Current controversies in Marine Ecology - with an emphasis on Coral reef systems

• Open vs closed populations (already Discussed)
  - The extent and importance of larval dispersal
• Maintenance of Diversity
  - Equilibrial hypotheses
  - Non-equilibrial hypotheses
• Stability
  - Metapopulation structure
  - Diversity - stability hypothesis
• Behavioral hypotheses
  - Sequential hermaphrodites
  - Larval settlement behavior

A) Review of Hypotheses for maintenance of diversity (summarized and reviewed by Connell '78)

Recall, Ho’s can be categorized into one of two general categories:

1) Equilibrium hypotheses
2) Non-equilibrium hypotheses

Test the possible importance of each hypothesis in a particular community by testing:

a) assumptions necessary for each hypothesis
b) predicted dynamics and structure of assemblage in response to a perturbation
c) test both observationally and /or experimentally

- involve settlement and post-settlement processes
- stress biotic interactions
- mostly competition based - competitive exclusion principle
- community structure and dynamics are predictable
- predictable return to pre-perturbation state!

Niche Diversification Hypothesis

Assumptions:

a) competition based (assumes resources are limiting)
b) resource partitioning (each species is a superior competitor for particular resources or within particular niche)
c) for test, assume perturbation does not alter resource availability, only diminishes species abundances

Predictions:

a) total number of individuals and total number of species limited by resources, ⇒ assemblage-wide carrying capacity (K)
b) relative abundance of spp. determined by relative niche availability ⇒ specific carrying capacity for each species
c) predictable composition and relative abundance
Niche Diversification Hypothesis

Either exclusion or niche partitioning

Resource gradient (types)

Niche Diversification Hypothesis

Species A

Species B

Number of individuals

Resource gradient (types)

Species A

Species B

Niche Diversification Hypothesis

Number of individuals

Resource Gradient (types)

Species A

Species B

Species C

Species D

Species E

Time

Proportional abundance

Total abundance

Species A

Species B

Species C

0.0
0.5
1.0

K

Number of individuals

Resource gradient (types)
Niche Diversification Hypothesis

Species A
Species B
Species C

Time
Proportional abundance
K
Total abundance
perturbation
Species composition returns to pre-perturbation state!!!

Compensatory Mortality

Assumptions:
a) competition based (assumes resources are limiting)
b) disturbance or generalist predator removes most abundant species, thereby freeing resources for competitively inferior, rarer species
c) for test, assume perturbation does not alter resource availability, only diminishes species abundances

Predictions:
a) inverse relationships in species abundances
b) most abundant species at any time suffers disproportionate mortality
**Predation Hypotheses (equilibrial-based)**

Different equilibrial-based mechanisms:

- **Compensatory mortality** (predators feed on most abundant species)
- Predators “switch” to feed on most abundant species, disproportionately reducing that species
- Induces competition for refuge from predation (i.e. overall K for assemblage)
- **Regulate** populations of prey species separately (density dependence)

Reviewed by Hixon (in Sale book) 1991

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**Predation Hypotheses (equilibrial-based)**

**Assumptions:**

a) Predator causes disproportionately higher mortality in most abundant prey species (competitive dominant)

b) Induces competition or otherwise regulates prey populations

c) Allows persistence of rare species or inferior competitors

**Predictions:**

a) Inverse relationships in species abundances

b) Most abundant species at any time suffers disproportionate mortality

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**Predation Hypothesis (compensatory or switching)**

Note similarity of predicted pattern with compensatory mortality

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**Predation Hypothesis (compensatory or switching)**

Note similarity of predicted pattern with compensatory mortality
Predation Hypotheses (equilibrial-based)

Predictions for recruitment patterns:
- **Compensatory mortality, switching** - differences in recruitment diminish over time as numbers converge
- **Induced competition for refuge** - pattern similar to niche diversification
- **Regulate** populations of prey species separately (density dependence) - leads to predictable relative abundance of recruits

Intermediate Disturbance
- discussed at length previously
- competition based – mediated by physical or biological disturbance
- Connell '78 (Science) - proposed to explain maintenance of species diversity
- species diversity is greatest at intermediate levels of diversity

A) Review of Hypotheses for maintenance of diversity (summarized and reviewed by Connell '78)

II. Non-equilibrium Hypotheses
- Various processes can be involved: competition, predation, disturbance, limited recruitment
- Relative and total abundance fluctuates **unpredictably**
- Species composition is **unpredictable**
- Species composition and abundance does NOT return to pre-perturbation state

Intermediate disturbance hypothesis

Logic
- a) Disturbance interrupts successional sequence by creating patches of different ages → different states of succession
- b) In absence of disturbance, succession leads to climax community characterized by monospecific stand of competitive dominant (or a few) → low diversity
- c) but, at extremely high levels of disturbance, nothing or only a few species of rapid colonizers (or disturbance tolerant species) would persist → low diversity
- d) Recall that competitively superior species typically have poor colonizing capabilities.
Logic cont’d:

e) At intermediate levels of disturbance, get a mix of patches with climax (old), early-fugitive (new), and middle succession w/ mix of both:

Lottery Hypothesis
(Connell’s “Equal Chance” Hypothesis)
Peter Sale 1977

Assumptions:
• competition based (resource limitation)
• larval pool saturates resource (space)
• no resource partitioning (all species equal competitors)
• likelihood of creating and acquiring resource (space) due to random chance (deaths and larval settlement unpredictable)
• equal likelihood of settlement from larval pool

but, requires some mechanism in plankton to maintain similar relative abundance of species in larval pool! Assumes species compositions on different reefs out of sync!

Lottery Hypothesis
(Connell’s “Equal Chance” Hypothesis)
Peter Sale 1977

Predictions:
• unpredictable as to what species will recruit to any location or at any time
• maximum total abundance across species (K)
• relative abundance of species fluctuates unpredictably
• including after perturbation
Lottery Hypothesis

Lottery Model – Storage Effect
(Hutchinson’s “Gradual Change” Hypothesis)
Bob Warner and Peter Chesson 1985

Assumptions:
• competition based (resource limitation)
• same assumptions as lottery hypothesis, but
• relative recruitment success of species changes through
time (akin to “gradual change” hypothesis)
• variable success due to variation in larval production,
planktonic conditions, settlement conditions
• species persist through bad recruitment periods and
“store” recruitment events in extended lifetime (age
classes) of adults

Predictions:
• same as Lottery Hypothesis but different mechanism

Recruitment Limitation Hypothesis
Peter Doherty 1983, Ben Victor 1986

Assumptions:
• Assumes high mortality of pelagic larvae limits number
of recruits to benthic populations
• Larval supply limits recruitment below that which is
required to saturate resources
• No competition so mortality is density-independent

Predictions:
• total numbers and relative abundance fluctuates
with variable larval supply
Recruitment Limitation Hypothesis

Species A
Species B
Species C

K
Total abundance
Species A
Species B
Species C

Time
Proportional abundance

“Pluralistic” Approach

Assumptions:
- probably a combination of several of the above
- varying in importance over scales of space and time
- because several of these competing hypotheses create similar patterns of variability in relative and combined numbers, helps to distinguish them experimentally
- involves orthogonal manipulations of competition, predation and disturbance

Predictions:
- relative importance of post-recruitment competition
- extent to which recruitment is modified by post-recruitment processes

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**Metapopulations**

- **Local Population:** “Population, subpopulation, deme” – Set of individuals that live in the same habitat patch and therefore interact with each other; most practically applied to “populations” living in such small patches that all individuals practically share a common environment.
- **Metapopulation:** Set of local populations within some larger area, where typically migration from one local population to at least some other patches is possible.

**Types of Metapopulations**

Metapopulation (Levins 1970, denBoer 1988)

- Traditional
- Central-Peripheral
- Metapopulation
- Source-Sink

**Formal Definitions** (Hanski and Simberloff 1997)

- **Local Population:** “Population, subpopulation, deme” – Set of individuals that live in the same habitat patch and therefore interact with each other; most practically applied to “populations” living in such small patches that all individuals practically share a common environment.
- **Metapopulation:** Set of local populations within some larger area, where typically migration from one local population to at least some other patches is possible.
Key Processes

- Extinction
  - usually a constant risk multiplied times number of occupied patches
- Colonization
  - dependent on number of occupied (sources of colonists) and empty (targets) patches
- Turnover
  - Extinction of local populations and establishment of new local populations in empty habitat patches by migrants from existing local populations

Diversity Stability Hypothesis

Key prediction with respect to stability

![Stability vs. Number of local populations graph](image)
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Example - Blue Headed Wrasse

- Initial phase males
- Females
- Terminal males
  - Arise from either initial phase males or females
- Initial phase males tend to group spawn with females
- Much rarer Terminal phase males hold territory and monopolize females

Sequential hermaphrodites - when to switch

When to switch?

Size

Fitness

Initial phase males or females
Terminal males
Pays to switch
How the number of terminal males affect the system

Number of Terminal Males

Fitness

Size

Fewer

More

Initial phase males or females

Terminal males

Larval settlement behavior

- Why have strong settlement behavior?
- Simple - Fitness (growth survivorship, fecundity increased by use of settlement behavior)
- Complex -

Settlement location very important

Likelihood of Using Cue

Reliability of Cue

Settlement location not very important