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

Class 8: Th September 25, 2008

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

NOTES:

Class schedule

Order of topics

- Today: 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]
- For Tuesday
  - 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:

Differentiated Instruction Projects: Environmental impacts of outer continental shelf oil exploration Due Thus 30 October with 10-15 min presentations & paper;

- I. **Quantitative analysis of biodiversity & species-environment relations**
  - Matlab-based analysis of benthic community structure on Georges Bank
  - No previous experience with Matlab required
    - 10+ hours needed to become familiar with programs
    - Will need access to program (Student version $99, or UMB)
    - Online help sessions
  - Will use West Falmouth oilspill and Georges Bank data
    - Can use R as an alternative
  - GIS analysis of George's Bank benthic community structure and the relation to environmental varialbes
  - Statistics: design an survey to assess baseline conditions and effects of drillling on the outter continental shelf.
- Ii **Ecology** (autecology & synecology)
  - What are the patterns of biodiversity on the outer continental shelf. Are there fundamental differences between East & West coast benthic ecology
  - Applied ecology
    - What were the effects of the 1969 Santa Barbara and Buzzards Bay oilspills?
    - What were the effects of the Exon Valdez oilspill?
  - Can one set of environmental guidelines apply to all OCS biogeograhic provinces
    - What are the major biogeographic differences between outer continental shelf communities in California, Acadian Province (including Georges Bank), Carolinian Province, Gulf of Mexico.
  - Can you desi
- III. **Law, Policy & Management**, with reference to benthos
  - How did effects of the 1969 oil spills in Santa Barbara and Buzzards Bay affect the regulation of OCS exploratikon
  - How is outer continental shelf oil exploration regulated?
  - How are the impacts of oil exploration assessed. Who pays? What is the role of the MMS.
  - Are there more effective ways to assess the effects of OCS exploration.

Slide 3 Differentiated Instruction Projects: Environmental impacts of outer continental shelf oil exploration

Due Thus 30 October with 10-15 min presentations & paper;

NOTES:

A few concluding slides on benthic diatoms

Slide 4 A few concluding slides on benthic diatoms

NOTES:

pH & species composition

N. salinarum replaced by *N. pygmaea*

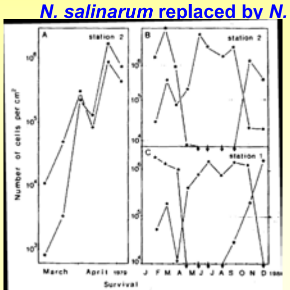


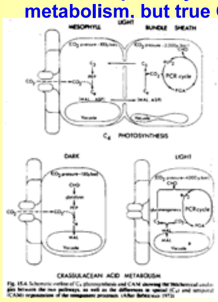
Fig. 3. Cell concentrations of *N. salinarum* (*) and *N. pygmaea* (●), calculated from total cell numbers and the relative species composition, during spring 1979 (A) and the year 1980 (B and C).

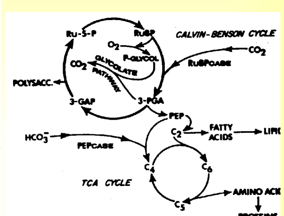
Slide 5 pH & species composition

NOTES:

Acclimation to low DIC

C3 & C4 photosynthesis; diatoms have a C4-like DIC metabolism, but true C4 requires multicellular carbon acquisition



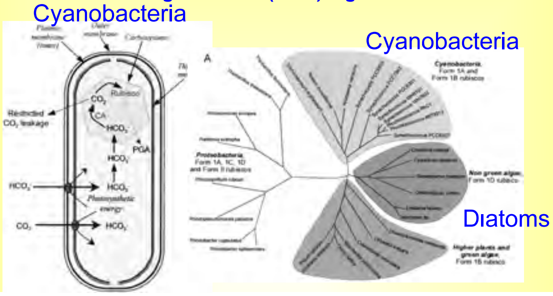


Slide 6 Acclimation to low DIC

NOTES:

Evolutionary History of DIC Concentrating mechanisms

Badger & Price (2003) Figs 1 & 2

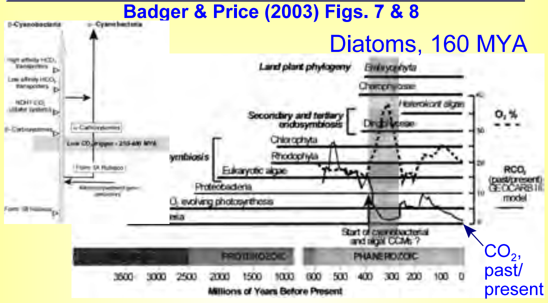


Slide 7 Evolutionary History of DIC Concentrating mechanisms

NOTES:

Cyanobacterial evolution & DIC concentrations; the end of nature?

Badger & Price (2003) Figs. 7 & 8



Slide 8 Cyanobacterial evolution & DIC concentrations; the end of nature?

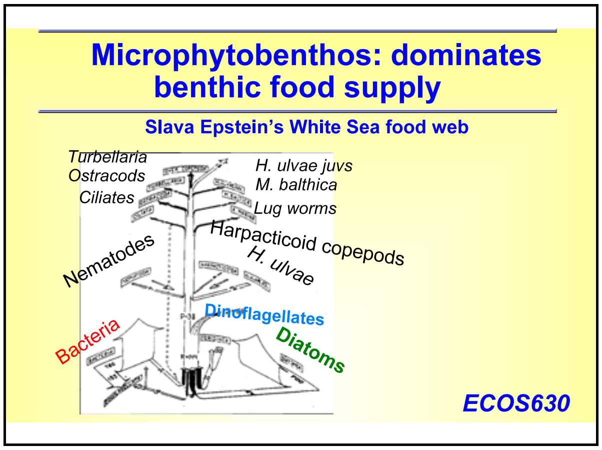
NOTES:

Latest word on the evolution of diatoms and relation to CO_2

- Kooistra, W. H. C. F., R. Gersonde, L. K. Medlin and D. G. Mann. 2007. The origin and evolution of the diatoms: their adaptation to a planktonic existence. Pp. 207-249 *in* P. G. Falkowski and A. H. Knoll, eds., Evolution of Primary Producers in the Sea. Elsevier, Amsterdam. 441 pp.
- Major ideas
  - The decline in atmospheric CO_2 is probably due to the latest phase of the 'Wilson cycle,' the opening of the Atlantic 150 mya, creating large broad continental margins with active deposition of organic matter
  - Diatoms are adapted for thriving under low CO_2 and high O_2 conditions.

