“Bipartite” life cycle of benthic marine fishes with pelagic larvae

“Closed” Populations
- Little or no exchange among populations
- Supply → Production

“Open” Populations
- Significant exchange among populations
- Supply ↔ Production

- Definitions:
  a) settlement - the permanent transition from the pelagic environment to the benthic environment
  i.e. from the planktonic dispersive stage to the sessile/sedentary benthic stage

  b) recruitment - broadly, the addition of individuals to a population
  theoretically, same as settlement, BUT rarely see/record settlement (brief, unpredictable, involves small propagules, often occurs at night)...

  operationally, what is recorded as a new addition to a population. (i.e. what you see the first time you see an individual)

Life History Traits
- (individual, heritable, species-wide)
- longevity, fecundity
- reproductive modes
- life cycle

Population Attributes
- distribution
- structure (size, age, genetic, spatial)
- dynamics

Community Attributes
- structure (composition, abundance)
- diversity
- biogeography
- dynamics
b) recruitment  (Keough and Downes 1982)

i) subjective, arbitrary as to when and what is measured
- daily, weekly, monthly, annually

ii) incorporates settlement and post-settlement mortality and movement

iii) therefore, estimate and relationship to settlement depends very much on:
- sampling frequency
- patterns of post-settlement mortality (density-independent and density-dependent)

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VIII. Settlement and Pre-settlement Processes

i) Stability, population regulation and complex life histories

A) Post-settlement processes - generally thought to be deterministic

i) competition: logistic growth (pop), niche diversification (comm)

- predation: functional response (pop), switching (pop), keystone (comm)

- physical environment: resource (space) limitation, carrying capacity, habitat partitioning

Species interactions all have predictable effects on populations and communities

but recall also,

ii) disturbance does not - disrupts patterns, can destabilize systems

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I) Stability, population regulation and complex life histories

B) Populations- can come to an equilibrium, therefore

Community- organization can be stabilized

because of feedbacks (involve mechanisms of regulation)
(e.g., biomedical or thermostat)

i) because the effects of ecological processes are manifested in next generation

- e.g., logistic growth curve

\[ \frac{dN}{dt} = rN \left( K - N \right) / K \]

remember, \( \frac{dN}{dt} = rN \left( K - N \right) / K \)

Which means that the change in a population (what it will be) depends on what the population size is now. As population approaches \( K \), present population size constrains the number of offspring it produces.
Limited Growth - caused by changes to birth and death rates that are density-dependent

Birth rate --- Death rate

Population (N) --- Population (N)

Rate

Rate

Per capita growth rate (r)

ii) So there's this feedback between generations

a) how? ➔ either birth rate decreases, or death rate increases with changes in population size

b) either way, assumption is that the feedback occurs locally ➔ local birth rates and local death rates affect size of population in next generation

Now...

C) Contrast simple life history: (cats, dogs, people)

Because of limited dispersal, this all occurs in the same local environment.

So, life stages interact directly and influence each other's performance as well as the next generation.

With complex "bipartite" life cycle of benthic marine organisms with pelagic larvae:

Larvae

survive, grow, develop, disperse

Pelagic Environment

reproduce --- settlement

Benthic Environment

Adult Juvenile

survive, grow, mature

Result of complex life history:

1) local supply of larvae (perhaps settlement) is decoupled from local reproduction ➔ settlers come from elsewhere

i.e., no coupling of local reproduction and next generation of settlers

therefore...

2) no potential for births as a feedback mechanism, theory suggest this could act to destabilize populations — we’ll come back to this

we’ve removed the importance of births in population regulation and replaced with variable settlement rates!
II) Open and closed populations (two extremes of a continuum)
A) closed population - population where individuals recruit back into (and replenish) population of parents
B) open population - population where individuals recruit to populations different from parents (decoupling of local offspring production from recruitment)

C) Reality - populations exist along a continuum of openness depending on...
1) spatial scale - increasing spatial scale of “population”, reduces openness

D) if increasing openness of population acts to destabilize populations then there should be a relationship between population variability and planktonic duration: (because no feedback from production)

Predict: closed populations should be less variable than open ones
Hypothesis: closed populations (species with shorter larval durations) should be less variable than open ones

Russell Schmitt tested the relationship predicted by this hypothesis using fish species in So. Cal. Bight

Temporal variability predicted

short planktonic duration

long planktonic duration

closed pop. s (surperches): intermediate variability driven by local habitat variability over time

fully open (long larval duration): highest variability driven by vagaries in the plankton

intermediate openness (limited larval duration): lowest variability

Conclusion: perhaps some population openness dampens variability by reducing both of these other sources of variability. i.e., some dispersal increases (homogenizes) scale at which population responds to habitat variability

III) Settlement and density dependence

A) The theoretical complications arising from open systems and no local feedbacks assume what?

1) That the number of adults is in large part determined by larval supply and the number of settlers:

e.g., Adults \( \propto \) (settlers):

\[
\text{Adults}_{(t+1)} = \text{Settlers}_t \times \text{Survival}_t
\]

2) if instead adult density is unrelated to larval supply / settlement, this means:

a) most influential processes occur post-settlement and, therefore,
b) decoupling between local reproduction and subsequent local settlement is unimportant to regulation and stability

### III) Settlement and density dependence

B) How would this occur? if post-settlement processes act in a (complete) density-dependent manner

1) example:

<table>
<thead>
<tr>
<th>Density-independent</th>
<th>Density-dependent</th>
</tr>
</thead>
<tbody>
<tr>
<td>settlers</td>
<td>survive</td>
</tr>
<tr>
<td>2</td>
<td>50%</td>
</tr>
<tr>
<td>10</td>
<td>50%</td>
</tr>
<tr>
<td>100</td>
<td>50%</td>
</tr>
</tbody>
</table>

| settlers | survive | adults |
| 2 | 100% | 2 |
| 10 | 20% | 2 |
| 100 | 2% | 2 |

Density-independent: same probability of surviving regardless of density

Density dependence: no relationship between adult # and settler #
brings us to another major paradigm in marine ecology.

IV) Recruitment limitation: [definition], occurs when number/rate of settlers (“recruits”) is sufficiently low (i.e. limited) because of low production or high mortality in the plankton that adult density remains below carrying capacity, thereby precluding competition:

simple case, assume single pulse of recruits (settlers):

Therefore, occurs

A) when density dependence doesn’t fully eliminate the relationship between # of adults and # settlers

B) evidence for recruitment limitation: most is from coral reef fish literature

e.g., Victor 1983, Doherty 1983, Doherty and Fowler 1994 (in readings)

Now, a more unified perspective typified by...

IV) Recruitment limitation

Classic invertebrate example is Connell 1985 JEMBE:

C) So as predicted, (d-i) settlement is important and limiting but only to a certain point, where (d-d) post-settlement processes eventually overwhelm variability in settlement (i.e. increasing settlers has no affect on population size)

D) Up to a certain level, settlement could affect stability [population size] because:

i) settlement affects local abundance, and

ii) settlement is unrelated to local production no linkage among generations and therefore more likely to be de-stabilizing!
IV) Recruitment limitation

<table>
<thead>
<tr>
<th>Density-independent</th>
<th>Density-dependent</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. Adults (t+1)</td>
<td>Settlement rate (t) (number per time)</td>
</tr>
</tbody>
</table>

E) After a certain level, settlement unimportant to stability or regulation (equilibrium set by carrying capacity) at which point:

i) settlement variability has no effect on local abundance (beyond some level of settlement always get same # of adults)

ii) only local processes affect local abundance