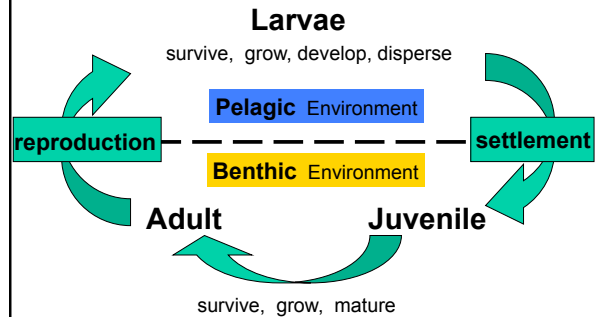


## Rocky Intertidal Ecology

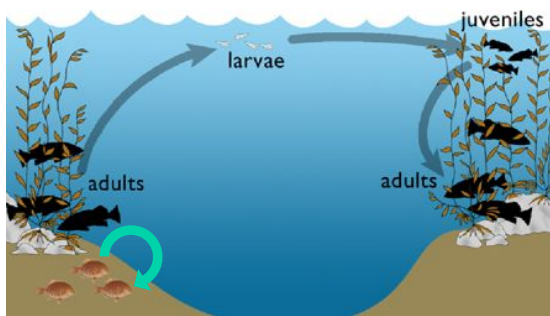
- I. Population Structure (review)
- II. Settlement & Recruitment
- III. Zonation
- IV. Experiments that changed Ecology



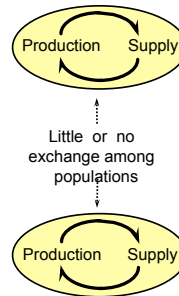
## “Bipartite” life cycle of benthic marine organisms with pelagic larvae review



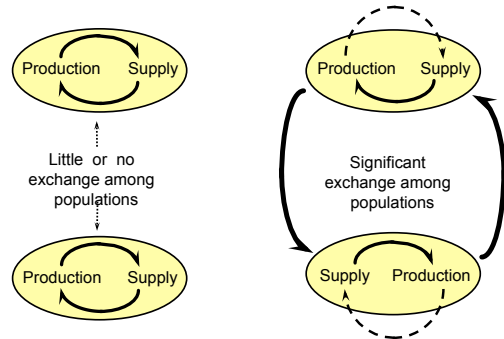
## “Bipartite” life cycle of benthic marine organisms with pelagic larvae review



## “Closed” Populations review



## “Open” Populations review



### Definitions:

**a) settlement** - the permanent transition from the pelagic environment to the benthic environment

(from the planktonic dispersive stage to the sessile/sedentary benthic stage)

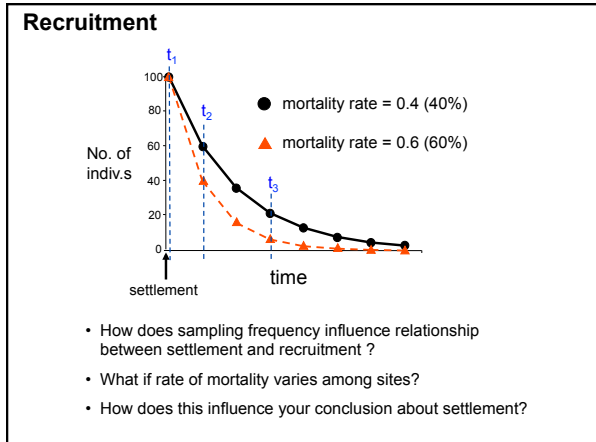
**b) recruitment** - the addition of individuals to a population

- could be same as settlement, BUT we rarely observe settlement (it is brief, unpredictable, involves small propagules, often occurs at night)...

- operationally, a **recruit** is what we **record** as a *new individual* in a population

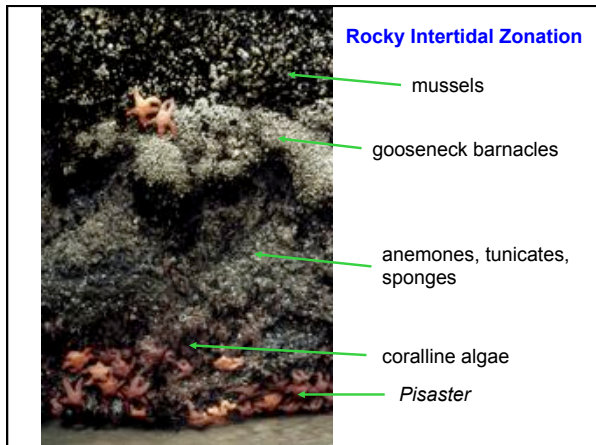
### **Recruitment** (Keough and Downes 1982)

- i) subjective, arbitrary as to when and what is measured (e.g., *daily, weekly, monthly, annually*)
- ii) incorporates settlement and post-settlement mortality and movement
- iii) therefore, this estimate and its relationship to settlement depends on:
  - **sampling frequency**
  - **patterns of post-settlement mortality** (density-independent and density-dependent)



**In the beginning...**  
when ecologists first wandered into the rocky intertidal...

I. **Pattern:** species distributed in discrete zones relative to elevation and tidal height



- i) zonation exhibited across a very short distance in intertidal
- implies very strong determinants of distribution and abundance
  - great opportunity to examine causes of zonation



- ii) Almost all of the **early ecological studies** on zonation concentrated on **processes affecting individuals after settlement** ("postsettlement": i.e., juveniles and adults in benthic habitat)

Reasons:

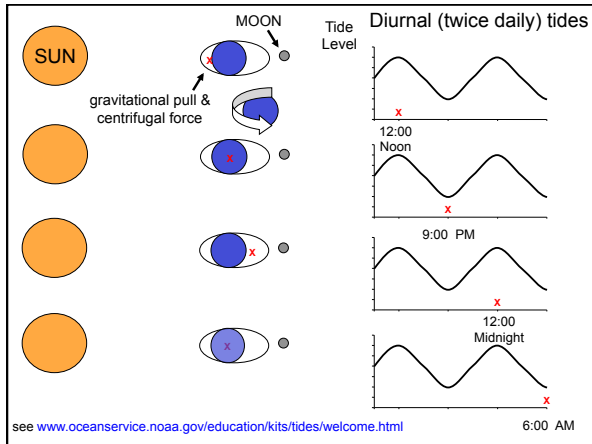
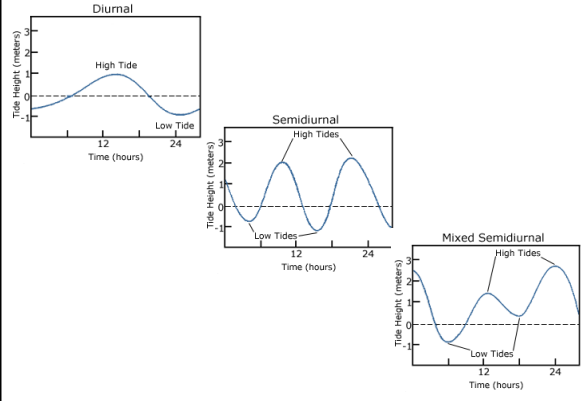
- i) those were the life stages for which patterns were described (zonation)
- ii) logistically easier to work on benthic stages than larvae
- iii) pool of larvae thought to be limitless (thus, what happened after settlement would be more important)

**II) Tides as a determinant of zonation patterns in intertidal**

- i) intertidal zone is an **ecotone** -- the interface of two distinct habitats: terrestrial & marine  
(higher more terrestrial tolerant; lower more marine tolerant)
- ii) what could cause such sharp boundaries in species distributions?
  - seemed clear that such boundaries had to be the result of **physical factors**  
(rapid shift in environmental conditions and successful species)
- iii) what was the most likely physical factor that could cause zonation in intertidal areas?

