## Benthic biodiversity (α, β, and γ) & Benthic population processes

**Class 9: Tu September 30, 2008**
**Class 10: Th October 2, 2008**

### Slide 1 Benthic biodiversity (α, β, and γ) & Benthic population processes

NOTES:

## Class schedule

**Order of topics**

- Tuesday: overview of benthic community structure, with a start of benthic population processes
  - Tools of the trade: alpha, beta & gamma
    - Gallagher, E. D. & K. E. Keay. 1998. Organism-sediment-contaminant interactions in Boston Harbor. Pp. 89-132 in K. D. Stolzenbach and E. E. Adams, eds., Contaminated Sediments in Boston Harbor. MIT Sea Grant College Program, Cambridge MA. 170 p. [There is a slightly expanded version of this document available as a pdf at http://www.es.umb.edu/edg/ECOS630/GallagherKeay98.pdf]
- Thursday, Competition, predation & pollution
  - Competition & predation in soft- and hard-bottom benthos
    - Gallagher, E. D., G. B. Gardner and P. A. Jumars 1990. Competition among the pioneers in soft bottom benthic succession: field experiments and analysis of the Gilpin-Ayala competition model. Oecologia *83*: 427-442.
    - Whitlatch, R. B. 1980. Patterns of resource utilization an coexistence in marine intertidal deposit-feeding communities. J. Mar. Res. *38*: 743-765.

### Slide 2 Class schedule

NOTES:

## Required reading, community structure

*Chapter 5: Global Patterns of Benthic Community Structure Especially Deep-Sea Diversity*

*Etter, R.J. and L. S. Mullineaux. 2001. Deep-sea communities. Pp. 367-393 in M. D. Bertness, S. D. Gaines, and M. Hay ,Eds., Marine Community Ecology. Sinauer Associates, Sunderland, Massachusetts. 550 pp*

*Gallagher, E. D. & K. E. Keay. 1998. Organism-sediment-contaminant interactions in Boston Harbor. Pp. 89-132 in K. D. Stolzenbach and E. E. Adams, eds., Contaminated Sediments in Boston Harbor. MIT Sea Grant College Program, Cambridge MA. 170 p. [There is a slightly expanded version of this document available as a pdf at http://www.es.umb.edu/edg/ECOS630/GallagherKeay98.pdf]*

*Jumars, P. A. and E. D. Gallagher. 1982. Deep-sea community structure: three plays on the benthic proscenium. Pages 217-255 in* W. G. Ernst and J. G. Morin, *eds.*, The environment of the deep sea; Rubey Volume II, Prentice-Hall, Englewood Cliffs, N.J.

### Slide 3 Required reading, community structure

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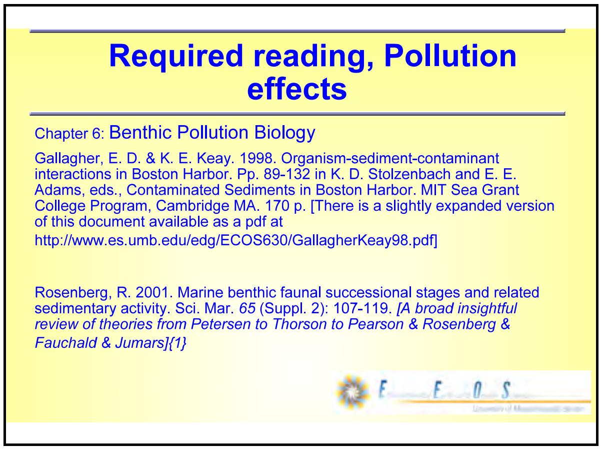


## Slide 4 Required reading, Pollution effects

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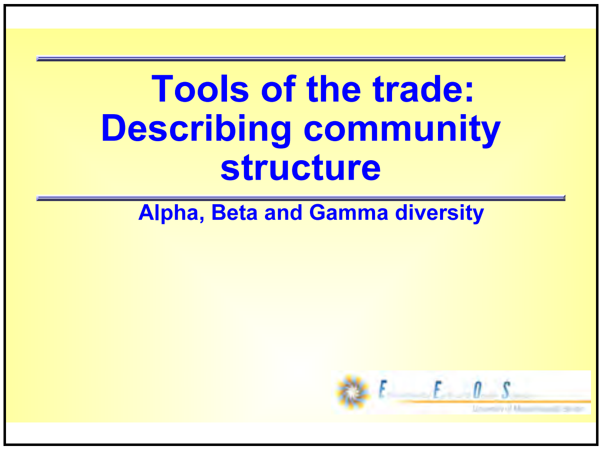


## Slide 5 Tools of the trade:

Describing community structure

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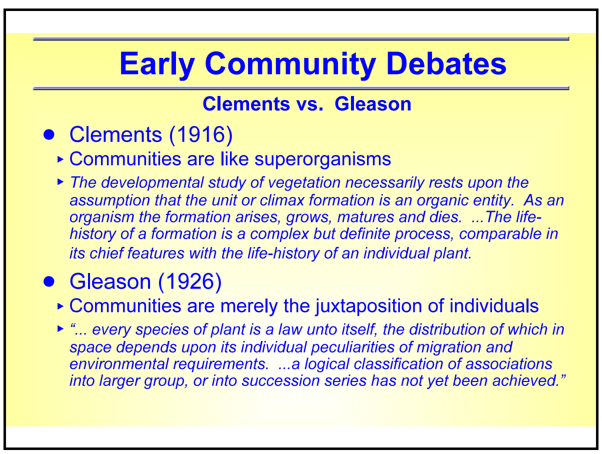


## Slide 6 Early Community Debates

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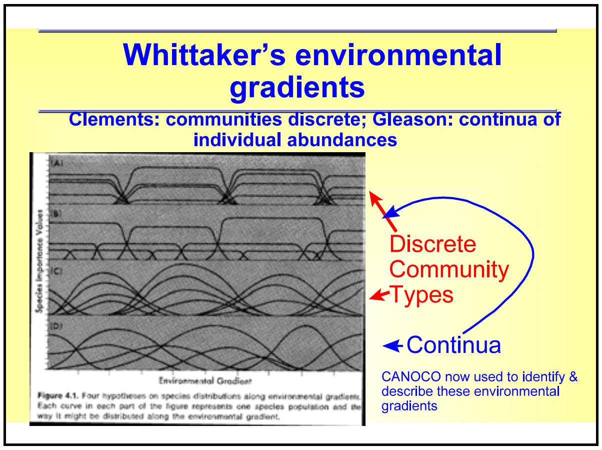
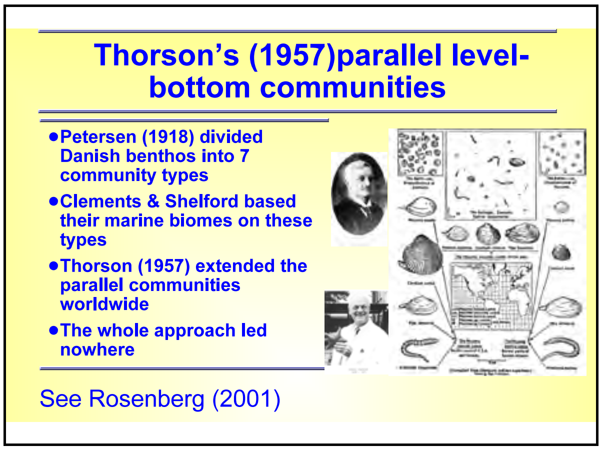



## Slide 7 Whittaker's environmental gradients

NOTES:




## Slide 8 Thorson's (1957)parallel level-bottom communities

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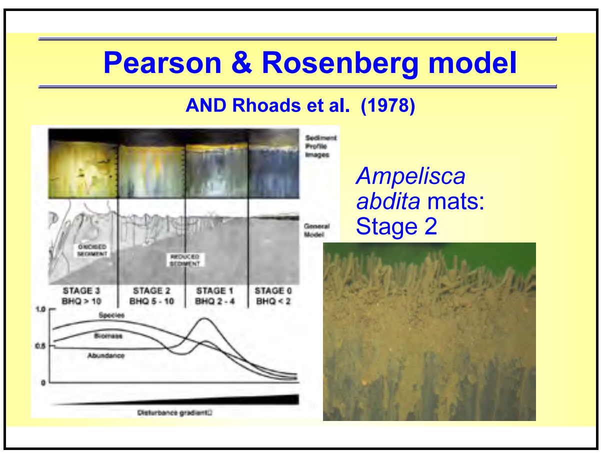
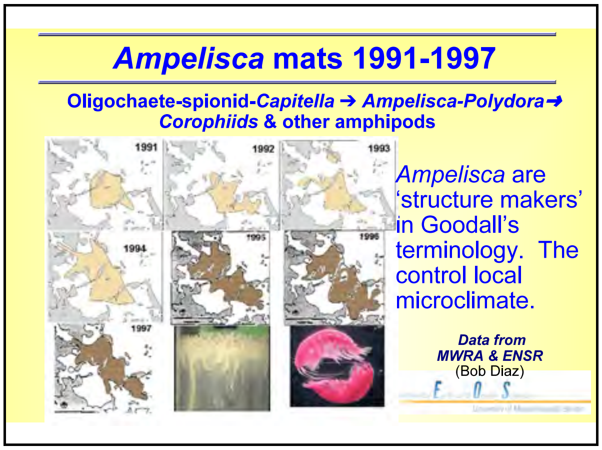



## Slide 9 Pearson & Rosenberg model

NOTES:

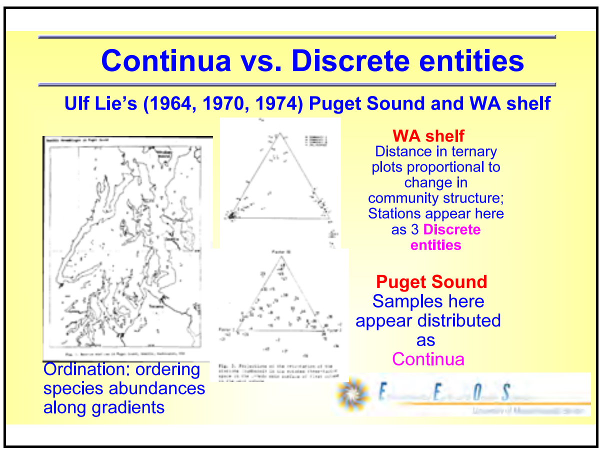



**Slide 10 Ampelisca mats 1991-1997**

NOTES:


**Slide 11 The 90's Ampelisca mats**

NOTES:




**Slide 12 Continua vs. Discrete entities**

NOTES:

## Reconciliations of Clements v. Gleason

**Watt (1947, 1954), Mills (1969), Brown (1995)**

- Watt (1947, 1954): Communities = Spatio-temporal mosaics
- Mills (1969)
  - *"A community is a group of potentially interacting populations that occur in a given area and are separable from other such groups by ecological survey"*
  - *Separation by survey?*
    - *Cluster analysis*
    - *Ordination*
- *Brown (1995, Macroecology, p. 35): "As in most such arguments in ecology, both protagonists were largely right; they were just talking about different things. Clements emphasized the emergent properties of ecosystems … Gleason focused on the idiosyncratic details."*

### Slide 13 Reconciliations of Clements v. Gleason

NOTES:

## Hubbell's (2001) community

Hubbell (2001, p. 5) bases his theory of neutral community structure on a restrictive definition of community, which is, as he notes, more similar to others' definition of guild: "…I define an ecological community as a group of trophically similar, sympatric species that actually or potentially compete in a local area for the same or similar resources" Hubbell (2001, p. 5) also adapts the definition of **metacommunity** for his neutral theory: "The metacommunity consists of all trophically similar individuals and species in a regional collection of local communities. However, unlike species in the local community, species may not actually compete because of separation in space or time." The usual definition of metacommunity would not restrict the class to trophically similar individuals, nor to those that are potential or actual competitors.