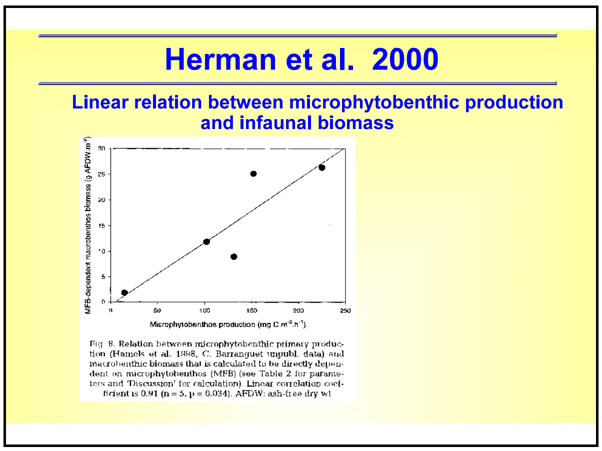
Slide 9 Latest word on the evolution of diatoms and relation to CO2

NOTES:



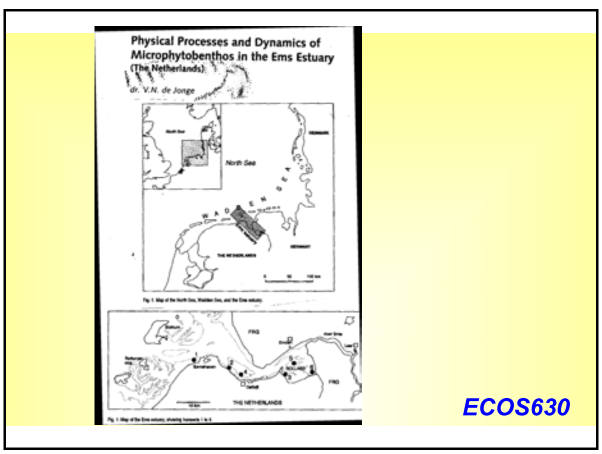
Slide 10 Microphytobenthos: dominates benthic food supply

NOTES:



Slide 11 Herman et al. 2000

NOTES:

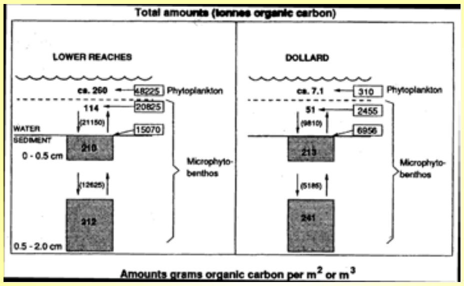


Slide 12

NOTES:

Photoautotrophic standing stock

From de Jonge (1994)

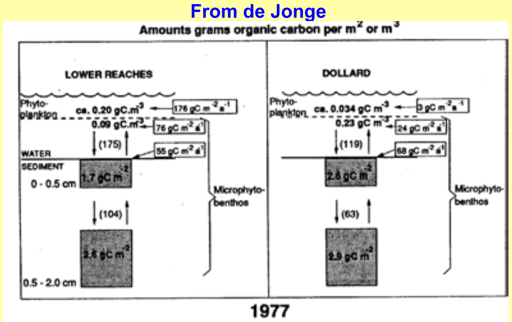


Slide 13 Photoautotrophic standing stock

NOTES:

Photoautotrophic production

From de Jonge



Slide 14 Photoautotrophic production

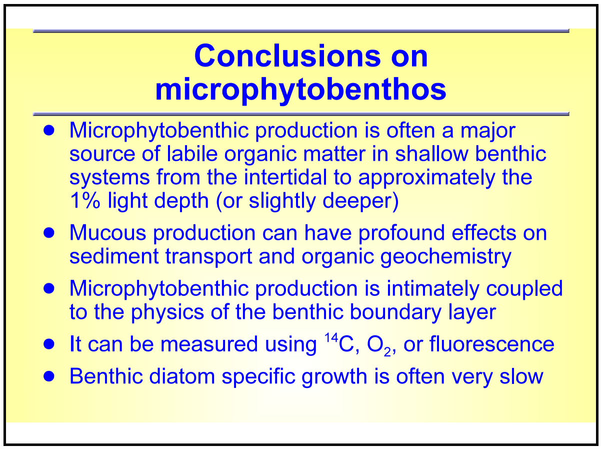
NOTES:

Microphytobenthos & phytoplankton

- Ems Dollard
  - Microphytobenthic production 60-250 mgC m^{-2} d^{-1}
  - 30% of phytoplankton are resuspended microphytobenthos
- Dollard (about 1 m deep)
  - 92% of Chl *a* from microphytobenthos
  - Production
    - 25% of total production from resuspended benthic diatoms
    - 53% from true phytoplankton
    - 22% from tidal flat production

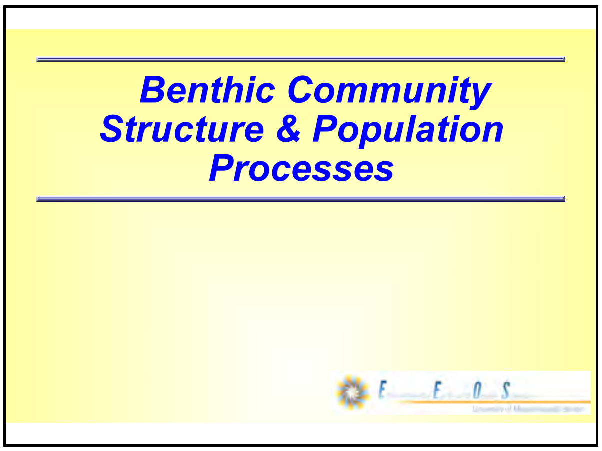
Slide 15 Microphytobenthos & phytoplankton

NOTES:



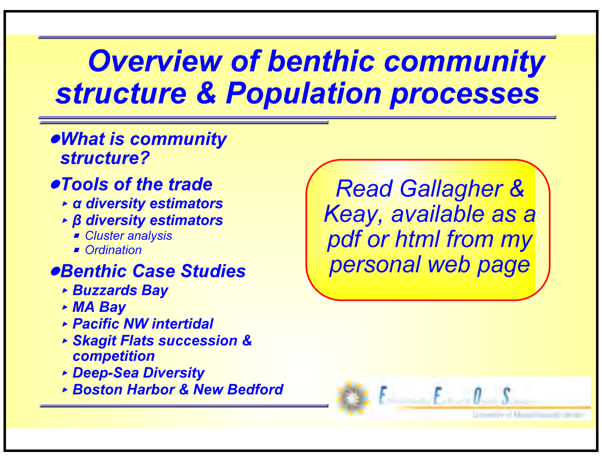
Slide 16 Conclusions on microphytobenthos

NOTES:



Slide 17 Benthic Community Structure & Population Processes

NOTES:



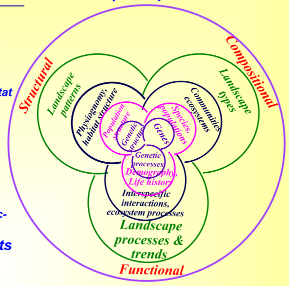
Slide 18 Overview of benthic community structure & Population processes

NOTES:

Biodiversity

Orians (1997) based on Norris (1990)

- **Compositional:**
  - species relative abundances
  - Should assess both alpha, beta and gamma diversity
- **Structural**
  - Distribution in space and in relation to habitat structure
    - Now being assessed through indirect and direct ordination methods (e.g. CANOCO)
  - Biomass spectra
  - Food web patterns (interval food webs)
  - Genetic diversity
- **Functional**
  - Energy flow and efficiencies
  - interactions: predation, competition, trophic-group amensalism
- **Synergistic effect of all 3 components**
  - Watt's spatial-temporal mosaic model
    - Benthos: Ralph Gordon Johnson, Bob Paine, Fred Grassle
  - Landscape ecology



Slide 19 Biodiversity

NOTES:

Controls of community structure

Gallagher & Keay (1998)

- Biogeography
  - Historical & Evolutionary factors
  - Barriers (Cape Cod)
- Physical factors (including long-term climate change: Pacific Decadal Oscillation, ENSO, NAO)
  - Salinity & temperature
  - Depth/light
  - Organic carbon concentration
  - Sediment grain size
- Larval supply rates: supply-side ecology
- Toxicity/anoxia
- Biological interactions

Slide 20 Controls of community structure

NOTES:

Tools of the trade: Describing community structure

Alpha, Beta and Gamma diversity

Slide 21 Tools of the trade:

Describing community structure

NOTES:

Early Community Debates

Clements vs. Gleason

- *Clements (1916)*
  - *Communities are like superorganisms*
  - *The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures and dies. ...The life-history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant.*
- Gleason (1926)
  - Communities are merely the juxtaposition of individuals
  - *"... every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements. ...a logical classification of associations into larger group, or into succession series has not yet been achieved."*

Slide 22 Early Community Debates

NOTES:

Whittaker's environmental gradients

Clements: communities discrete; Gleason: continua of individual abundances

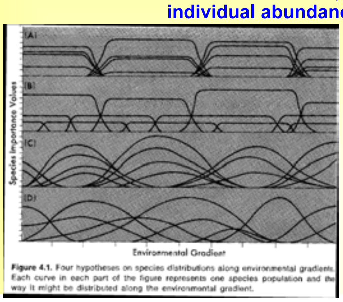


Figure 4.1. Four hypotheses on species distributions along environmental gradients. Each curve in each part of the figure represents one species population and the way it might be distributed along the environmental gradient.

Discrete Community Types

Continua

CANOCO now used to identify & describe these environmental gradients

Slide 23 Whittaker's environmental gradients

NOTES:

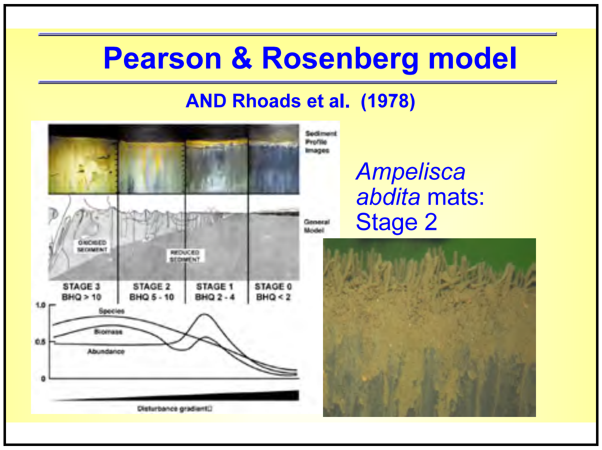
Thorson's (1957)parallel level-bottom communities

- **Petersen (1918) divided Danish benthos into 7 community types**
- **Clements & Shelford based their marine biomes on these types**
- **Thorson (1957) extended the parallel communities worldwide**
- **The whole approach led nowhere**

See Rosenberg (2001)

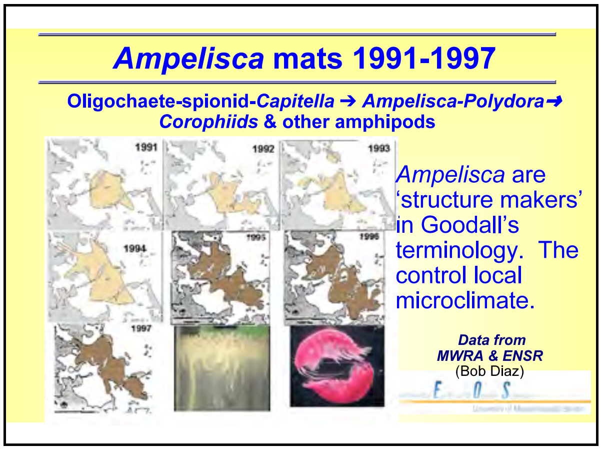
Slide 24 Thorson's (1957)parallel level-bottom communities