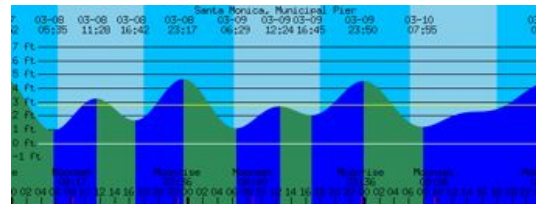
-- **Tides!**

**II) Tides as a determinant of zonation patterns in intertidal**



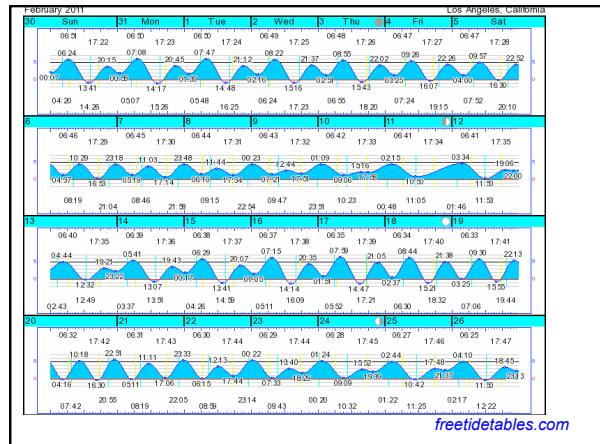
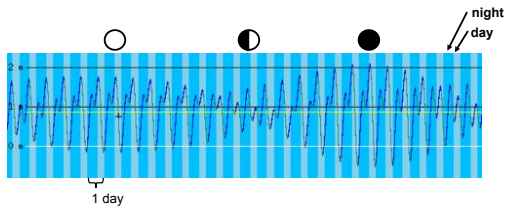
Topography of ocean basin modifies tidal current so that the 2 high tides (and 2 low tides) per day are not same height.

- this is referred to as **mixed semi-diurnal tides**



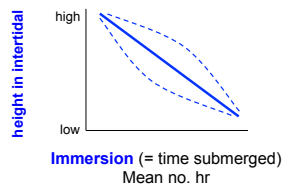
mean sea level <http://tbone.biol.sc.edu/tide/>  
 0 ft mark at MLLW (mean lower low water)  
 = mean lowest tides over the year at that location

- when moon is on the same side as sun (new moon), or opposite sun (full moon), tides are **strong (spring tide)**
- when moon is 90° to sun and moon, tides are **weak (neap tide)**
- time of a tide lags ~ 50 minutes each day because moon rotates 12° around the earth each day



## II) Tides as a determinant of zonation patterns in intertidal

- a) *Tides are sinusoidal* -- might lead you to believe that the relationship between **immersion time** (time underwater) and **tidal height** decreases smoothly (and linearly or gently curvilinear) with increasing tidal height:

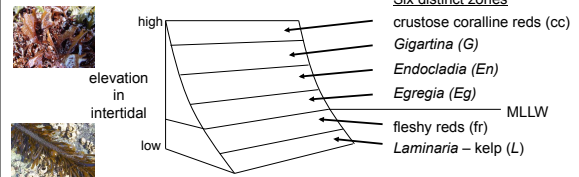


Does this correspond intuitively to sharp breaks in zonation patterns?

An early example exploring effects of immersion (tides) on zonation...

### b) Example: Doty 1946 (Ecology 27:315-328)

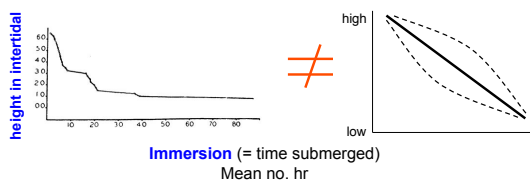
- i) **Pattern:** sampled distributions of species of macroalgae along CA and Oregon coasts and found:



- ii) **General hypothesis:** tidal fluctuation and differential tolerance to immersion causes zonation of species in intertidal

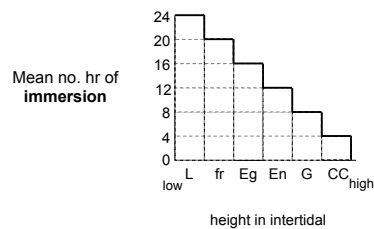
- iii) **Specific hypothesis:** species zones will correlate with discrete zones of immersion ("critical tide levels")

- iv) **Test:** Calculated the actual immersion times over the tidal range:



- v) **Results:** dramatic non-linear steps in immersion...

- iv) **Test:** Calculated the actual immersion times over the tidal range:



- v) **Results:** dramatic non-linear steps in immersion that correlated with algal zonation!

- vi) **Conclusion:** physical factors - immersion - control species distribution and determine zonation of species in intertidal

**c) Questions / observations:**

- i) **Should upper and lower limits both be set by physical factors?**
  - Where do intertidal species come from?
  - Why would physical factors determine lower limit?
- ii) critical tidal levels were less good at explaining animal distributions; particularly mobile animals – does this cause rejection or modification of the general hypothesis?
- iii) **Alternative hypotheses?**

<p><u>Upper limits</u></p> <ul style="list-style-type: none"> <li>a) radiation (UV)</li> <li>b) desiccation</li> <li>c) thermal stress</li> <li>d) freshwater</li> <li>e) lack of settlement - larval supply</li> <li>f) food availability</li> <li>g) biotic interactions</li> </ul>	<p><u>Lower limits</u></p> <ul style="list-style-type: none"> <li>a) submersion</li> <li>b) lack of settlement - larval supply</li> <li>c) biotic interactions</li> </ul>
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**c) Questions / observations:**

- iv) How best to distinguish among these alternative hypotheses?
- v) What processes or mechanisms are responsible for each alternative?

**III) Connell and the experimental revolution**

- a) Most ecological field studies prior to study we are to examine were purely descriptive (like Doty's)

Joe Connell



PhD in **Millport, Scotland**  
Ecology 1961; Ecol. Monographs 1961

**THE INFLUENCE OF INTERSPECIFIC COMPETITION AND OTHER FACTORS ON THE DISTRIBUTION OF THE BARNACLE, *CHTHAMALUS STELLATUS***

JOSEPH H. CONNELL  
*Department of Biology, University of California, Santa Barbara, Santa Barbara, California*

**INTRODUCTION**

Most of the evidence for the occurrence of interspecific competition in animals has been gained from laboratory populations. Because of the small amount of direct evidence for its occurrence in nature, competition has sometimes been assigned a minor role in determining the distributions of animal communities.

Indirect evidence exists, however, which suggests that competition... influenced the distribution of the barnacle.

**Cited over 1000 times!**

In the course of an investigation of the animals of an intertidal rocky shore I noticed that the adults of 2 species of barnacles occupied 2 separate horizontal zones with a small area of overlap, whereas the young of the species from the upper zone were found in much of the lower zone. The upper species, *Cthamalus stellatus* (Pall.) thus settled but did not survive in the lower zone. It seemed probable that this species was outcompeted by the lower one, *Balanus balanoides* (L.), in a struggle for a common resource which was in short supply. In the rocky intertidal region, space for attachment and growth is often extremely limited. This paper is an account of some observations and experiments designed to test the hypothesis that the absence in the lower zone of adults of *Cthamalus* was due to interspecific competition with *Balanus* for space.


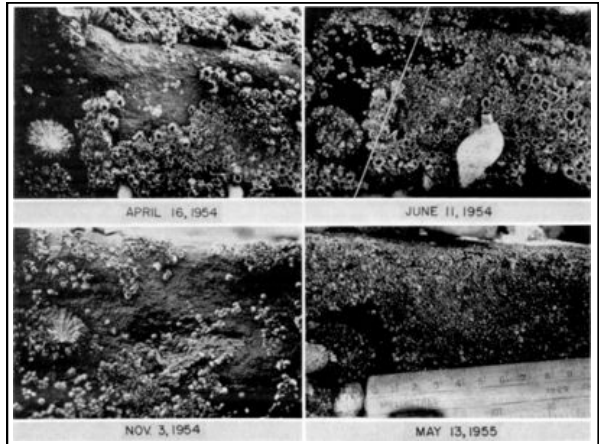
I would like to thank Prof. C. M. Yonge and the staff of the Marine Station, Millport, for their help, discussions and encouragement during the course of this work. Thanks are due to the following for their critical reading of the manuscript: C. S. Ebbot, F. V. Frank, G. Hardin, N. C. Hammon, E. Oran, T. Park and his students, and my wife.

**Distribution of the species of barnacles**

The upper species, *Cthamalus stellatus*, has its central distribution in the Mediterranean; it reaches its northern limit in the Shetland Islands, north of Scotland. At Millport, adults of this species occur between the levels of mean high water of neap and spring tides (M.H.W.N. and M.H.W.S.; see Figure 3 and Table 1). In southwest England and Ireland, adult *Cthamalus*

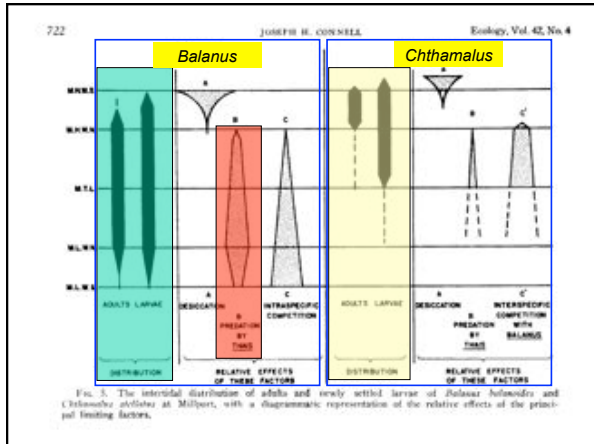
**III) Connell and the experimental revolution**

- b) **System:** two species of barnacles and a carnivorous gastropod in the rocky intertidal:
  - i) *(Semi)Balanus balanoides* - a large barnacle
  - ii) *Cthamalus stellatus* – a small barnacle
  - iii) *Thais (Nucella) lapillus* – predatory snail

**c) Pattern:** disjunct vertical distribution of adults of the two barnacle species in intertidal zone

- 1) adult distributions more restricted than recruit distribution:
  - at upper limits for both species
  - at lower limits for *Cthamalus*
- 2) distribution of *Cthamalus* and *Balanus* overlap extensively as recruits but little as adults
- 3) *Thais* only found in adult distribution of *Balanus*



d) Hypotheses (and circumstantial evidence)

1) Upper limits

- a) set by settlement distribution?
  - inconsistent with observation that settlement occurs higher than adult distribution

- b) species interactions? (untested by Connell)

Why untested?

- i) *Chthamalus* - few organisms above it (including predators)
- ii) *Balanus* - no evidence from other work that *Chthamalus* negatively affects *Balanus*

d) Hypotheses (and circumstantial evidence)

1) Upper limits

- c) Heat stress / desiccation - data and observations were consistent with this hypothesis (mechanism untested)
  - i) settlement did occur above adult distribution for both species (rejects settlement hypothesis)
  - ii) much greater mortality for juveniles above adult distribution

d) Hypotheses (and circumstantial evidence)

2) Lower limits

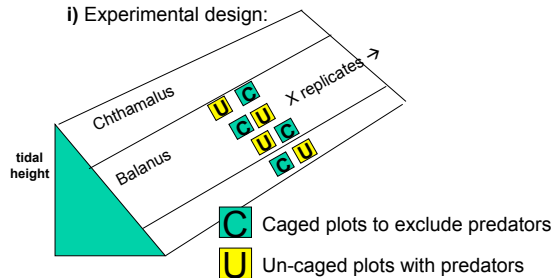
a) *Balanus*

- i) set by settlement distribution?
  - perhaps, because lower limits of both recruits and adults are similar
- ii) set by predation by *Thais*?
  - Connell tested by experiments with cages
  - paired replicates at different tidal heights within and below range of *Balanus*

d) Hypotheses (and circumstantial evidence)

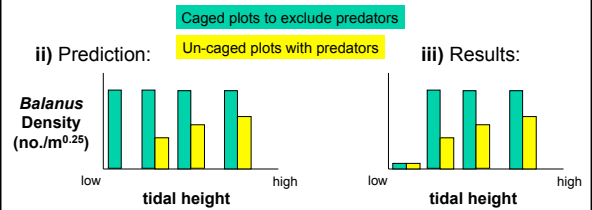
2-a-ii) Lower limit of *Semibalanus* set by predation?

i) Experimental design:



d) Hypotheses (and circumstantial evidence)

2-a-ii) Lower limit of *Balanus* set by predation?



- a) predation was more intense at lower limits, but...
- b) *Balanus* were not completely excluded at any tidal height
- c) lower limit not entirely set by predation
- 3) other Biological Interactions? e.g., competition with algae (untested)
- 4) Physical factors? — immersion— untested — why?

d) Hypotheses (and circumstantial evidence)

2) Lower limits

b) *Chthamalus*

i) Physical processes — immersion

- placed rocks with *Chthamalus* juveniles in tidepools (of same tidal ht)
- compared survivorship to those not in tidepools
- no major difference in survivorship
- conclusion: immersion not important

ii) Settlement distribution — unlikely

- settlement distribution much lower than adult distribution
- indicates post-settlement mortality

d) Hypotheses (and circumstantial evidence)

2) Lower limits

b) *Chthamalus*

iii) Predation/Competition — tested both at once (allows for test of multiple causality and interaction among factors)

- attached rocks with juvenile *Chthamalus* and *Balanus* at several tidal heights
- removed *Balanus* from 1/2 of each rock
- half of rocks at each tidal height were enclosed in cages (to exclude predators)

d) Hypotheses (and circumstantial evidence)

2-b-iii) Lower limits of *Chthamalus* set by predation and/or competition?

i) Experimental design:

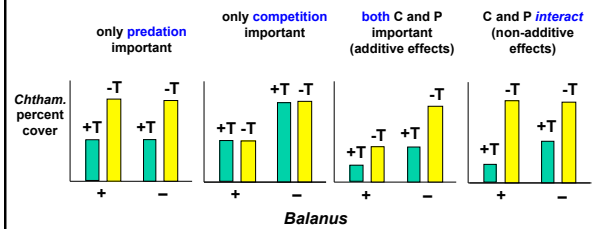
	<i>Balanus</i>	
	+	-
+	+	+
-	-	-

- remove *Balanus* from 1/2 of each rock
- half of rocks at each tidal height were enclosed in cages (to exclude predators)

d) Hypotheses (and circumstantial evidence)

2-b-iii) Lower limits of *Chthamalus* set by predation and/or competition?

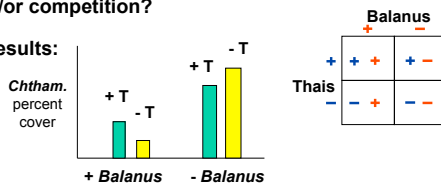
ii) Predictions:



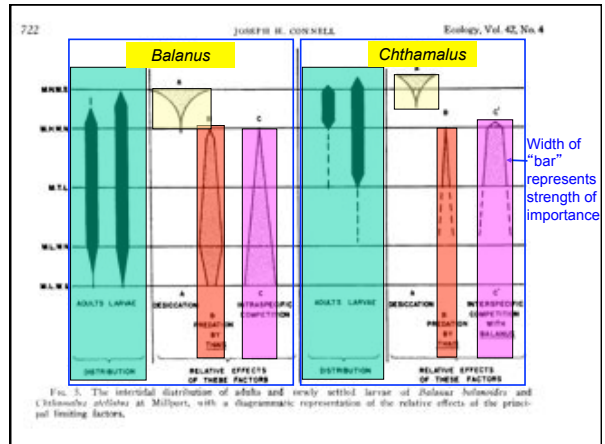
d) Hypotheses (and circumstantial evidence)

2-b-iii) Lower limits of *Chthamalus* set by predation and/or competition?

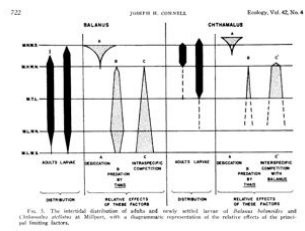
ii) Results:



- *Balanus* limits *Chth* distribution and abundance (competition)
- *Thais* normally does not control *Chth* by itself
- *Balanus* and *Thais* jointly affect *Chth* distribution and abundance
- *Thais* eats *Balanus*, enhancing *Chth* distribution and abundance



### III) Connell and the experimental revolution



#### Impacts:

- 1) "Connell's rule": upper limits set by physical processes, lower limits set by species interactions
- 2) The dawn of appreciation and exploration of experimental field ecology