### Slide 14 Hubbell's (2001) community

NOTES:

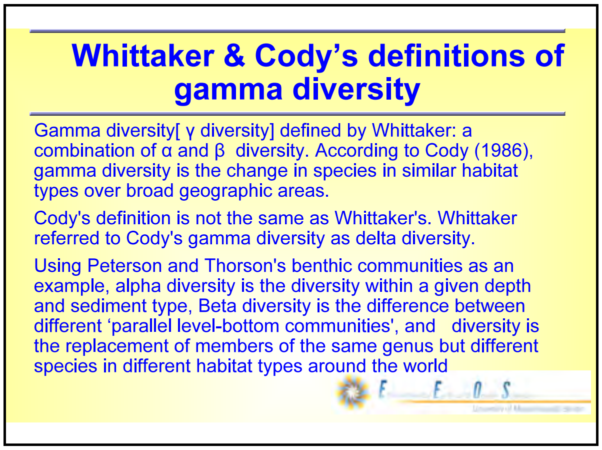
## Components of diversity

**Whitaker's alpha, beta, and gamma diversity**

- **Alpha (α) diversity**
  - The species diversity at a site, sometimes in a sample
  - Consisting of:
    - Species richness
    - Species equitability or evenness
- **Beta (β) diversity**
  - Change in diversity along environmental gradients
  - Usually measured with faunal similarity indices, rate of change is often described using the half-change unit
  - Displayed using classification or ordination
- **Gamma (γ) diversity**
  - Change in species composition among large-scale regions
  - For example, Puget Sound's subtidal benthos much more diverse than Gulf of Maine or the entire Eastern shelf

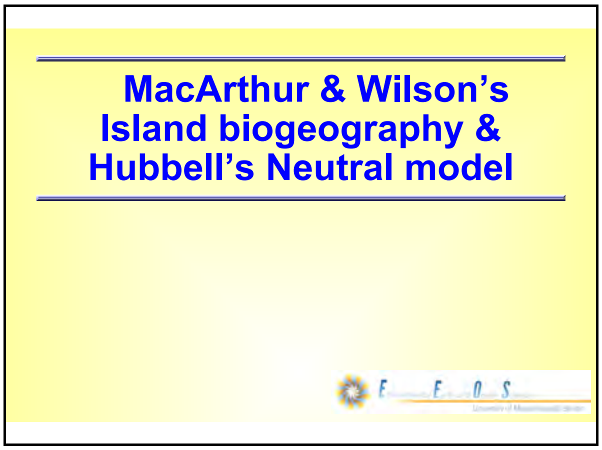
### Slide 15 Components of diversity

NOTES:




**Slide 16 Whittaker & Cody's definitions of gamma diversity**

NOTES:




**Slide 17 MacArthur & Wilson's Island biogeography & Hubbell's Neutral model**

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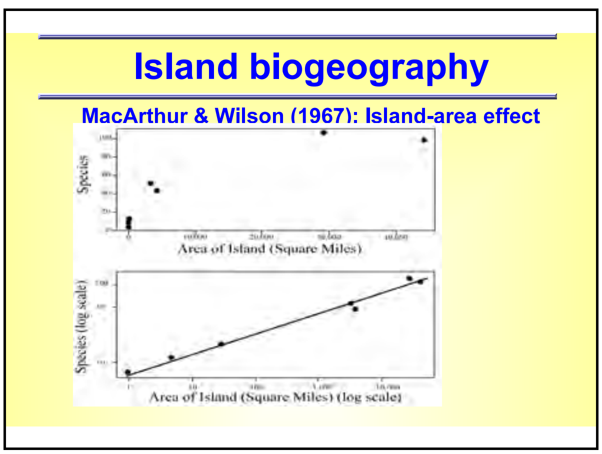
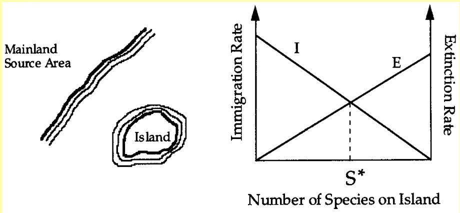



**Slide 18 Island biogeography**

NOTES:

## Island biogeography

**MacArthur & Wilson (1967)**
**Hubbell (2001) Figure 1.2**

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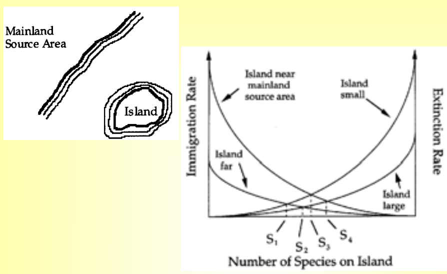
### Slide 19 Island biogeography

NOTES:

## Effects of island distance & size

**MacArthur & Wilson, Hubbell (2001) Fig. 1.3**

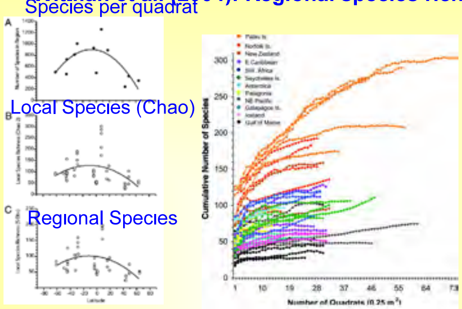



### Slide 20 Effects of island distance & size

NOTES:

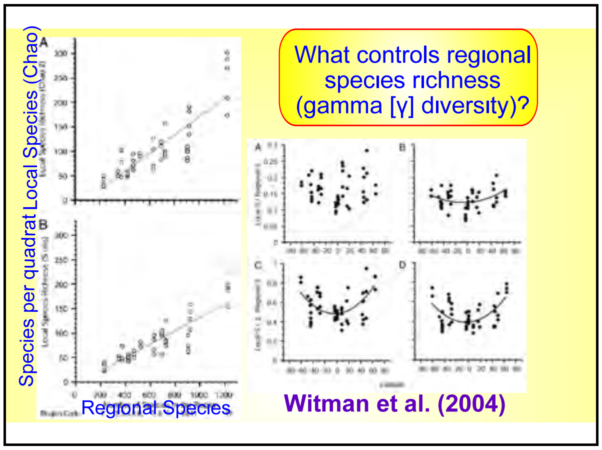
## Hard substrate α diversity

**Witman et al. (2004): Regional species richness**




### Slide 21 Hard substrate α diversity

NOTES:




**Slide 22**

NOTES:

## Conclusions from Witman et al. (2004)

*"Both regional and local species richness displayed significant unimodal patterns with latitude, peaking at low latitudes and decreasing toward high latitudes. The latitudinal diversity gradient was represented at the scale of local sites because local species richness was positively and linearly related to regional species richness. The richness of the regional species pool explained 73-76% of local species richness....'These findings imply that even in the most diverse regions of the world, the number of species coexisting in local communities of epifaunal invertebrates is influenced by the size of the regional species pool (type I). No saturation is evident.'*

**Slide 23 Conclusions from Witman et al. (2004)**

NOTES:

## Information Content Indices

**Shannon's H' for populations & Brillouin's H for samples**

$$H' = -\sum_{i}^{S} p_i \log p_i ,$$

*where,*

$p_i$ = *frequency of species i in sample.*

$$p_i = \frac{N_i}{N}$$

$N_i$ = *Number of individuals of species i.*

$N$ = *Total individuals in sample.*

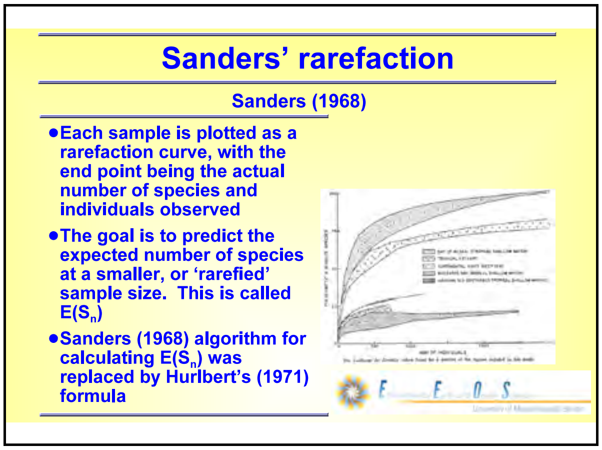
$S$ = *Number of species.*

*log could be base 2, 10, or natural log.*

$$\text{Brillouin's } H = \frac{1}{N} \log\left(\frac{N!}{N_1!\, N_2! \ldots N_s!}\right)$$

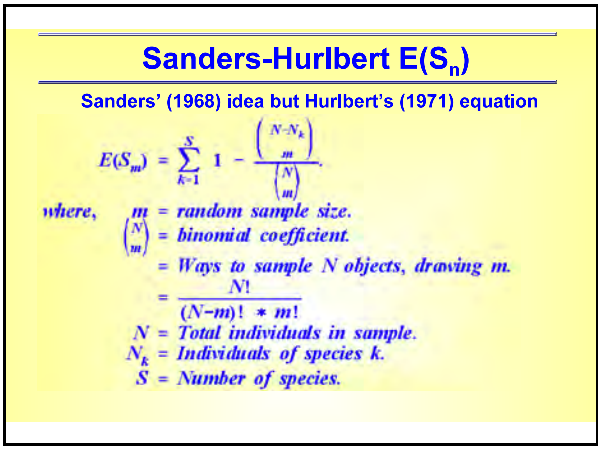
**Slide 24 Information Content Indices**

NOTES:



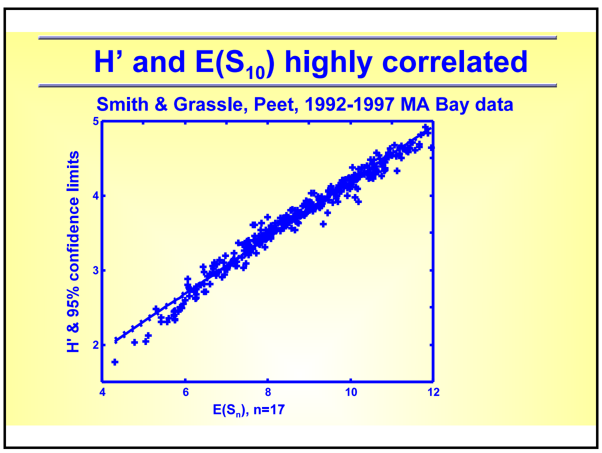

**Slide 25 Sanders' rarefaction**

NOTES:




**Slide 26 Sanders-Hurlbert E(Sn)**

NOTES:

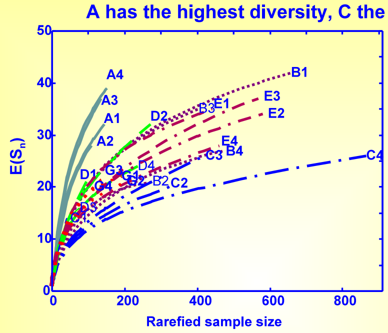



**Slide 27 H' and E(S10) highly correlated**

NOTES:

## GEEP Fjord gradient

A has the highest diversity, C the lowest




Species per grab is a poor indicator of species richness!

**Slide 28 GEEP Fjord gradient**

NOTES:

## Fisher's log-series alpha

Fisher, Corbet & Williams (1943); Only the number of species & individuals required; Fails 2 of Pielou's criteria

$$S = -\alpha \ln(1-x)$$

where, $\alpha$ = constant, dependent on diversity alone, and
$x$ = variable dependent on sample size.

$$\frac{S}{N} = \left[\frac{(x-1)}{x}\right] \ln(1-x).$$

Motomura niche preemption model:
The 1st species colonizing the environment takes of x% of the space. Of the space remaining, the 2nd species takes up x percent. Now, the third species settling in takes up x percent of the remaining space, and so on.