NOTES:



Slide 25 Pearson & Rosenberg model

NOTES:



Slide 26 Ampelisca mats 1991-1997

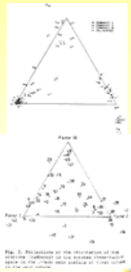
NOTES:

Slide 27 The 90's Ampelisca mats

NOTES:

Continua vs. Discrete entities

Ulf Lie's (1964, 1970, 1974) Puget Sound and WA shelf



WA shelf
Distance in ternary plots proportional to change in community structure; Stations appear here as 3 **Discrete entities**

Puget Sound
Samples here appear distributed as Continua

Ordination: ordering species abundances along gradients

Slide 28 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 29 Reconciliations of Clements v. Gleason

NOTES:

Components of diversity

Whitaker's alpha, beta, and gamma diversity

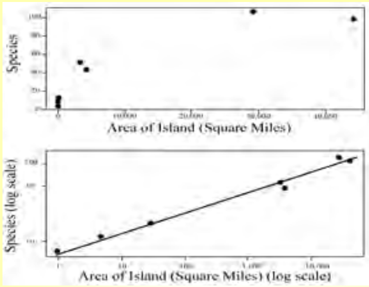
- **Alpha (α) diversity**
  - The species diversity at a site, sometimes in a sample
  - Consisting of:
    - Species richness
    - Species equitability or evenness
- **Beta (β) diversity**
  - Change in diversity along environmental gradients
  - Usually measured with faunal similarity indices, rate 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 30 Components of diversity

NOTES:

Island biography

MacArthur & Wilson (1967): Island-area effect

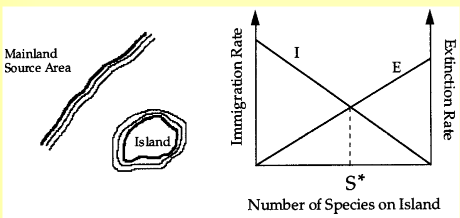


Slide 31 Island biogeography

NOTES:

Island biogeography

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



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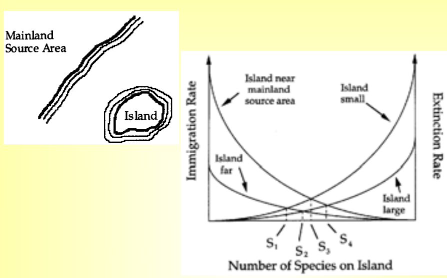
Slide 32 Island biogeography

NOTES:

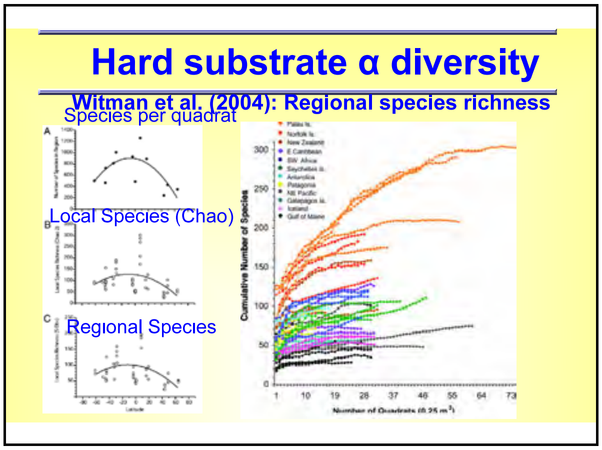
Effects of island distance & size

MacArthur & Wilson, Hubbell (2001) Fig. 1.3



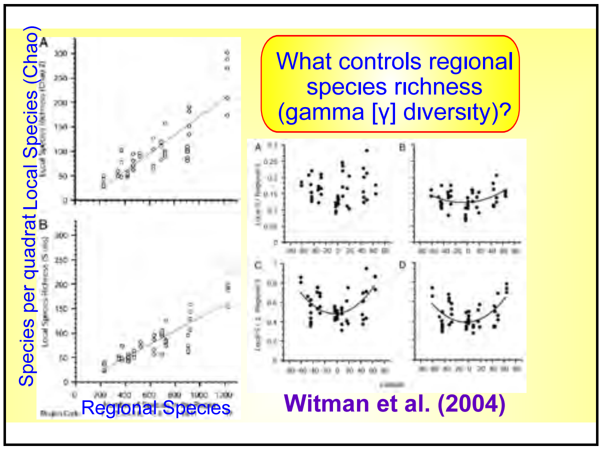
Slide 33 Effects of island distance & size

NOTES:



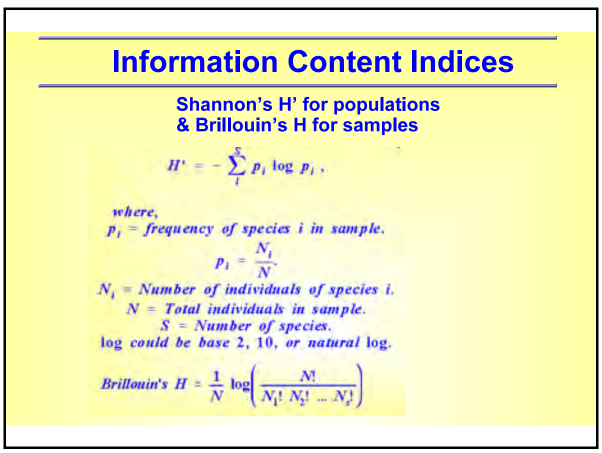
Slide 34 Hard substrate α diversity

NOTES:



Slide 35

NOTES:



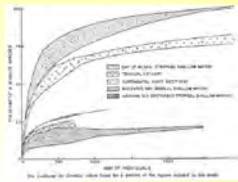
Slide 36 Information Content Indices

NOTES:

Sanders' rarefaction

Sanders (1968)

- Each sample is plotted as a rarefaction curve, with the end point being the actual number of species and individuals observed
- The goal is to predict the expected number of species at a smaller, or 'rarefied' sample size. This is called $E(S_n)$
- Sanders (1968) algorithm for calculating $E(S_n)$ was replaced by Hurlbert's (1971) formula



Slide 37 Sanders' rarefaction

NOTES:

Sanders-Hurlbert $E(S_n)$

Sanders' (1968) idea but Hurlbert's (1971) equation

$$E(S_m) = \sum_{k=1}^{S} 1 - \frac{\binom{N-N_k}{m}}{\binom{N}{m}}.$$

where,

m = random sample size.

$\binom{N}{m}$ = binomial coefficient.

= Ways to sample N objects, drawing m.

$= \frac{N!}{(N-m)! * m!}$

N = Total individuals in sample.

N_k = Individuals of species k.

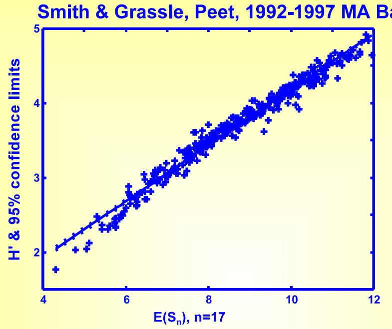
S = Number of species.

Slide 38 Sanders-Hurlbert E(Sn)

NOTES:

H' and $E(S_{10})$ highly correlated

Smith & Grassle, Peet, 1992-1997 MA Bay data

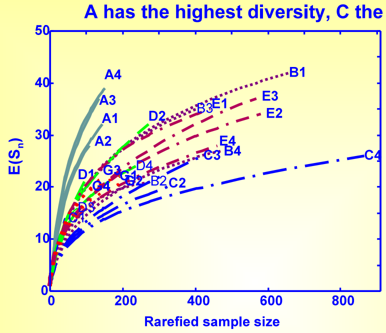


Slide 39 H' and E(S10) highly correlated

NOTES:

GEEP Fjord gradient

A has the highest diversity, C the lowest



Species per grab is a poor indicator of species richness!

Slide 40 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, α = constant, dependent on diversity alone, and
x = variable dependent on sample size.

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

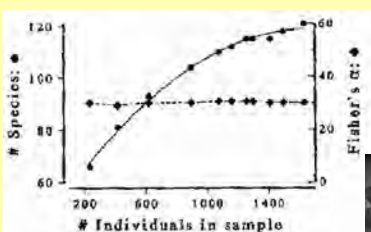
Motomura niche preemption model.
The 1st species colonizing the environment takes of x% of the space. Of the space remaining, the 2nd species takes up x percent. Now, the third species settling in takes up x percent of the remaining space, and so on.

Slide 41 Fisher's log-series alpha

NOTES:

Fisher's log-series α

Figure from Rosenzweig, replotted from Williams (1964)

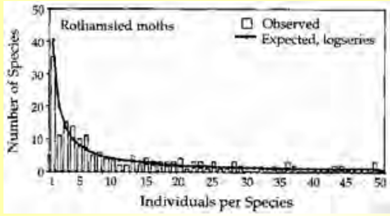


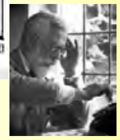
Slide 42 Fisher's log-series α

NOTES:

Log-series fit to moth data

Hubbell (2001) Figure 2.1





Slide 43 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

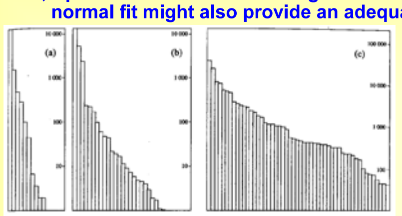


Figure 6.1 Fish catches (abundances) in (a) the Barents Sea, (b) the Indian Ocean, and (c) the Red Sea. Along the abscissa, species are arranged in order of decreasing frequencies. The ordinates of histograms are logarithmic. Adapted from Margalef (1974).

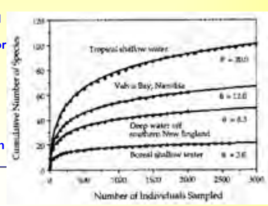
Slide 44 Fish species abundance patterns

NOTES:

Hubbell's (2001) neutral model

Fisher's α ≈ $\Theta = 2 J_M v$, Fundamental biodiversity No.

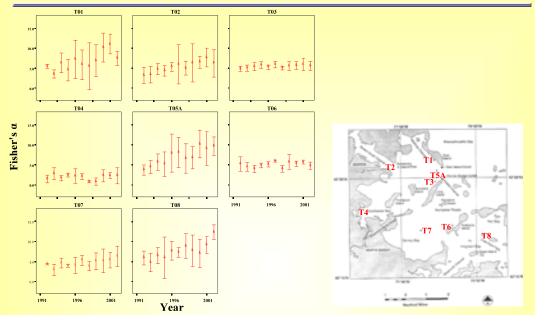
- Hubbell's (2001) unified neutral model argues that
  - Local species frequencies can be modeled as a zero-sum game. 1 species increases at the expensive of the others
  - For model simplicity, all species are assumed to be equivalent
  - Local diversity is controlled by competition for limiting resources and immigration from the regional metacommunity
- Regional species richness strongly affects local community structure
  - Modeled using m, the immigration rate from the metacommunity and
  - θ, the fundamental biodiversity number, which is asymptotically indentical to Fisher's α



Slide 45 Hubbell's (2001) neutral model

NOTES:

Fisher's α & Boston Harbor Recovery



Slide 46 Fisher's α & Boston Harbor Recovery

NOTES:

Species evenness

Pielou's J'. the most common index of evenness

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

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.

$$\text{Pielou's } J' = \frac{H'}{H'_{max}}$$

Slide 47 Species evenness

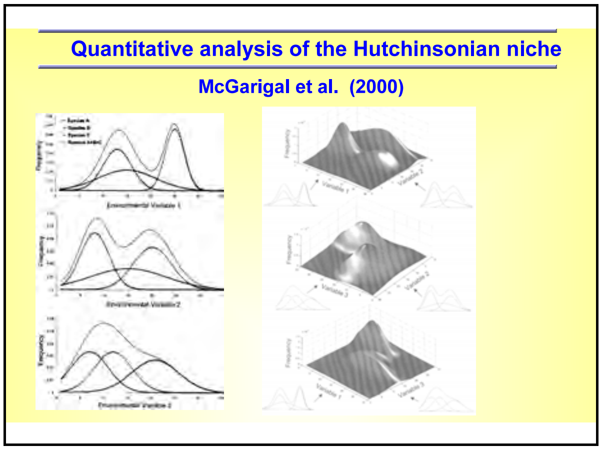
NOTES:

Beta diversity

Similarity & dissimilarity indices, Cluster analysis & ordination

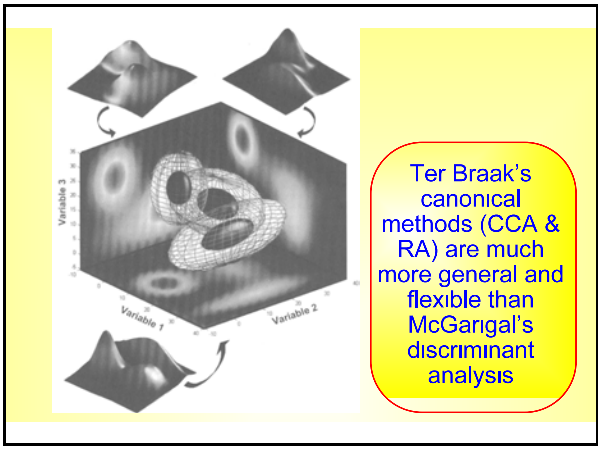
Slide 48 Beta diversity

NOTES:



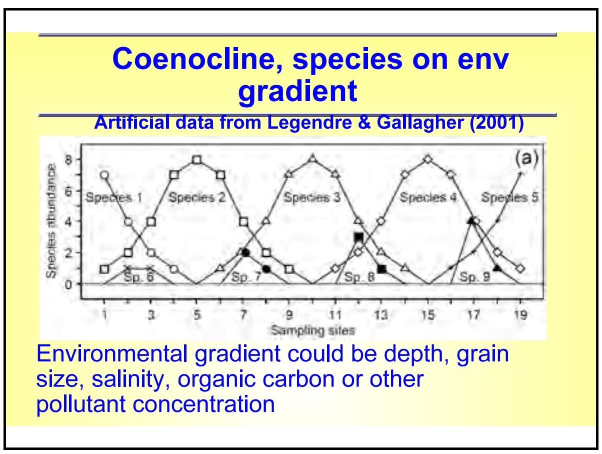
Slide 49 Quantitative analysis of the Hutchinsonian niche

NOTES:



Slide 50

NOTES:



Slide 51 Coenocline, species on env gradient

NOTES:

Ordination: ordering samples

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

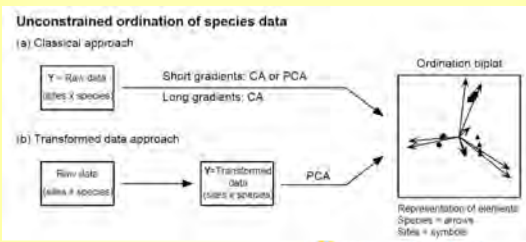
- Direct: Plot species abundances along measure of environmental gradient
- Indirect ordination or indirect gradient analysis
  - Principal components analysis, Principal coordinates analysis, Correspondence analysis
    - Do the ordination using PCA, PCoA, or CA or other methods
    - External variables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

Slide 52 Ordination: ordering samples

NOTES:

Ordination biplots: PCA & CA

See Legendre & Gallagher (2001)
http://www.es.umb.edu/edgwebp.htm



Slide 53 Ordination biplots: PCA & CA

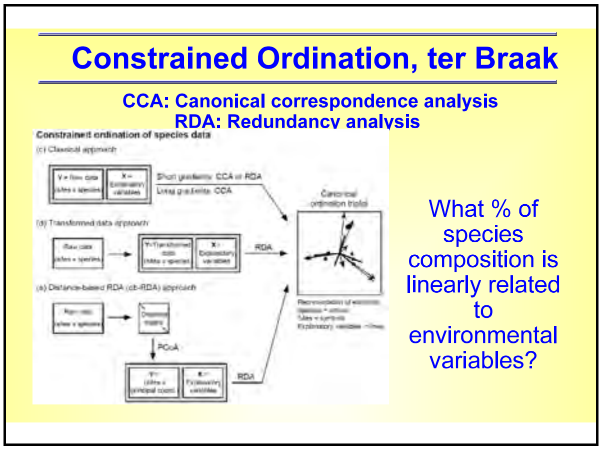
NOTES:

When should you use canonical methods (Canonical CA, 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

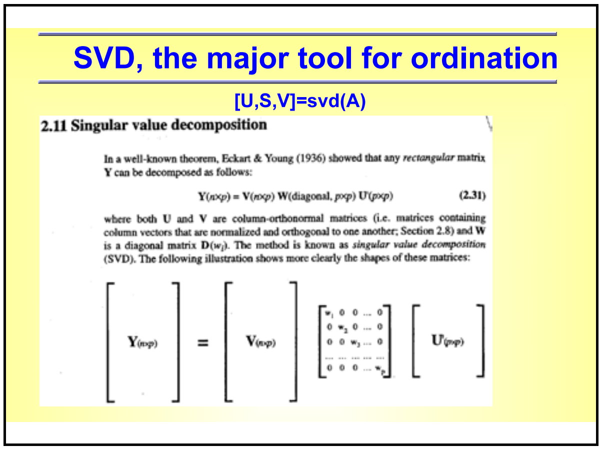
Slide 54 When should you use canonical methods (Canonical CA, Redundancy Analysis, Discriminant Analysis)?

NOTES:



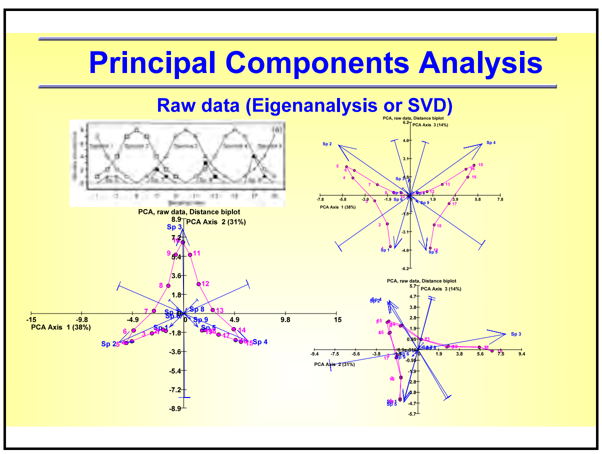
Slide 55 Constrained Ordination, ter Braak

NOTES:



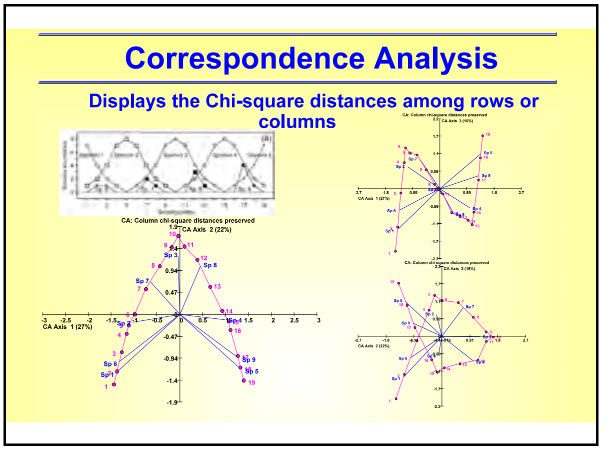
Slide 56 SVD, the major tool for ordination

NOTES:



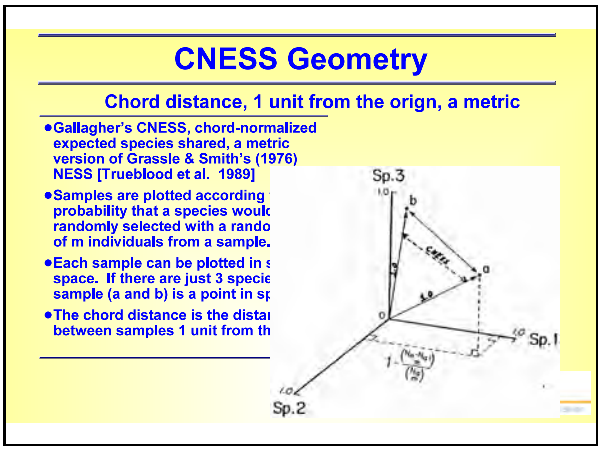
Slide 57 Principal Components Analysis

NOTES:



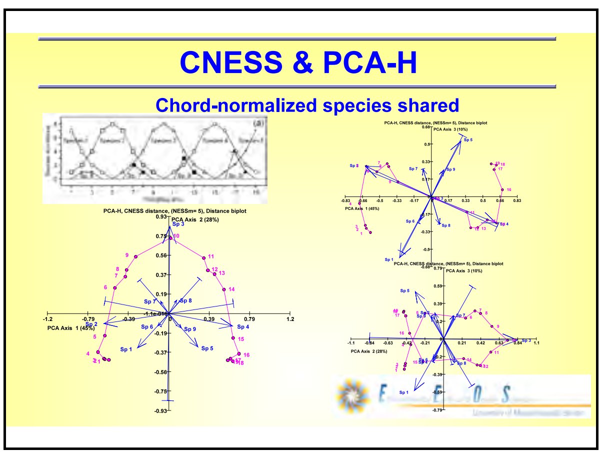
Slide 58 Correspondence Analysis

NOTES:



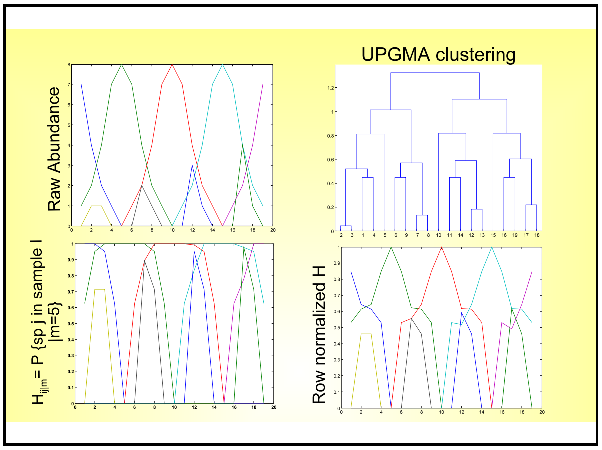
Slide 59 CNESS Geometry

NOTES:



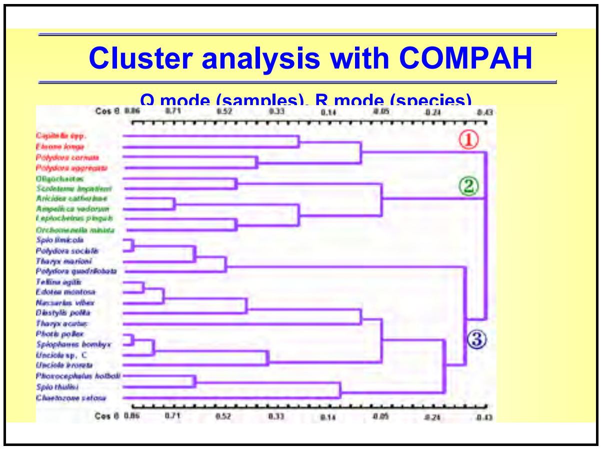
Slide 60 CNESS & PCA-H

NOTES:



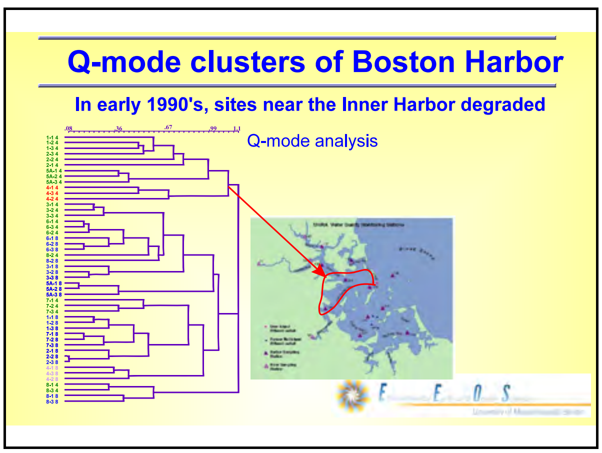
Slide 61

NOTES:



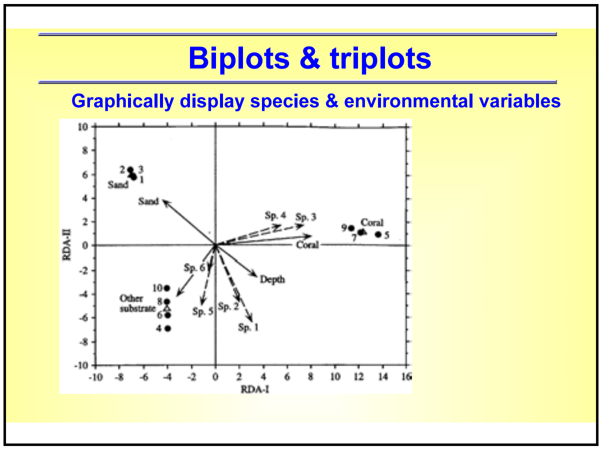
Slide 62 Cluster analysis with COMPAH

NOTES:



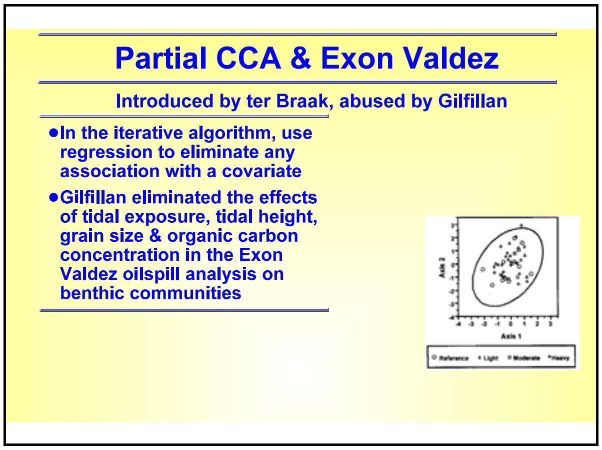
Slide 63 Q-mode clusters of Boston Harbor

NOTES:



Slide 64 Biplots & triplots

NOTES:



Slide 65 Partial CCA & Exon Valdez

NOTES:

Slide 66 Benthic Communities and Populations

Case 1: Buzzards Bay

Case 2: MA Bay

Case 3: Pacific NW Intertidal

Case 4: Skagit Intertidal

Case 5: Deep-Sea & Hydrothermal Vents

Case 6: Boston Harbor

NOTES:

Benthic Community Structure
Case Study 1: Buzzards Bay & Case Study 2: MA Bay

Sanders (1960) & Gallagher MWRA analyses

Slide 67 Benthic Community Structure

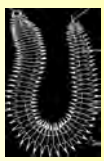
Case Study 1: Buzzards Bay & Case Study 2: MA Bay

NOTES:

Sanders (1960)

Buzzards Bay Station R

- *Sampled Station R – a mud station – 20 grab samples over 729 days*
- *Used a 300-μm mesh sieve*
- *Described the community by its numerically dominant and characteristic taxa the polychaete worm Nephtys incisa & the protobranch bivalve Nucula annulata.*
- Described the community as being remarkably stable
- Resampled by Boyer & Whitlatch 20 y later – little changed



N. incisa

Slide 68 Sanders (1960)

NOTES:

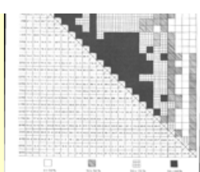
Sanders' (1960): Buzzards Bay

% Similarity & a trellis diagram

% Similarity = Sanders' (1960) Dominance Affinity:

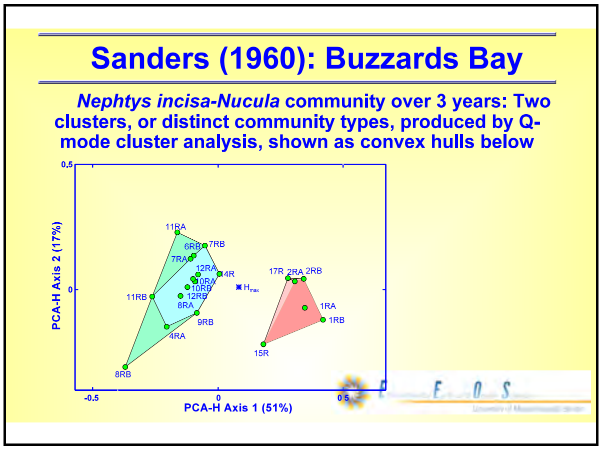
$$SIM_{ij} = \sum_{k=1}^{S} \min\left(\frac{x_{ki}}{\sum_{k=1}^{S} x_{ki}}, \frac{x_{kj}}{\sum_{k=1}^{S} x_{kj}}\right).$$

where, x_{ki} = Abundance of species k in sample i.
S = Number of species



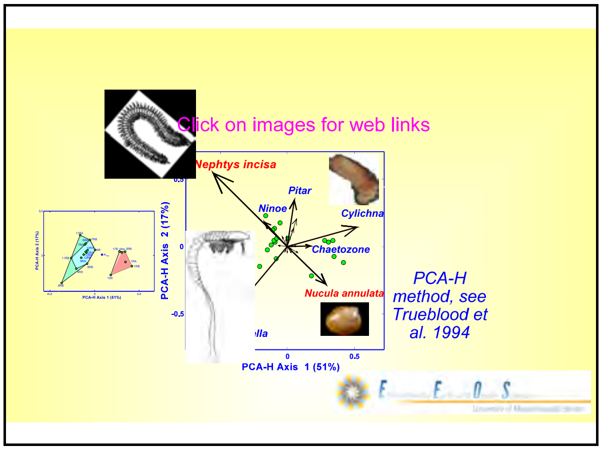
Slide 69 Sanders' (1960): Buzzards Bay

NOTES:



Slide 70 Sanders (1960): Buzzards Bay

NOTES:



Slide 71

NOTES: