C) Processes affecting settlement

III. The evolution of behavioral cues (for settlement)

2) Larval behavior

a) Utility of behavioral cues
   - larval period critical – relocation after settlement is difficult or impossible... life-long fitness consequences
   - consequence of settlement
     i) indicates “good” habitat / conditions for the species
     ii) facilitates reproduction (particularly) for individuals that are sessile
     iii) safety in numbers (e.g., swamping predators)

b) Why not always have cues? — costs

b) Why not always have cues? two kinds of costs... (mistakes)

   1) cue is inappropriate...
      leads to settlement in inappropriate conditions
   2) places without cue are in fact appropriate...
      think about coral heads without blue chromis

   probability of evolving response to cue

   reliability of cue

   cost of mistake (not using cue)

   high

   low

   = death

IV. Contribution of larval behavior to vertical zonation patterns

A) Processes affecting zonation → 4 possibilities

1) Larvae may be stratified in water column (behavior or hydrodynamic effects) and land at different tidal heights

Adult pattern (zonation):

Given...

i) the costs of adapting to inappropriate cues,

ii) how many species exhibit this behavior to so many different kinds of cues

iii) the implied strength of selection for these behavioral responses

iv) the importance of settlement as a life-long consequence for fitness (especially for sessile species)...

settlement must be an extremely important stage in the life cycle of a marine organism

can all this behavior at settlement contribute to those patterns that drove ecologists to study intertidal ecology (i.e. patterns of zonation)?
IV. Contribution of larval behavior to vertical zonation patterns

A) Processes affecting zonation → 4 possibilities

2) Larvae may (1) be mixed in water column, (2) exhibit settlement behavior (3) settle within appropriate zone

Adult pattern (zonation):

3) Larvae may (1) be mixed in water column, (2) show no settlement behavior (3) settle randomly and (4) die back to appropriate zonation (post-settlement processes!)

Adult pattern (zonation):

B) Stratification of larvae in water column

Grosberg 1982, senior thesis! seminal paper never repeated to my knowledge

a) System: Santa Cruz harbor, 2 species of barnacle on pier pilings

i) *Balanus glandula* - upper intertidal barnacle

ii) *Balanus crenatus* - lower intertidal barnacle

b) Pattern:

![Graph showing tide height and adult density](image)
c) Question: What causes vertical zonation?

d) Hypotheses:
   i) HA1: early post-settlement mortality limits species distribution (sensu Connell)
   ii) HA2: stratification of larvae limits distribution → via behavior

e) Test:
   i) HA1 early post-settlement mortality
   10 x 10 cm plates
   Sampled weekly during a period of high settlement - allows detection of 1–7 day old individuals

f) Results:

B) Stratification of larvae in water column

Question: What causes vertical zonation?

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Question: What causes vertical zonation?
e) Results — differ between species:
1) 94% of glandula larvae taken in surface waters (irrespective of tidal sequence)
2) 98% of crenatus larvae were collected < 0 m mllw, meaning their distribution in water column changed as a function of tide

f) Conclusions—
1) Distribution of adults determined by position of larvae in water column
2) Larval distribution set by two different behaviors:
   a) B. glandula stays in surface water, which over tidal sequences travels from about -1.2 to 1.8 m (abundances correspond to time at tidal height)
   b) B. crenatus stays below a particular tidal level — orients to bottom?

C) Interactive effects of vertical distribution of larvae and biogenic structure on the spatial and temporal patterns of recruitment
Example: Carr 1994 Ecology

a) Question: Does kelp provide settlement habitat for reef fishes, and if so, does the temporal and spatial variability of kelp influence patterns of fish recruitment?

b) System: Forests of giant kelp, Macrocystis pyrifera and the kelp bass, Paralabrax clathratus at Santa Catalina Island.

Example:

- **Hypothesis 1**: If giant kelp influences recruitment, there will be a positive relationship between abundance of kelp and kelp bass recruits
- **d) Pattern:** and test of first hypothesis:
  Greater density of kelp bass settlers in areas of a reef with giant kelp compared to areas without
**d) Pattern:** among reefs and years...

Density of kelp bass settlers increases with increasing density of giant kelp... but it is not linear!

**c) Hypothesis 2:** Local kelp bass recruitment should respond to manipulated density of giant kelp

**e) Conclusions:**

i) Local and “regional” patterns of kelp bass recruitment are influenced by dynamics of giant kelp abundance

ii) The relationship is not based strictly on plant density, but on biomass (shelter!). Because kelp biomass changes with plant density, recruitment relationship is asymptotic.

iii) Giant kelp facilitates recruitment of kelp bass by providing habitat that they encounter as they pass over reefs

**Settlement (post-settlement): habitat structure**

1. *Macrocystis* (kelp bass in southern California)
   - e.g., Carr 1994, Ecology
   - positive correlation between recruitment and kelp density - demonstrated experimentally

2. *Macrocystis* (kelp surfperch in southern California)
   - e.g., Anderson 1994, MEPS
   - manipulated presence of giant kelp canopy and monitored recruitment

3. Sea urchins (blue-banded goby in southern California)
   - e.g., Hartney and Grorud 2002, Oecologia
   - manipulated presence of urchins and monitored recruitment
**Seagrass beds**

**Linear spatial scales**
- 1 cm
- 10 m
- 100 m
- 1 km
- 10 km
- 1 dm
- 100 km
- 1000 km
- 10000 km

**Temporal scale**
- 1 hour
- 1 min
- 1 day
- 1 week
- 1 month
- 1 year
- 1 decade
- 100 yrs
- 1000 yrs

**Surface**
- Waves
- Tides
- Langmuir cells
- Migration
- Coastally trapped waves
- Seasonal upwelling
- Mesoscale eddies
- ENSO
- PDO

**Internal waves**
- Kelp forests
- Small-scale fronts, plumes, runoff

**V. (Early) post-settlement processes as sources of variation in recruitment**

a) Recall that “recruitment” estimates occur at some point subsequent to settlement

b) Do post-settlement processes alter patterns of settlement and recruitment?

c) Can post-settlement processes cause density-dependent mortality that would (de-couple) patterns of settlement and recruitment?

d) How important are competition and predation as sources of variation in recruitment AND density-dependent mortality?

**Sources of spatial and temporal variation in recruitment**

- Competition
- Predation
- Survival
- Growth
- Movement

**Early post-settlement: competition**

Conspecific and interspecific resident effects
- e.g., Steele 1997a, Ecology
- Black-eyed and blue-banded gobies in So. California
- Manipulated presence of adults of both
- Settlement of black-eyed (-) “influenced” in presence of adult conspecifics
- Settlement of black-eyed not influenced by presence of adult blue-banded
- Settlement of blue-banded (+) influenced in presence of adult conspecifics
- Settlement of blue-banded not influenced in presence of adult black-eyed
V. (Early) post-settlement processes as sources of variation in recruitment

General approach:

i) To test for predator effects, manipulate presence and absence of predators

ii) To test for density-dependence, manipulate density of settlers

iii) To test for density dependence caused by predation, manipulate BOTH orthogonally

Conclusions

(1) Post-settlement mortality is a source of variation in recruitment

(2) Predation is an important source of post-settlement mortality

(3) Predation is also a source of density-dependent mortality, which can decouple estimates of settlement and recruitment (think about this with respect to testing for recruitment limitation)