**Slide 29 Fisher's log-series alpha**

NOTES:

## End Lecture 9, Start Lecture 10

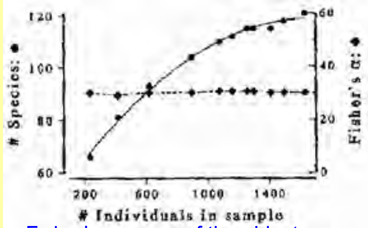
**Slide 30 End Lecture 9,**

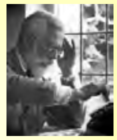
Start Lecture 10

NOTES:

## Fisher's log-series α

**Figure from Rosenzweig, replotted from Williams (1964)**



Fisher's α is one of the oldest diversity indices. Relatively insensitive to sample size but it is still 'biased'

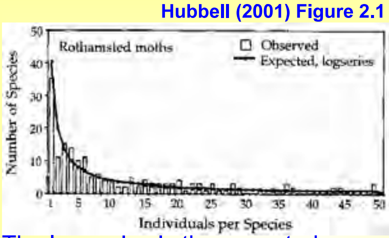
Bias *cf.*, The difference between the expected value and the true value of a parameter *cf.*, unbiased estimator

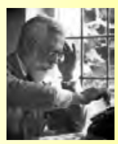
### Slide 31 Fisher's log-series α

NOTES:

## Log-series fit to moth data

**Hubbell (2001) Figure 2.1**



The log series is the expected distribution of allele frequencies under Kimura's neutral evolution model

### Slide 32 Log-series fit to moth data

NOTES:

## Fish species abundance patterns

**All could be fit to log-series, Legendre & Legendre Fig. 6.1; Species ranked in decreasing abundance; a log-normal fit might also provide an adequate fit**

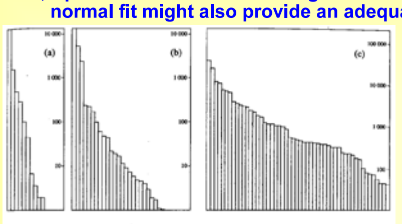
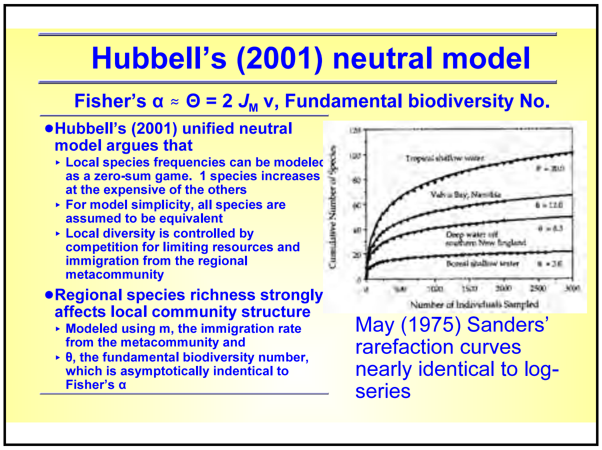



**Figure 6.1** Fish catches (abundances) in (a) the Barents Sea, (b) the Indian Ocean, and (c) the Red Sea. Along the abscissa, species are arranged in order of decreasing frequencies. The ordinates of histograms are logarithmic. Adapted from Margalef (1974).

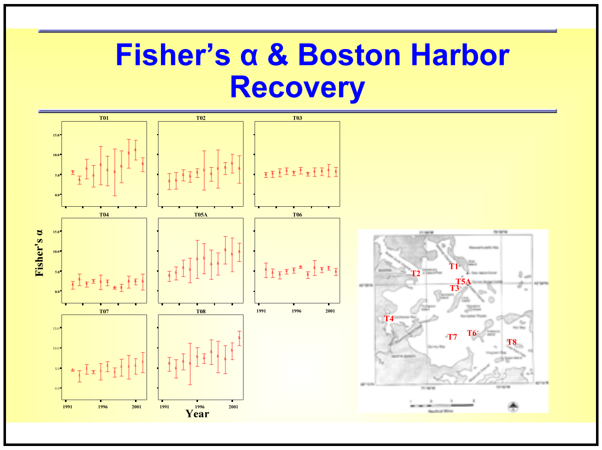
### Slide 33 Fish species abundance patterns

NOTES:



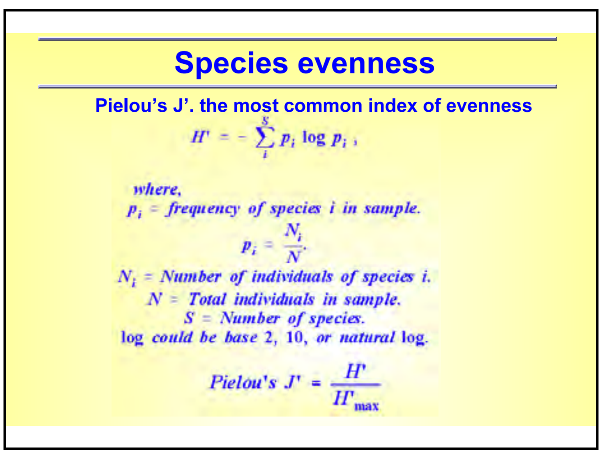

## Slide 34 Hubbell's (2001) neutral model

NOTES:



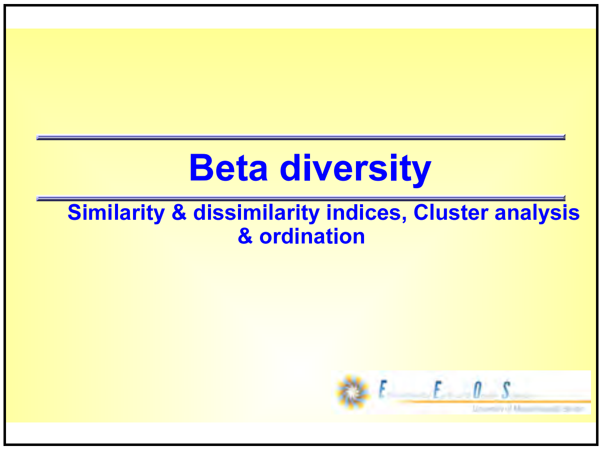

## Slide 35 Fisher's α & Boston Harbor Recovery

NOTES:



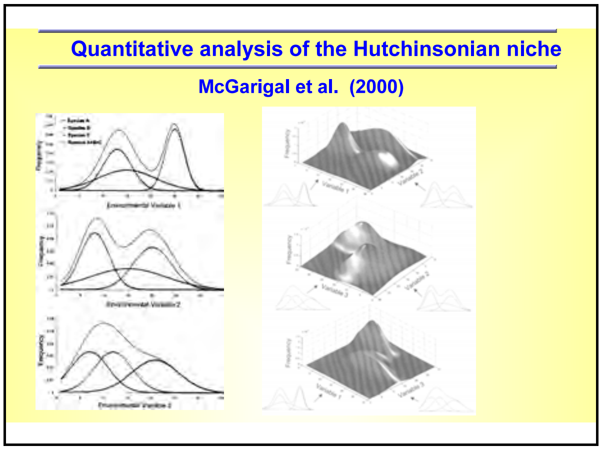

## Slide 36 Species evenness

NOTES:



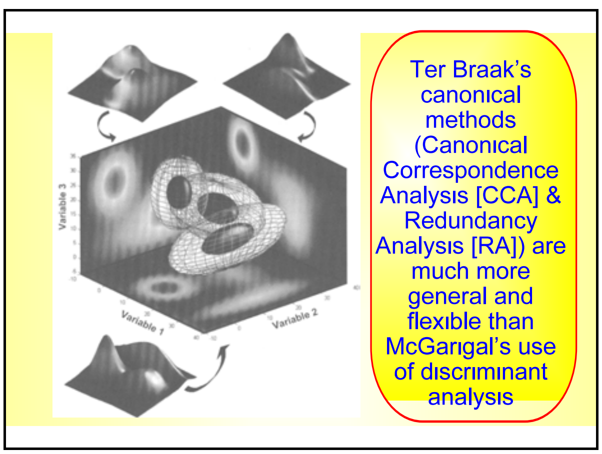

## Slide 37 Beta diversity

NOTES:




## Slide 38 Quantitative analysis of the Hutchinsonian niche

NOTES:




## Slide 39

NOTES:

## Ordination: ordering samples

**PCA, PcoA, CA, CCA, RDA, db-RDA**

- Direct: Plot species abundances along measure of environmental gradient
- Indirect ordination or indirect gradient analysis
  - Principal components analysis, Principal coordinates analysis, Correspondence analysis
    - Do the ordination using PCA, PCoA, or CA or other methods
    - External variables don't control the ordination
    - Look for association with environmental variables
  - Canonical or 'constrained' methods
    - Redundancy analysis
    - Canonical correspondence analysis

**Slide 40 Ordination: ordering samples**

NOTES:

## When should you use canonical methods (Canonical correspondence analysis, Redundancy Analysis, Discriminant Analysis)?

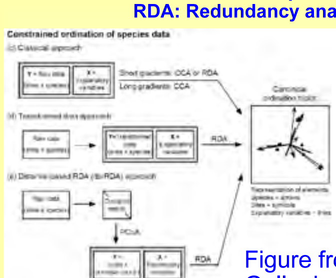
- To explain rather than describe patterns
  - What variables are really linearly associated with the major changes in community composition?
  - What are the patterns of covariation among species and pollutant variables?
- To test hypotheses about group differences (treatment groups can be set as dummy variables)
  - Exon Valdez Oilspill study, Gilfillan
  - Anderson & Legendre's benthic experiments: adding a predator or disturbance
- Discriminant analysis: to produce a classification function to classify groups

**Slide 41 When should you use canonical methods (Canonical correspondence analysis, Redundancy Analysis, Discriminant Analysis)?**

NOTES:

## Constrained Ordination

**CCA: Canonical correspondence analysis**
**RDA: Redundancy analysis**

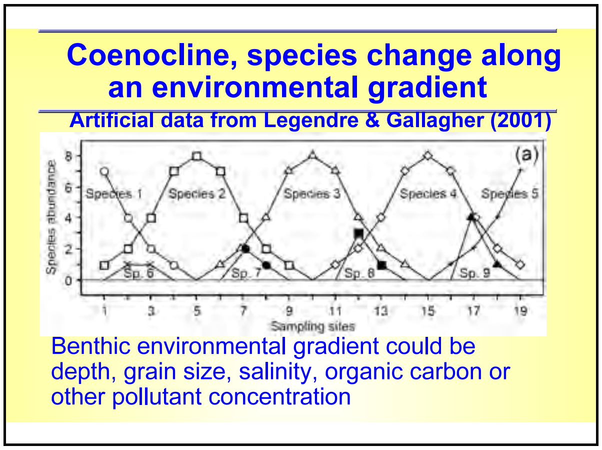



What % of species composition is linearly related to environmental variables?

Figure from Legendre & Gallagher (2001)

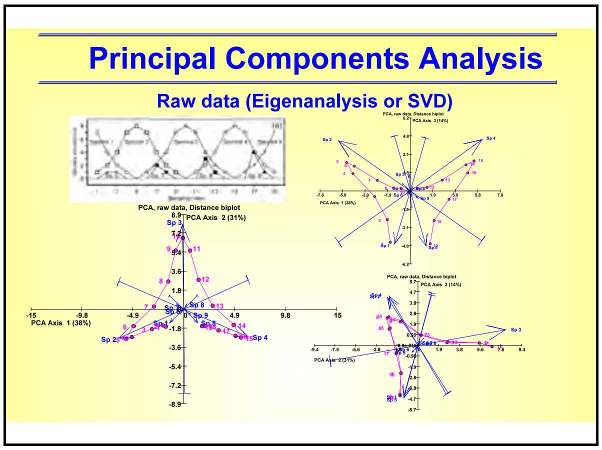
**Slide 42 Constrained Ordination**

NOTES:



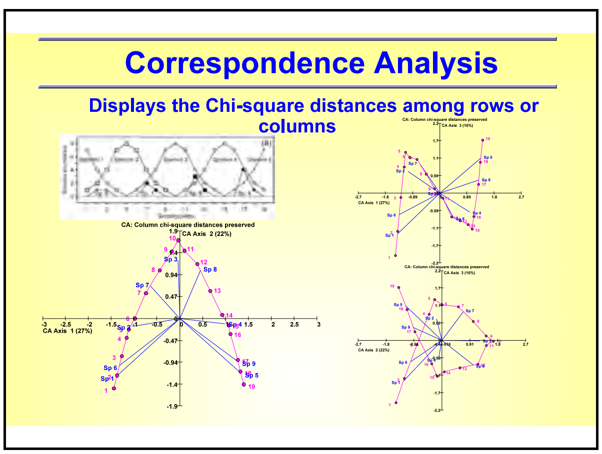

**Slide 43 Coenocline, species change along an environmental gradient**

NOTES:




**Slide 44 Principal Components Analysis**

NOTES:



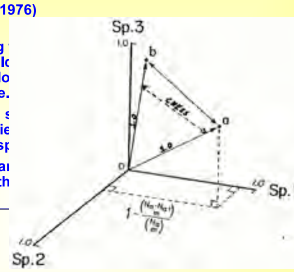

**Slide 45 Correspondence Analysis**

NOTES:

## CNESS Geometry

### Chord distance, 1 unit from the orign, a metric

- Gallagher's CNESS, chord-normalized expected species shared, a metric version of Grassle & Smith's (1976) NESS [Trueblood et al. 1989]
- Samples are plotted according probability that a species woulc randomly selected with a rando of m individuals from a sample.
- Each sample can be plotted in s space. If there are just 3 specie sample (a and b) is a point in sp
- The chord distance is the distan between samples 1 unit from th

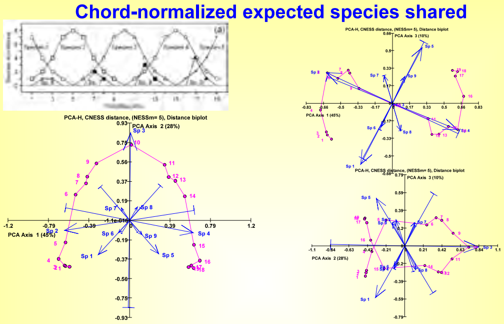



## Slide 46 CNESS Geometry

NOTES:

## CNESS & PCA-H

### Chord-normalized expected species shared



## Slide 47 CNESS & PCA-H

NOTES:

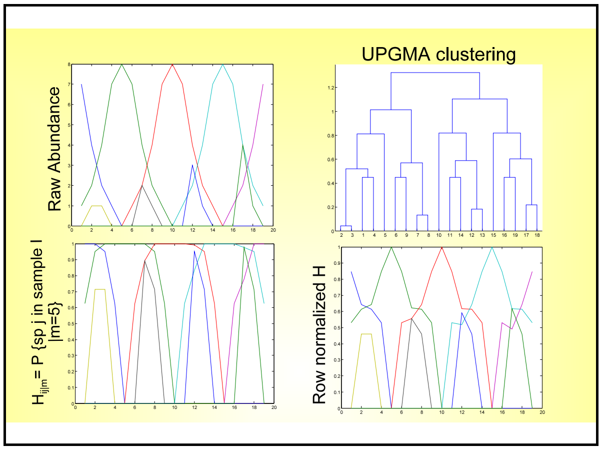
## Advantages of CNESS & PCA-H

### Over Correspondence Analysis

- Ordination diagrams are graphical displays of CNESS distances,which have a direct ecological interpretation
  - Based on the expected species shared from random draws of the community
  - Correspondence analysis (CA): graphical display of chi-square distances.
- CA suffers from the 'rare' and dominant species effects: trivial species can dominate the analysis or,
- A few dominant species can control the ordination
- Sample size, m, can be changed to make the index more or less sensitive to abundant or variable species

## Slide 48 Advantages of CNESS & PCA-H

NOTES:




## Slide 49

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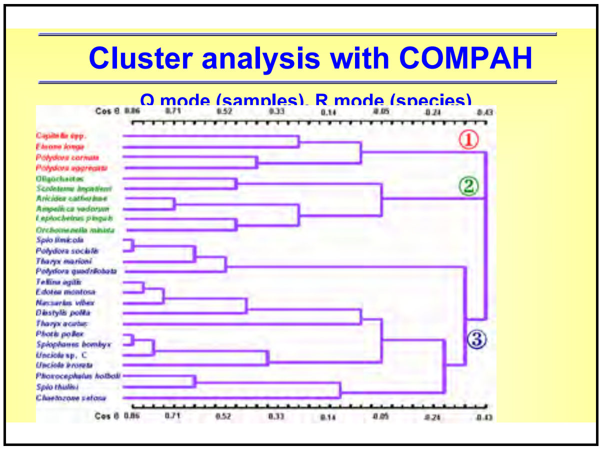
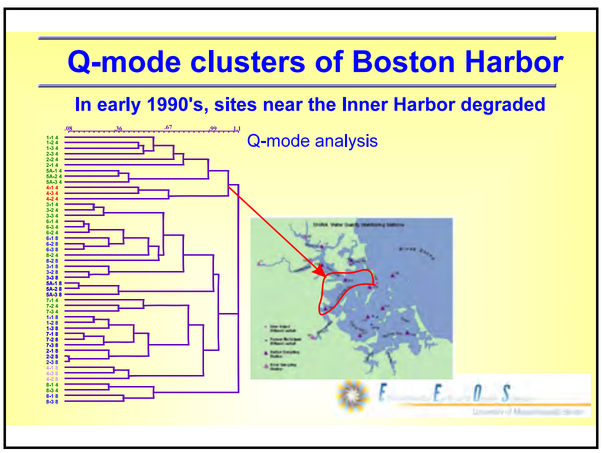



## Slide 50  Cluster analysis with COMPAH

NOTES:




## Slide 51  Q-mode clusters of Boston Harbor

NOTES:

## Biplots & triplots

Graphically display species & environmental variables

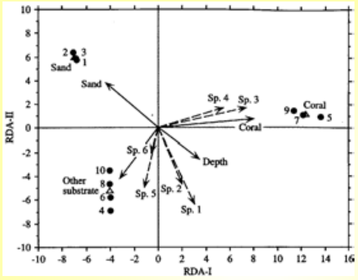



Figure from Legendre & Legendre, Numerical Ecology

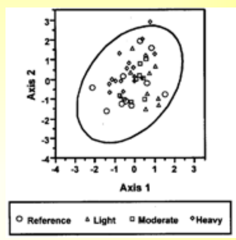
**Slide 52 Biplots & triplots**

NOTES:

## Partial CCA & Exon Valdez

Gilfillan et al. Used canonical correspondence analysis to conclude that oil had little effect on community structure

- In the iterative algorithm, use regression to eliminate any association with a covariate
- Gilfillan eliminated the effects of tidal exposure, tidal height, grain size & organic carbon concentration in the Exon Valdez oilspill analysis on benthic communities




**Slide 53 Partial CCA & Exon Valdez**

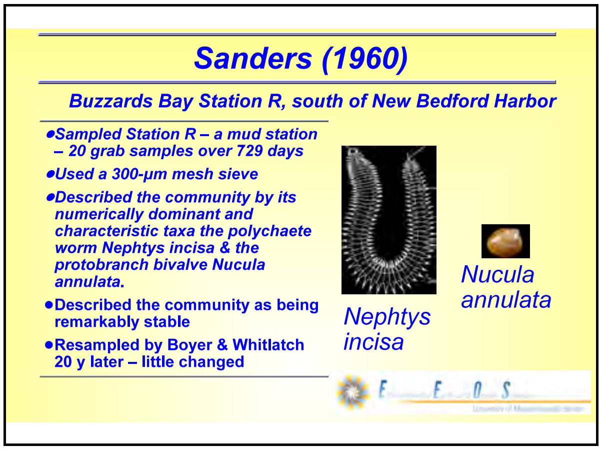
NOTES:

## *Benthic Communities and Populations*

- *Case 1: Sanders' Buzzards Bay St. R*
- *Case 2: Massachusetts Bay*
- *Case 3: Pacific NW Intertidal*
- *Case 4: Skagit Intertidal*
- *Case 5: Deep-Sea & Hydrothermal Vents*
- *Case 6: Boston Harbor*

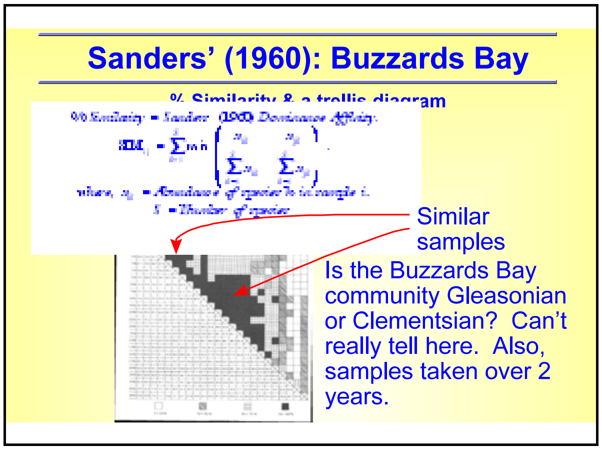
**Slide 54 Benthic Communities and Populations**

NOTES:



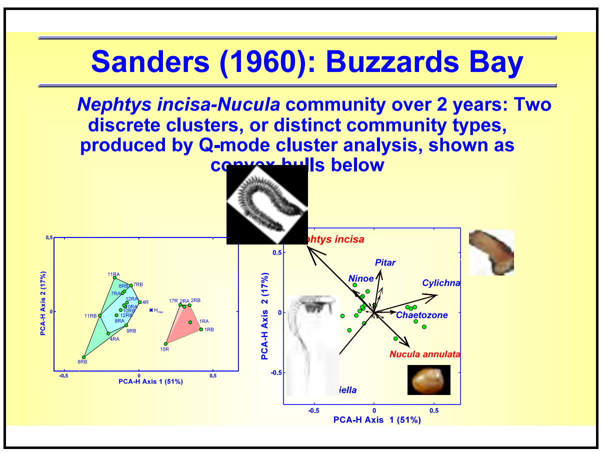

## Slide 55 Sanders (1960)

NOTES:



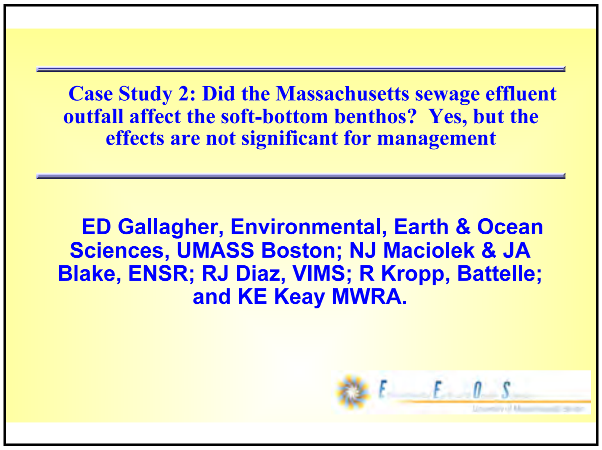

## Slide 56 Sanders' (1960): Buzzards Bay

NOTES:



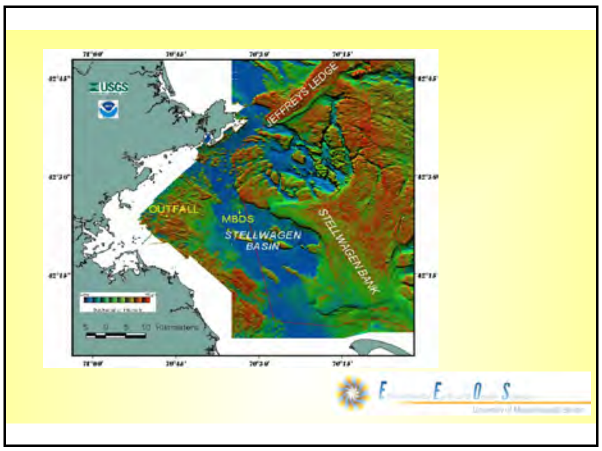

## Slide 57 Sanders (1960): Buzzards Bay

NOTES:



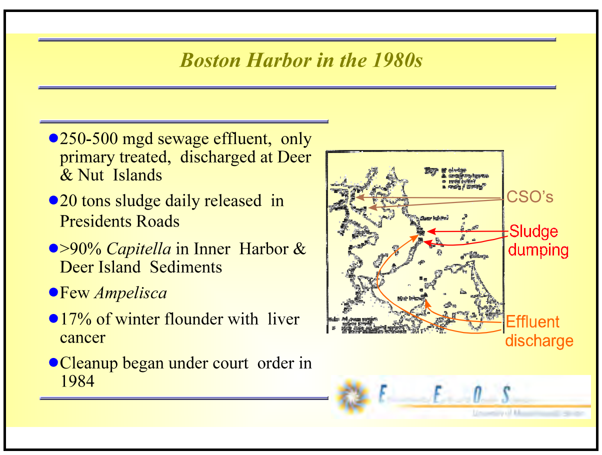

**Slide 58 Case Study 2: Did the Massachusetts sewage effluent outfall affect the soft-bottom benthos? Yes, but the effects are not significant for management**

NOTES:



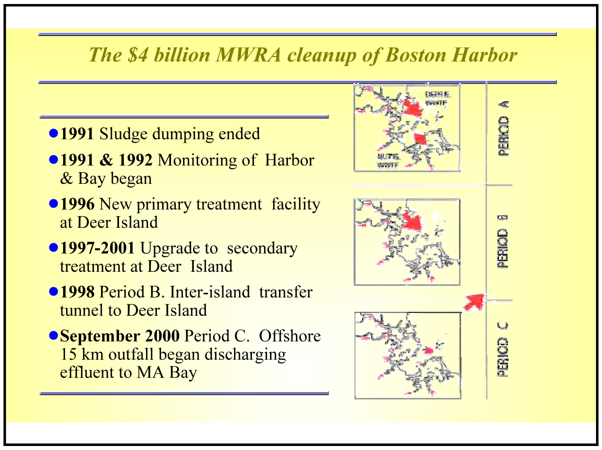

**Slide 59 Boston Harbor & the Western Gulf of Maine**

NOTES:



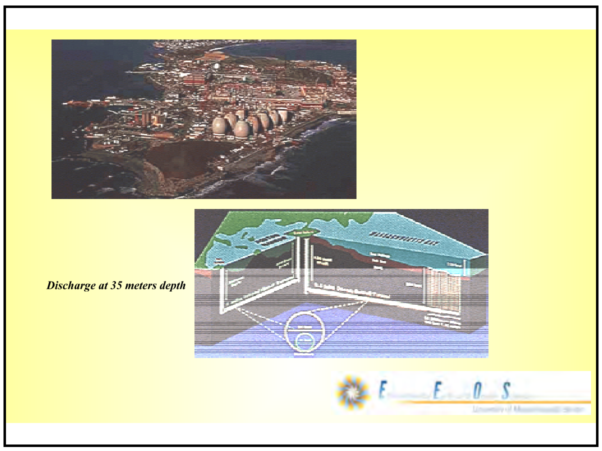

**Slide 60 Boston Harbor in the 1980s**

NOTES:



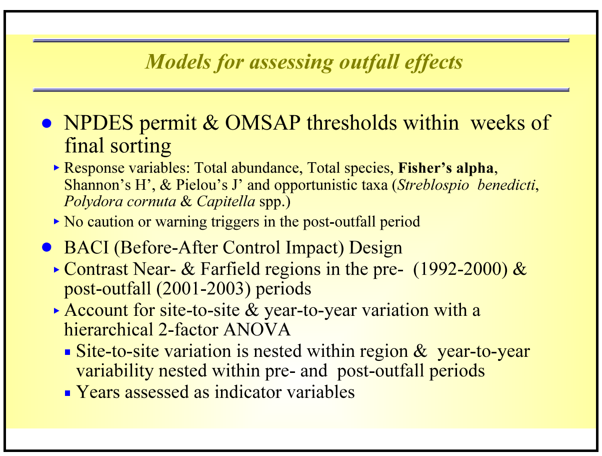

**Slide 61 The $4 billion MWRA cleanup of Boston Harbor**

NOTES:



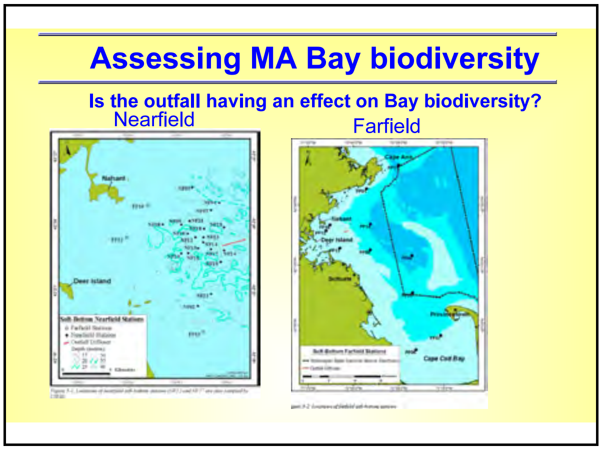

**Slide 62 The Deer Island Treatment Facility & Tunnels**

NOTES:



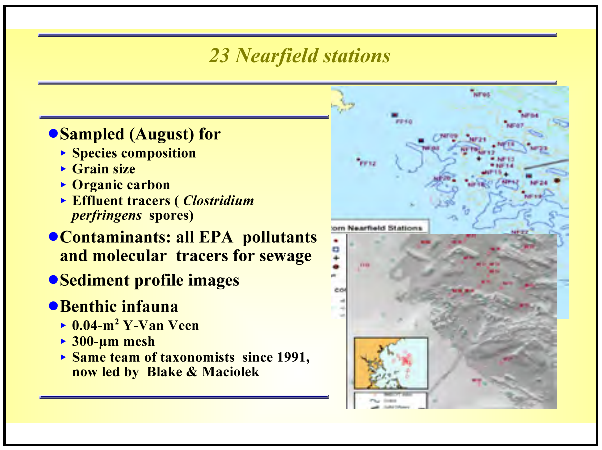

**Slide 63 Models for assessing outfall effects**

NOTES:



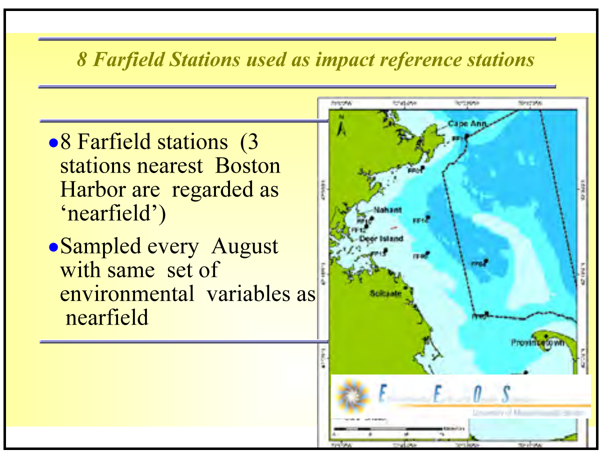

**Slide 64 Assessing MA Bay biodiversity**

NOTES:



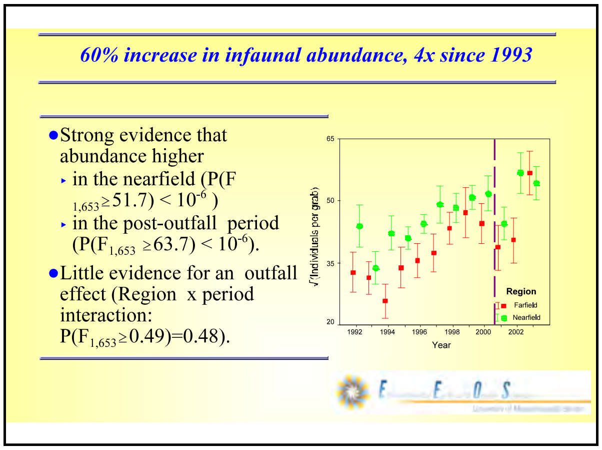

**Slide 65 23 Nearfield stations**

NOTES:



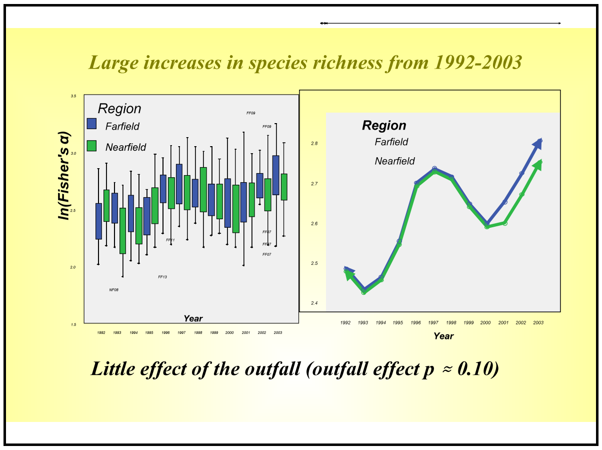

**Slide 66 8 Farfield Stations used as impact reference stations**

NOTES:



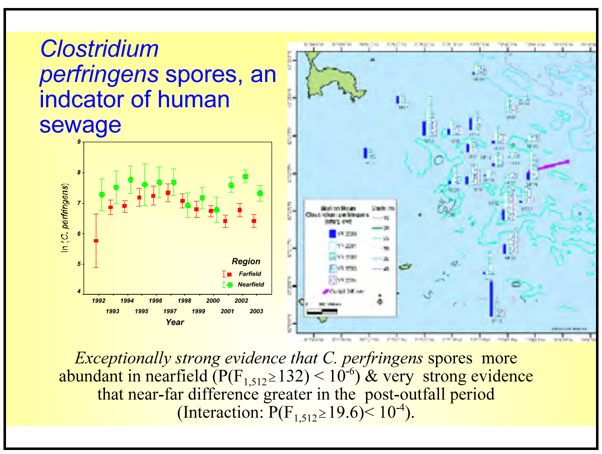

## Slide 67 60% increase in infaunal abundance, 4x since 1993

NOTES:



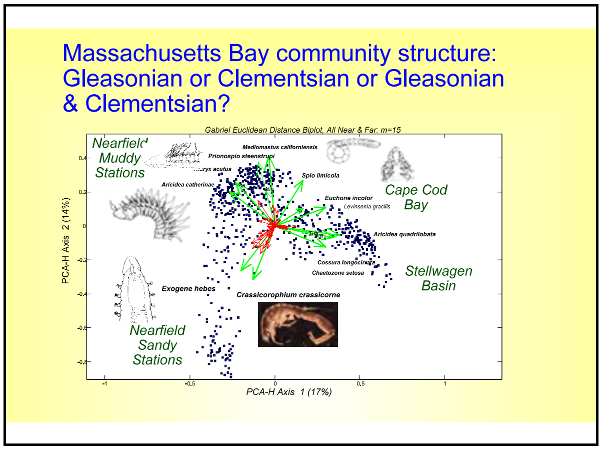

## Slide 68

NOTES:




## Slide 69 Outfall effects: C. Pefringens abundance changed due to outfall

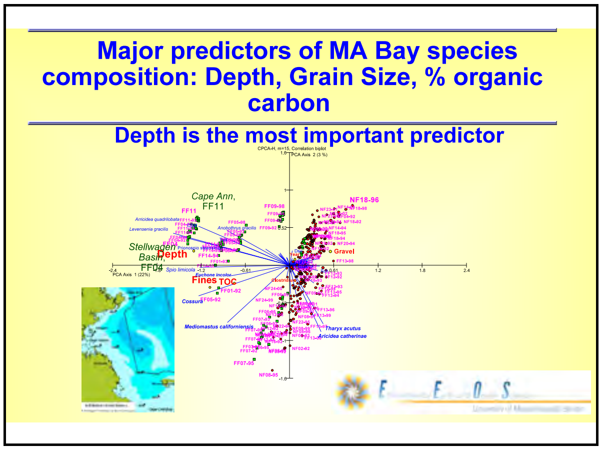
NOTES:




**Slide 70 Community structure in MA Bay:**

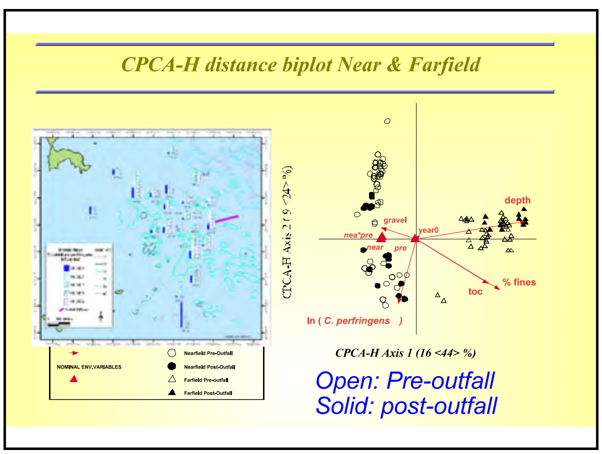
PCA-H, ordination of CNESS

NOTES:



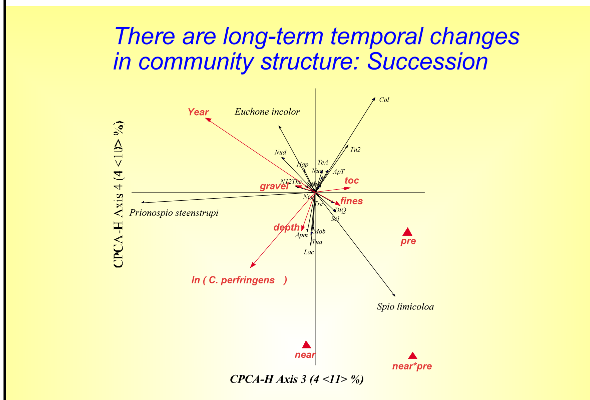

**Slide 71 Major predictors of MA Bay species composition: Depth, Grain Size, % organic carbon**

NOTES:



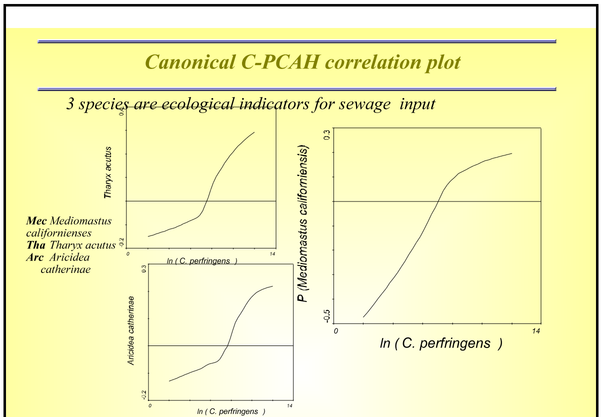

**Slide 72 CPCA-H distance biplot Near & Farfield**

NOTES:




**Slide 73 Long-term changes in numerical dominants**

NOTES:




**Slide 74 Canonical C-PCAH correlation plot**

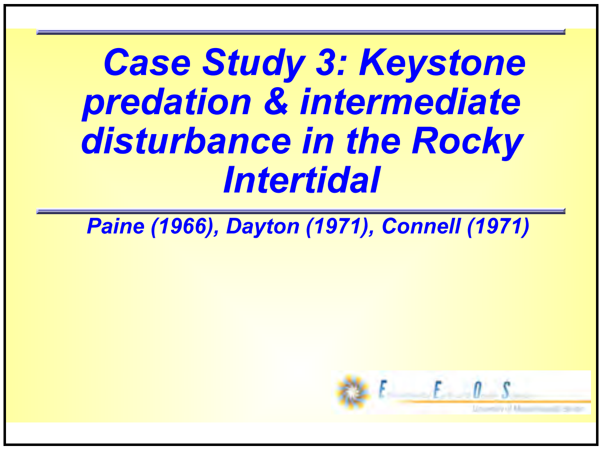
NOTES:

## Why has MA Bay species richness increased?

- The Perfect storm hypothesis: *The infaunal communities are recovering from disturbance by storms in October-November 1991.*
- The NAO hypothesis: *Massachusetts Bay benthos is exhibiting a long-term pattern of change, with 1993 and 2000-2001 minima associated with negative NAO events in 1988 and 1996.*
- The eutrophication hypothesis: *Massachusetts Bay could be undergoing eutrophication*
- Methodological differences: *the increases in species richness are due to improvements in our knowledge of the MA Bay fauna*
- *Ecological drift*
- *Changes in predation or disturbance*
- *Reductions in pollution input*

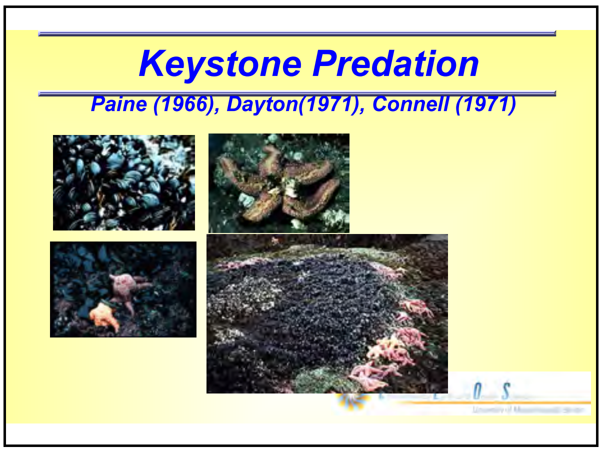
**Slide 75 Why has MA Bay species richness increased?**

NOTES:



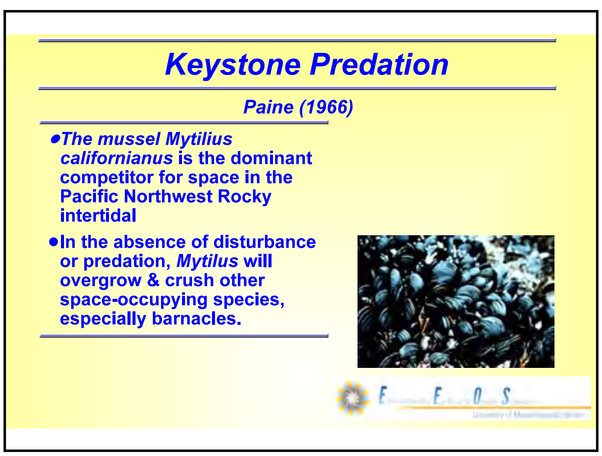

**Slide 76 Case Study 3: Keystone predation & intermediate disturbance in the Rocky Intertidal**

NOTES:



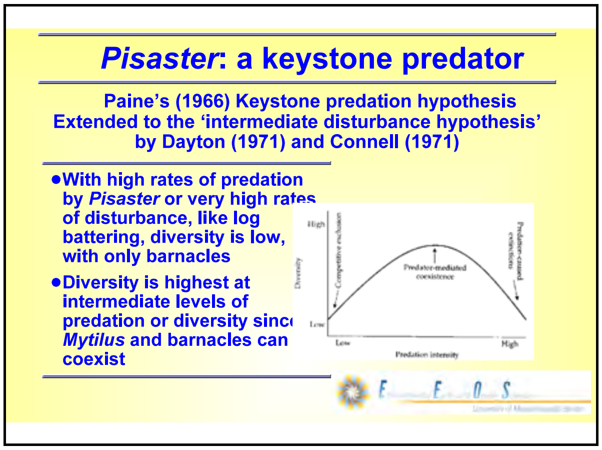

**Slide 77 Keystone Predation**

NOTES:



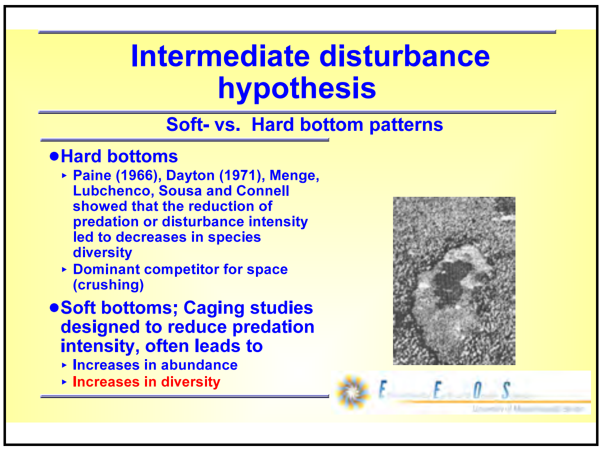

**Slide 78 Keystone Predation**

NOTES:



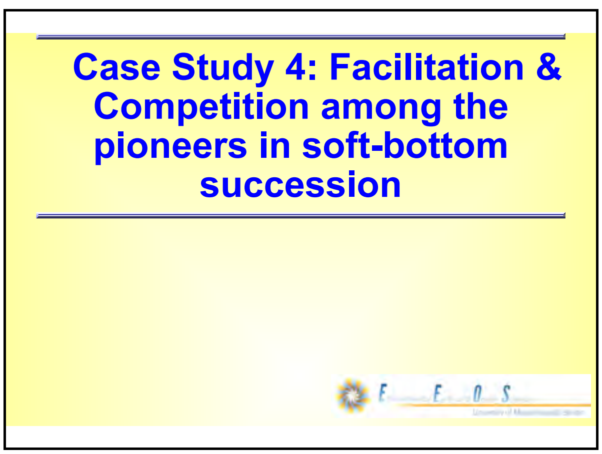

## Slide 79 Pisaster: a keystone predator

NOTES:



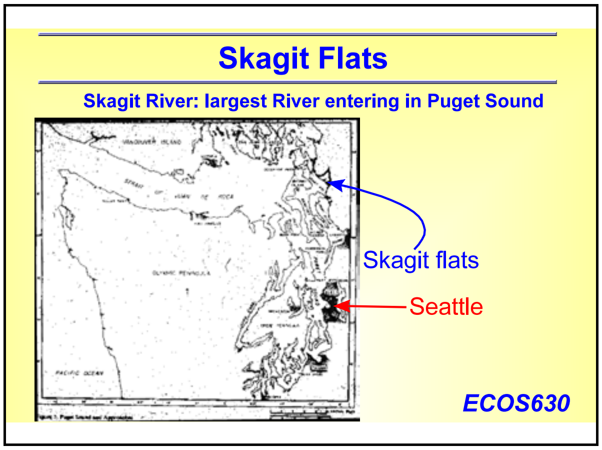

## Slide 80 Intermediate disturbance hypothesis

NOTES:



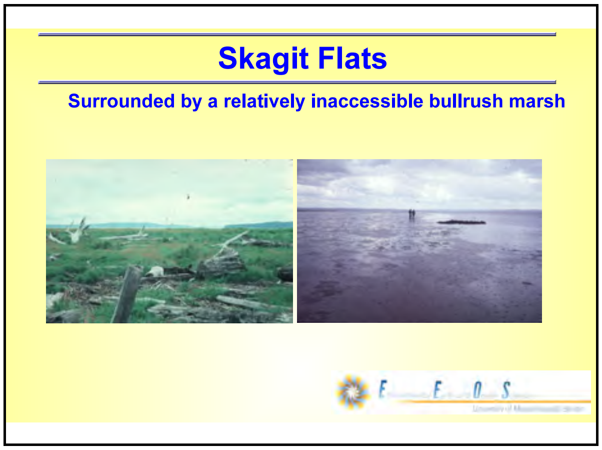

## Slide 81 Case Study 4: Facilitation & Competition among the pioneers in soft-bottom succession

NOTES:



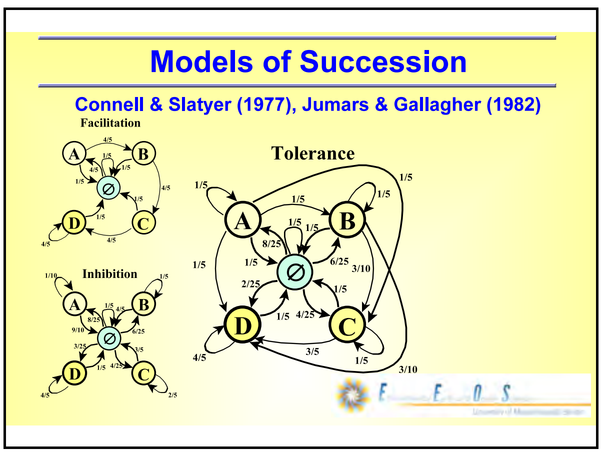

**Slide 82 Skagit Flats**

NOTES:



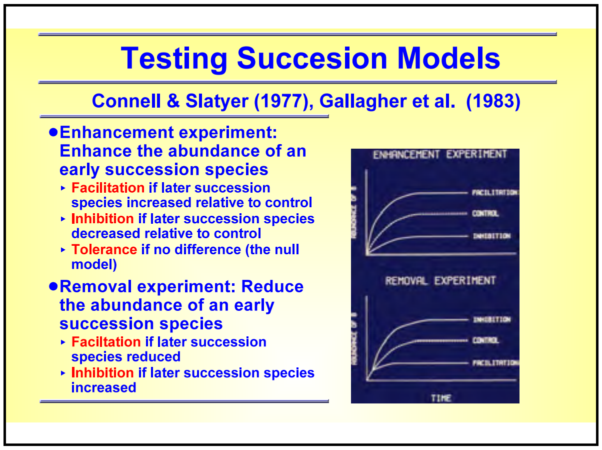

**Slide 83 Skagit Flats**

NOTES:



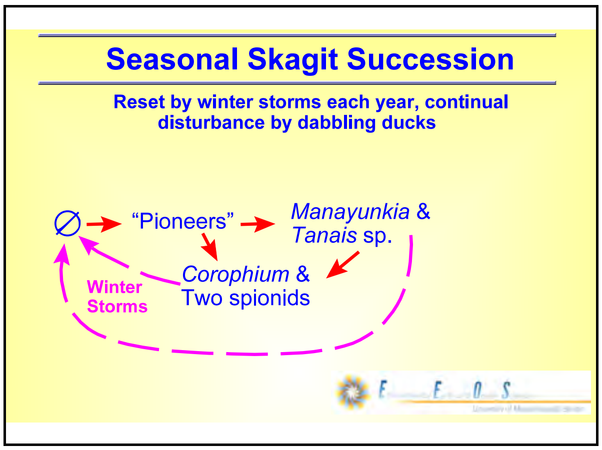

**Slide 84 Models of Succession**

NOTES:



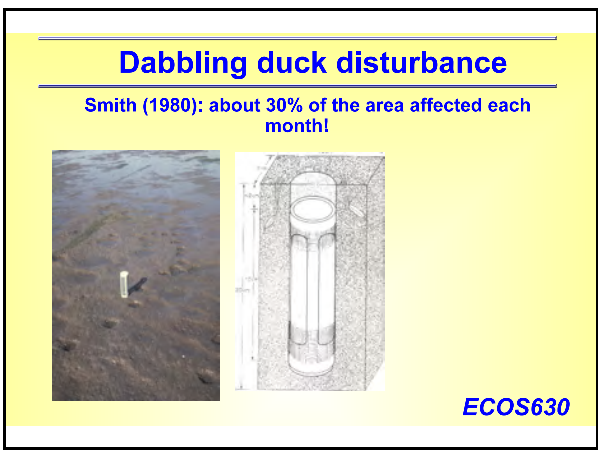

## Slide 85 Testing Succesion Models

NOTES:




## Slide 86 Seasonal Skagit Succession

NOTES:

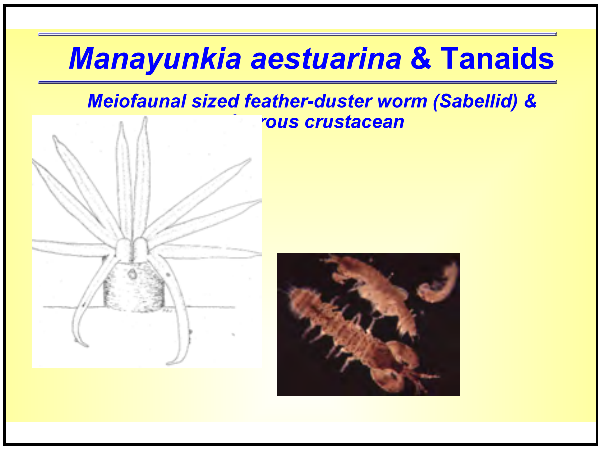



## Slide 87 Dabbling duck disturbance

NOTES:

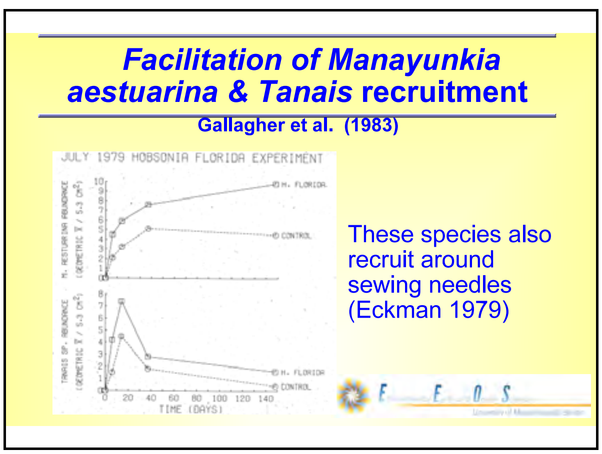

**Slide 88 Controlled field experiments**

NOTES:




**Slide 89 Manayunkia aestuarina & Tanaids**

NOTES:

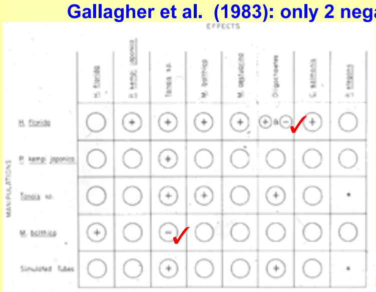



**Slide 90 Facilitation of Manayunkia aestuarina & Tanais recruitment**

NOTES:

## Facilitation is a major soft-bottom successional mechanism

**Gallagher et al. (1983): only 2 negative effects**



**Slide 91 Facilitation is a major soft-bottom successional mechanism**

NOTES:

## Predation & Soft bottom benthos

- Blegvad (1928) fish caging experiment
- Young & Young (1977): Caging leads to higher diversity!
  - Young et al. (1976): caging artifacts
    - Cage may have harbored predators
    - Flow effects
  - Peterson: Competitive exclusion rare in soft-bottom benthos
- Reise & Gray: predation relatively unimportant

**Slide 92 Predation & Soft bottom benthos**

NOTES:

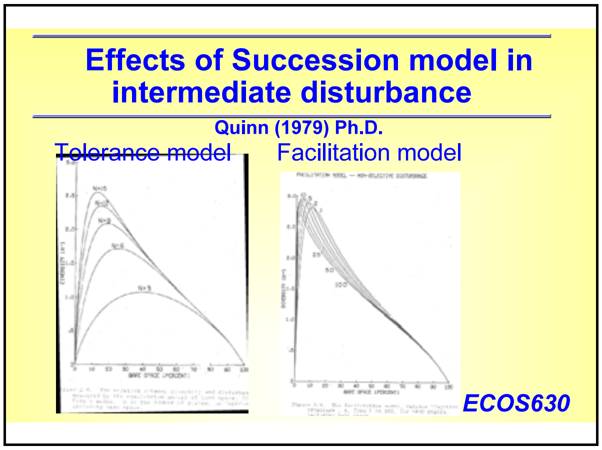
## Caging in the soft-bottom benthos

**Add a cage - diversity usually goes up**

- Caging experiments in the soft-bottom benthos often result in higher diversity, not lower as in the rocky intertidal
- Explanations:
  - caging artifacts (predators weren't really excluded, changes in recruitment)
  - Differences in the succession model: inhibition in the rocky intertidal, facilitation in the soft-bottom benthos

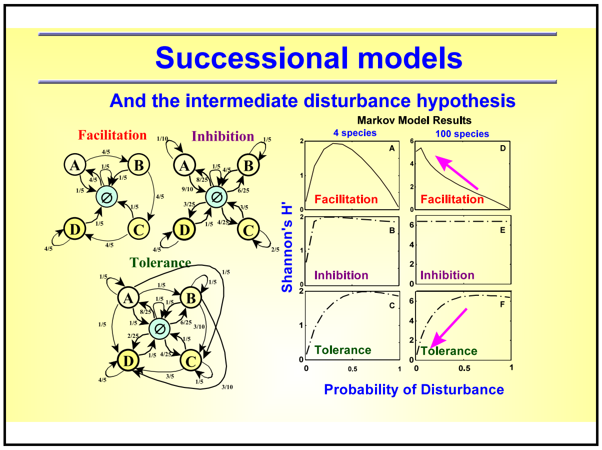
**Slide 93 Caging in the soft-bottom benthos**

NOTES:



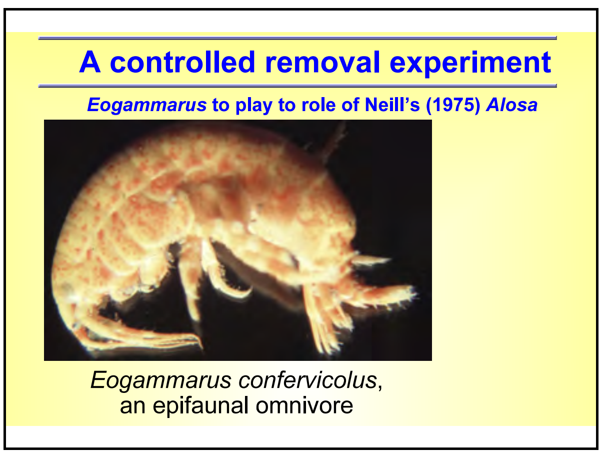

**Slide 94 Effects of Succession model in intermediate disturbance**

NOTES:




**Slide 95 Successional models**

NOTES:

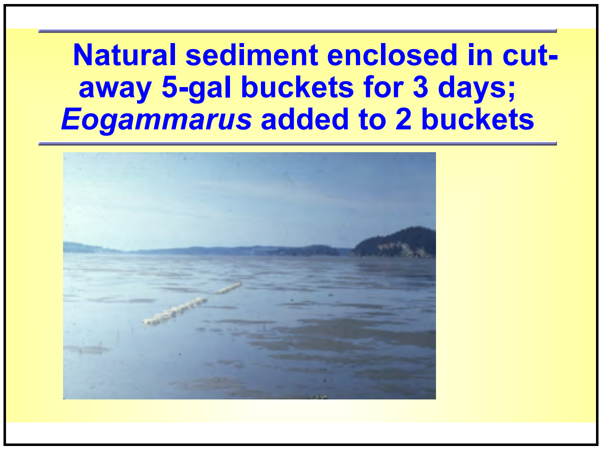



**Slide 96 A controlled removal experiment**

NOTES:


**Slide 97 Eogammarus is an omnivore**

NOTES:

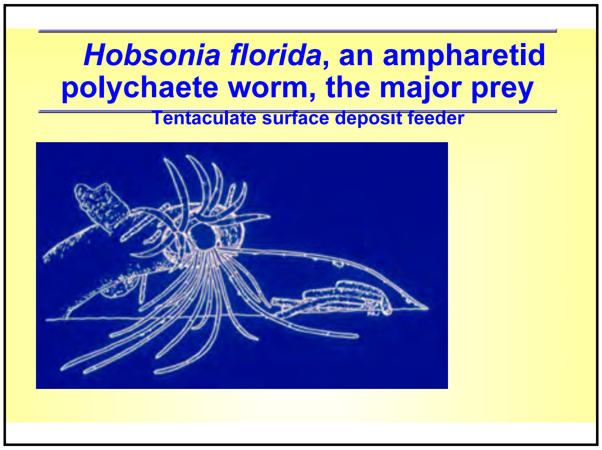



**Slide 98 Natural sediment enclosed in cut-away 5-gal buckets for 3 days; Eogammarus added to 2 buckets**

NOTES:

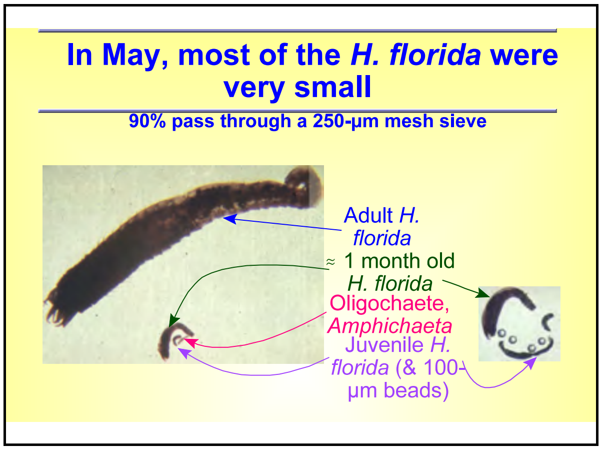

**Slide 99 Buckets enclosed with 1-mm mesh to retain Eogammarus**

NOTES:



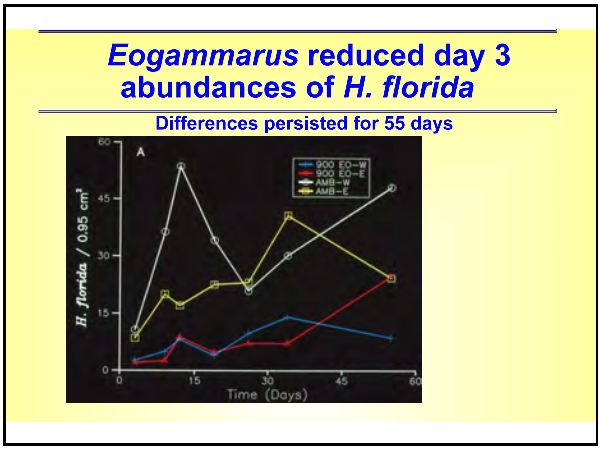

**Slide 100 Hobsonia florida, an ampharetid polychaete worm, the major prey**

NOTES:



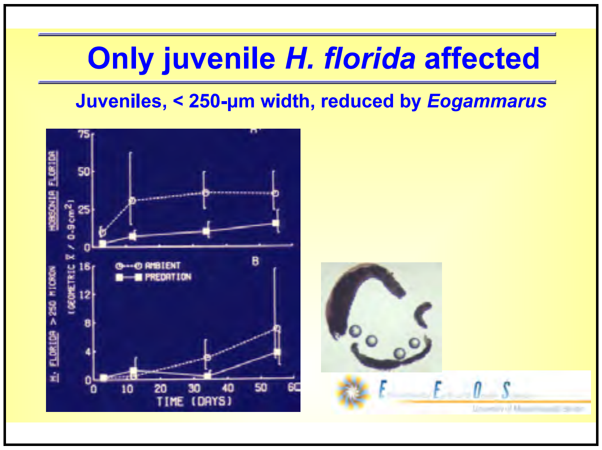

**Slide 101 In May, most of the H. Florida were very small**

NOTES:



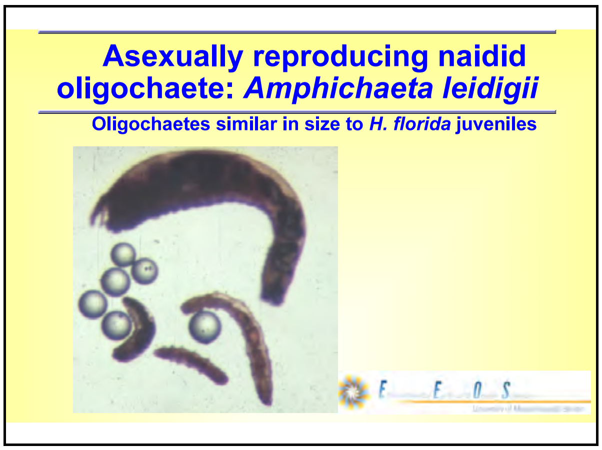

**Slide 102 Eogammarus reduced day 3 abundances of H. Florida**

NOTES:



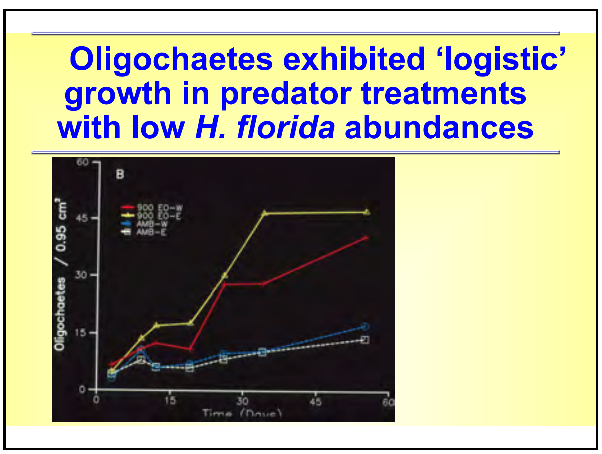

**Slide 103 Only juvenile H. Florida affected**

NOTES:




**Slide 104 Asexually reproducing naidid oligochaete: Amphichaeta leidigii**

NOTES:

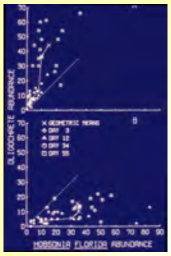



**Slide 105 Oligochaetes exhibited 'logistic' growth in predator treatments with low H. Florida abundances**

NOTES:

## Two distinct population growth trajectories

**In predator treatment, oligochaetes > *H. florida***
**In natural community, *H. florida* > Oligochaetes**




### Slide 106 Two distinct population growth trajectories

NOTES:

## What is competition?

- Competition: 'the shared utilization of a resource that is demonstrably in short supply.'
- "competition is occurring if the increase in the growth rate in one population leads to the decline in the growth rate of another."
  - *"intraspecific competition occurs if increasing density of the population leads to a decrease in the per capita*
  - Density dependence

### Slide 107 What is competition?

NOTES:

## Types of competition

**Exploitative ('scramble') vs. Interference**

In **exploitative, or scramble competition**, the effects of competition are caused by the consumption of the shared resource.

In **interference competition**, one individual or group of individuals prevents another individual or group of individuals from gaining access to the resource.

### Slide 108 Types of competition

NOTES:

## Competition vs. Predation vs. Density independence

- Competition for resources is the key factor limiting population growth:
  - Lack's & Darwin's finches
  - A. J. Lotka's logistic growth
  - Connell's barnacles crushing each other in the Scottish intertidal
- Predation is the key limiting factor
- Andrewartha & Birch (1954): Neither factor controls populations. It is climate & the environment

**Slide 109 Competition vs. Predation vs. Density independence**

NOTES:

## Lotka-Volterra competition

**An extension of the logistic equation: invoked to explain high-deep sea diversity in both equilibrium and non-equilibrium explanations**

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 - \alpha_{12} N_2}{K_1}\right)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 - \alpha_{21} N_1}{K_2}\right)$$

where, $\alpha$ = Interspecific competition coefficient.
$K$ = Carrying capacity.
$r$ = maximum per capita growth rate.

**Slide 110 Lotka-Volterra competition**

NOTES:

## Model Estimates

**Interspecific competiton coefficients ≈ 1**
**See Gallagher et al. (1990) for fitting methods**

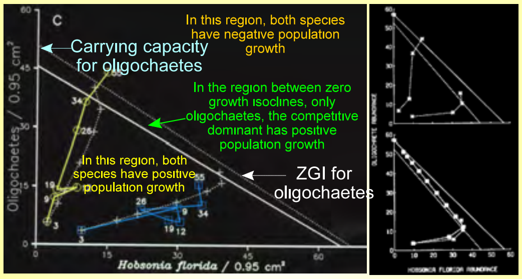
| Taxon | Doubling Time | Carrying Capacity | Competition Coefficient ($\alpha_{ij}$) |
| --- | --- | --- | --- |
| Oligochaetes | 5.8 Days | 57 | 1.005 |
| Hobsonia florida | 2.8 Days | 45 | 0.857 |

**Slide 111 Model Estimates**

NOTES:

## Trajectories fit by Lotka-Volterra model

A race to the zero-growth isoclines

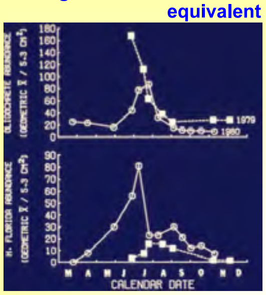



### Slide 112 Trajectories fit by Lotka-Volterra model

NOTES:

## Ambient community: 1979 v. 1980

Oligochaetes & *H. florida* appear to be competitively equivalent species



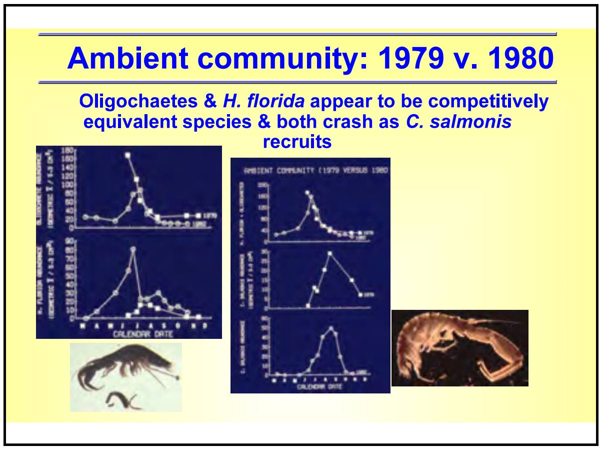

### Slide 113 Ambient community: 1979 v. 1980

NOTES:

## *Corophium salmonis*, a large interface feeder, recruits to the sandflat each July AS ADULTS

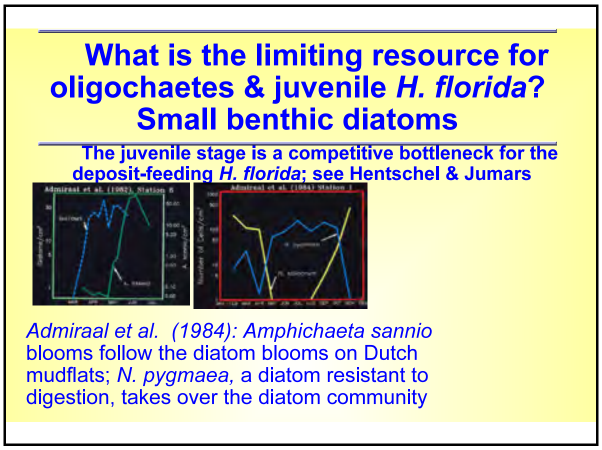
### Slide 114 Corophium salmonis, a large interface feeder, recruits to the sandflat each July AS ADULTS

NOTES:




**Slide 115 Ambient community: 1979 v. 1980**

NOTES:




**Slide 116 What is the limiting resource for oligochaetes & juvenile H. Florida? Small benthic diatoms**

NOTES: