immigration</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>5</td>
<td>0.50</td>
</tr>
<tr>
<td>20</td>
<td>5</td>
<td>0.25</td>
</tr>
<tr>
<td>50</td>
<td>5</td>
<td>0.10</td>
</tr>
<tr>
<td>100</td>
<td>5</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Regulation in Metapopulations
- can get regulation in a metapopulation without “biological” density dependence in the subpopulations
  - must have dispersal among subpopulations
  - must have asynchronous fluctuations in abundance in subpopulations
  - get “mathematical” density dependence

Asynchronous

Synchronous

IV. Intrapopulation Structure

Contrary to assumptions of simple mathematical models (e.g., Logistic Growth), not all individuals in a population are the same!

**Intrapopulation Structure** is the relative abundance of individual traits among individuals in a population:
- age
- size
- stage (e.g., larvae, juveniles, adults)
- sex
- genetic (genotypes)
- spatial

For example, the probability of survival and fecundity change with age

Survivorship Curves

Fecundity Curves

For example, size matters — bigger fish produce far more offspring
**V. Life History Strategies**

**Live fast, die young?**

Evolution can affect many basic attributes of the life history of an organism:

- age at maturity
- reproductive pattern (repeated vs. “big bang”)
- fecundity (offspring per bout)
- lifespan

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**Reproductive Pattern**

- Semelparity (“Big Bang”) — reproduce once
- Iteroparity — reproduce multiple times

Why do one instead of the other?

- semelparous
- iteroparous

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**Different life history strategies have evolved in response to different patterns of environmental variability**

**r-selection vs. K-selection**

- **r-selection**
  - unstable environments
    - low densities relative to K
    - highly variable densities (in response to environmental variation)
    - selects for high r to utilize unlimited resources
  - K-selection
  - stable environments
    - near K
    - relatively constant densities
    - selects for low r, but high competitive ability to garner resources

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**Pressures that cause r- or K-selection and attributes of r- and K-selected species**

<table>
<thead>
<tr>
<th>Selective Pressures</th>
<th>r-selection</th>
<th>K-selection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Climate</td>
<td>unpredictable</td>
<td>constant</td>
</tr>
<tr>
<td>Mortality</td>
<td>density-independent</td>
<td>density-dependent</td>
</tr>
<tr>
<td>Density</td>
<td>variable, low relative to K</td>
<td>constant, near K</td>
</tr>
<tr>
<td>Competition</td>
<td>weak</td>
<td>strong</td>
</tr>
</tbody>
</table>

**Expected attributes**

<table>
<thead>
<tr>
<th>Trait</th>
<th>r-selection</th>
<th>K-selection</th>
</tr>
</thead>
<tbody>
<tr>
<td>r</td>
<td>high</td>
<td>low</td>
</tr>
<tr>
<td>maturity</td>
<td>early</td>
<td>late</td>
</tr>
<tr>
<td>ontological development</td>
<td>rapid</td>
<td>slow</td>
</tr>
<tr>
<td>brood size</td>
<td>high</td>
<td>low</td>
</tr>
<tr>
<td>size of offspring relative to parents</td>
<td>small</td>
<td>large</td>
</tr>
<tr>
<td>lifespan</td>
<td>short</td>
<td>long</td>
</tr>
</tbody>
</table>