Reimannian Benthic Ecology: Competition, Predation & Deep-Sea Diversity

Class 11: October 7, 2008

Slide 1 Reimannian Benthic Ecology: competition, Predation, Deep-Sea Diversity

NOTES:

Class schedule

Order of topics

- Tuesday (9/30): 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 (10/2): 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.
- Today: Reimannian Ecology: competion, predation and theories of deep-sea diversity

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

NOTES:

Required reading, Pollution effects for Thursday

Chapter 6: Benthic Pollution Biology

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]

Rosenberg, R. 2001. Marine benthic faunal successional stages and related sedimentary activity. Sci. Mar. *65* (Suppl. 2): 107-119. *[A broad insightful review of theories from Petersen to Thorson to Pearson & Rosenberg & Fauchald & Jumars]{1}*

Slide 4 Required reading, Pollution effects for Thursday

NOTES:

Reimannian Ecology

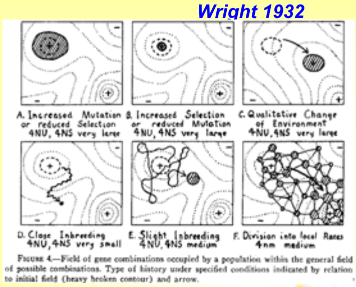
- *Herman Reimann was asked in 1953 by one of his examiners, Carl Friedrich Gauss, to prepare a talk on the topic 'The hypotheses which underlie geometry.' He delivered his lecture in 1854, describing geometry in more than 3 dimensions. Gauss immediately praised him, and his lecture material was published in 1854.*
  - *Reimann described how a metric tensor with 10 parameters could describe a surface in 4 dimensions, no matter how curved or distorted.*
  - *In a classic example of verisimilitude, Einstein found that*
- *In ecology and evolutionary biology, there are two major concepts involving higher dimensional space.*
  - *Sewell Wright's (1932) adaptive landscapes to describe evolution and genetic drift*
  - *Hutchinson's (1944, 1957) definition of the niche*
  - *Both topics play a role in understanding processes controlling benthic community structure*

Slide 5 Reimannian Ecology

NOTES:

Wright's adaptive landscapes

Wright 1932



Contours indicate fitness

Slide 6 Wright's adaptive landscapes

NOTES:

Hutchinson's n-dimensional niche

Two definitions of niche, see Chase & Leibold (2003)

- 1) Grinnell (1917): the place in the environment that a species occupies
  - Verbally mapped all the necessary conditions for a species' existence: physiological tolerances, morphological limitations, feeding habits and interactions with other species
  - Hutchinson (1944, 1957): the niche is an n-dimensional hypervolume.
- 2) Elton (1927): the niche of a species is the functional role of the species within within the food web and its impact on the environment
- A new definition by Chase & Leibold (2003): the joint description of the zero net growth isocline (ZNGI) of an organism along with the impact vector on that ZNGI in the multivariate space defined by the set of environmental factors that are present

Slide 7 Hutchinson's n-dimensional niche

NOTES:

Benthic Communities and Populations

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

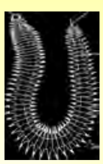
Slide 8 Benthic Communities and Populations

NOTES:

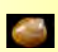
Sanders (1960)

Buzzards Bay Station R, south of New Bedford Harbor

- 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



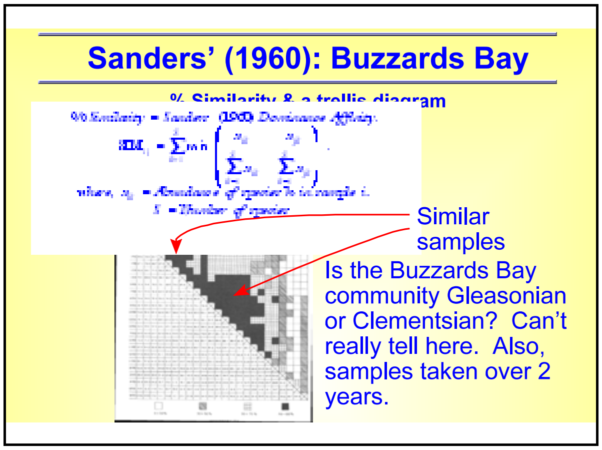
Nephtys incisa



Nucula annulata

Slide 9 Sanders (1960)

NOTES:



Slide 10 Sanders' (1960): Buzzards Bay

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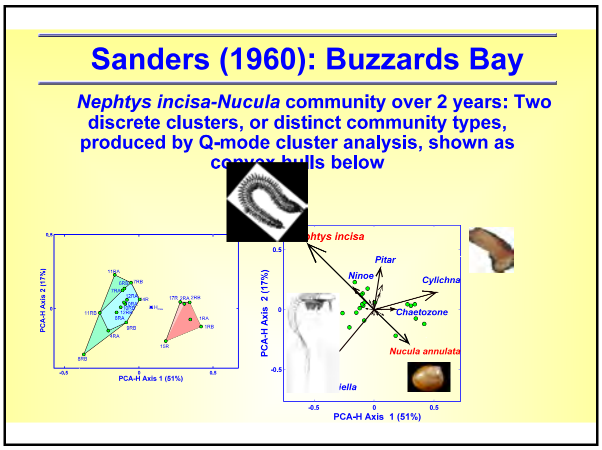

Slide 11 Sanders (1960): Buzzards Bay

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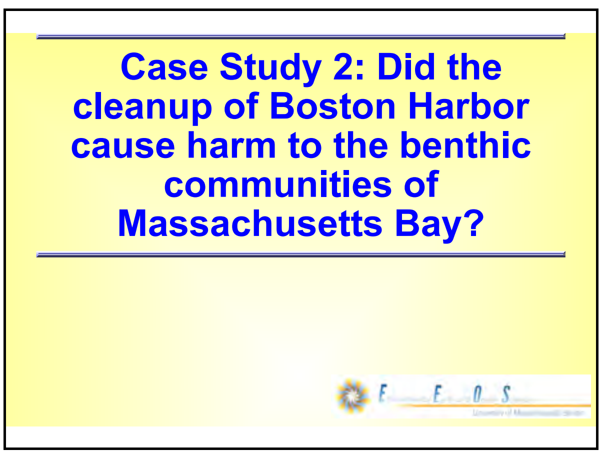
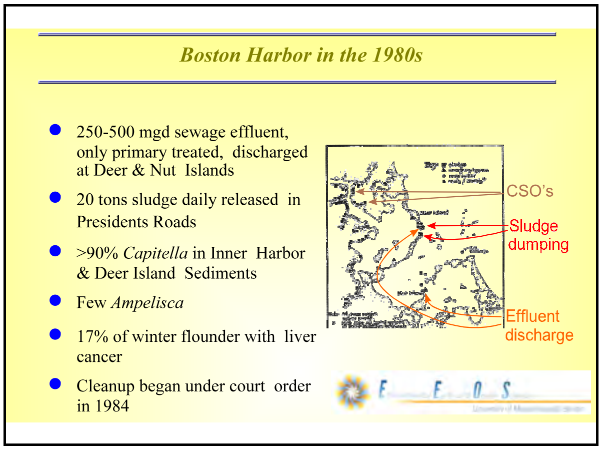


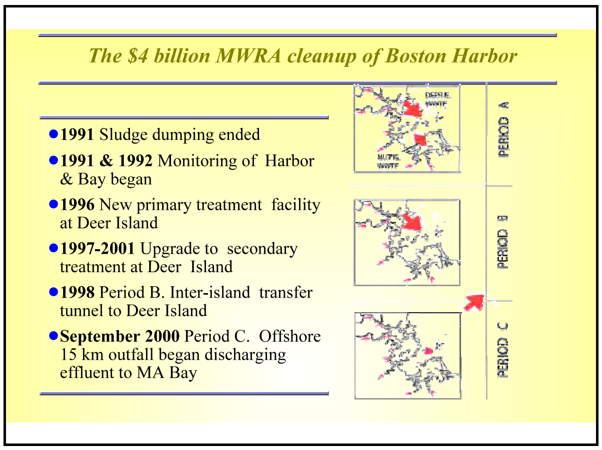
Slide 12 Case Study 2: Did the cleanup of Boston Harbor cause harm to the benthic communities of Massachusetts Bay?

NOTES:



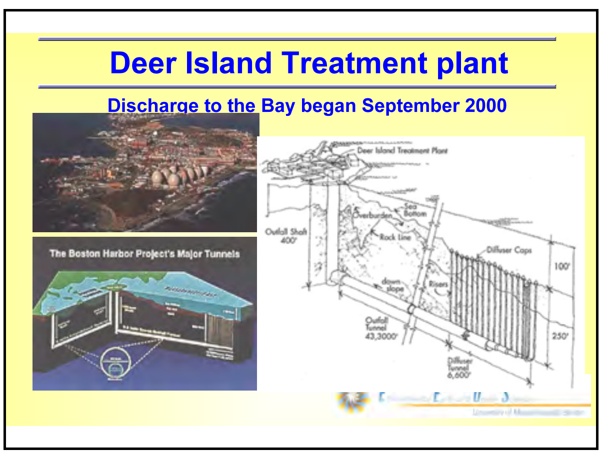
Slide 13 Boston Harbor in the 1980s

NOTES:



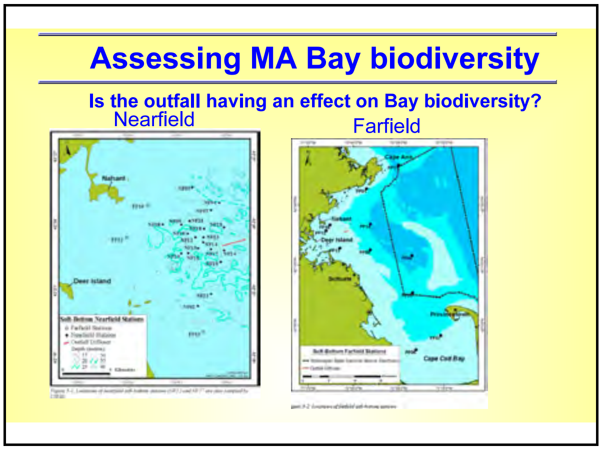
Slide 14 The $4 billion MWRA cleanup of Boston Harbor

NOTES:



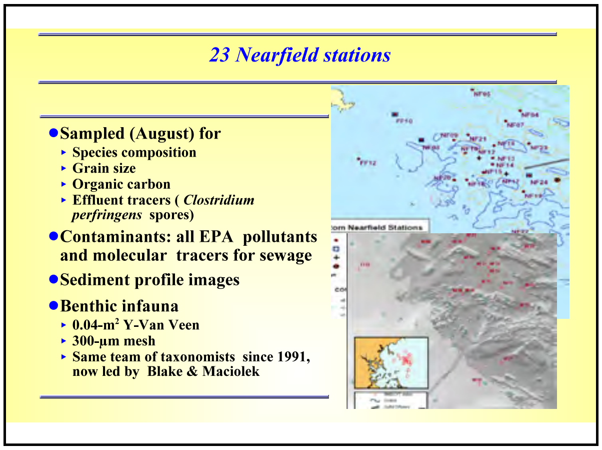
Slide 15 Deer Island Treatment plant

NOTES:



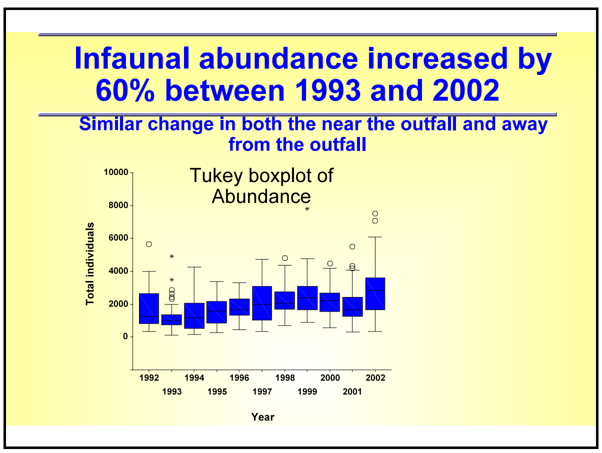
Slide 16 Assessing MA Bay biodiversity

NOTES:



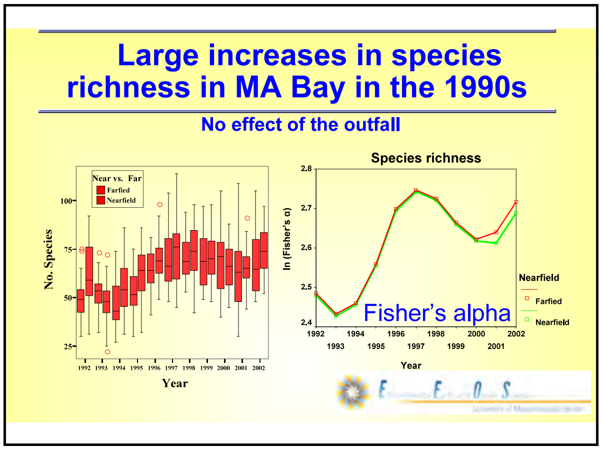
Slide 17 23 Nearfield stations

NOTES:



Slide 18 Infaunal abundance increased by 60% between 1993 and 2002

NOTES:



Slide 19 Large increases in species richness in MA Bay in the 1990s

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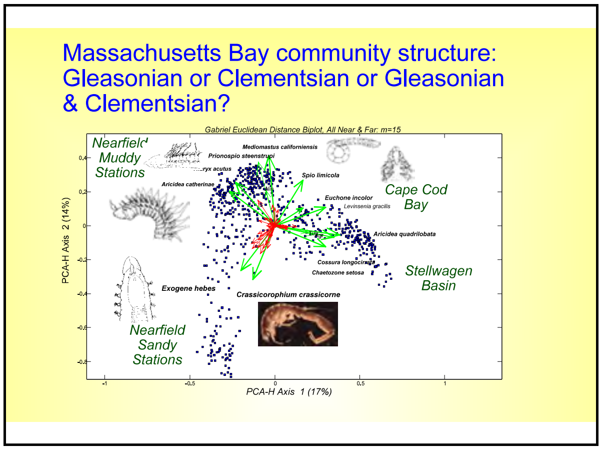

Slide 20 Community structure in MA Bay:

PCA-H, ordination of CNESS

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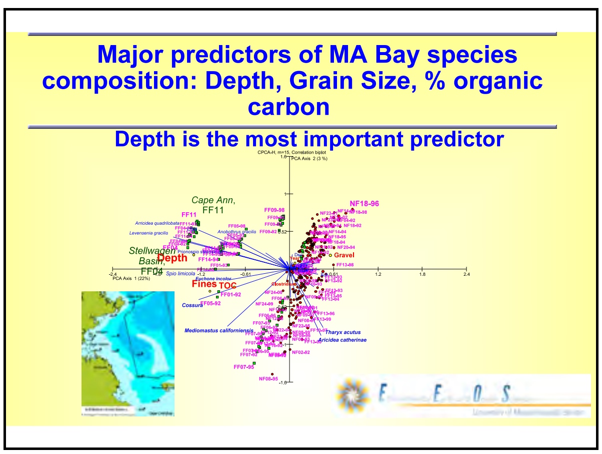
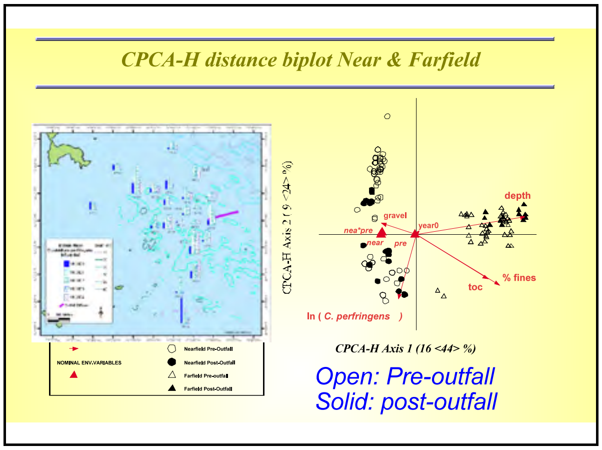


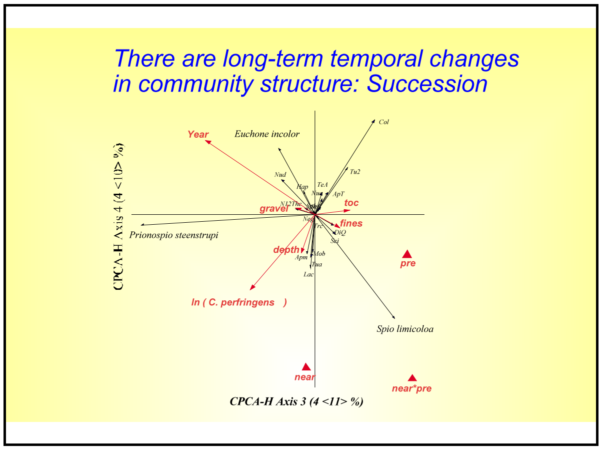
Slide 21 Major predictors of MA Bay species composition: Depth, Grain Size, % organic carbon

NOTES:



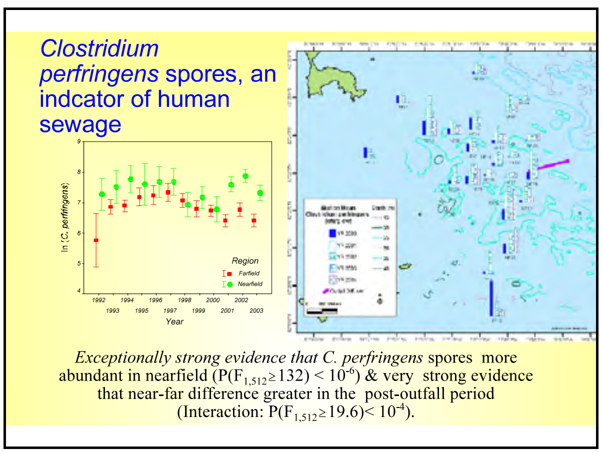
Slide 22 CPCA-H distance biplot Near & Farfield

NOTES:



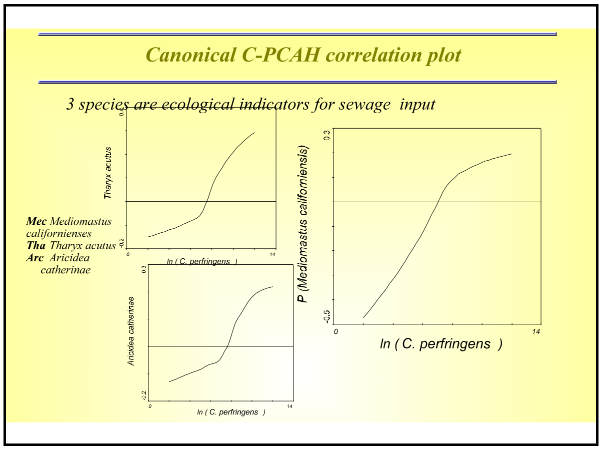
Slide 23 Long-term changes in numerical dominants

NOTES:



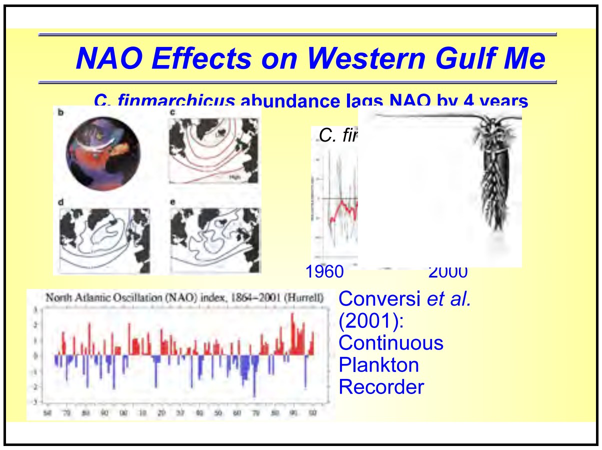
Slide 24 Outfall effects: C. Pefringens abundance changed due to outfall

NOTES:



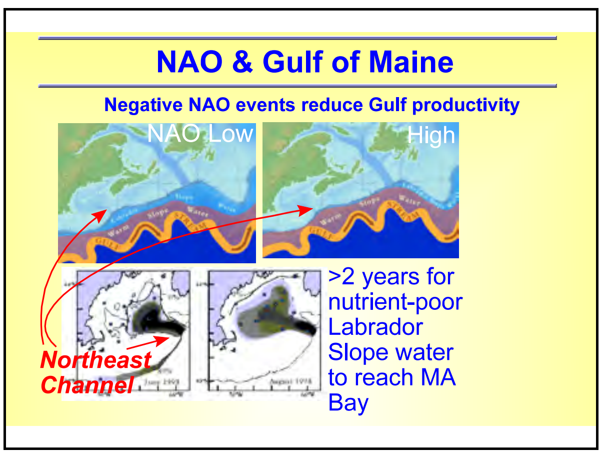
Slide 25 Canonical C-PCAH correlation plot

NOTES:



Slide 26 NAO Effects on Western Gulf Me

NOTES:



Slide 27 NAO & Gulf of Maine

NOTES:

Long-term cyclic trends in NAO

Hakkinen & Rhines Science (2004)

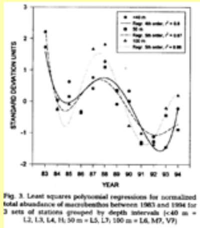
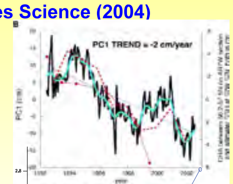
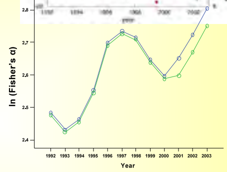


Fig. 3. Least squares polynomial regressions for normalized total abundance of macrobenthos between 1983 and 1994 for 3 sets of stations grouped by depth intervals





Tunberg & Nelson (1998): Swedish benthic communities

Slide 28 Long-term cyclic trends in NAO

NOTES:

Conclusions on MA Bay

- Boston Harbor has improved dramatically since the early 1990's
  - Most of the improvement was in the late 80s
    - Much of the increases in species richness occurred after the early 1982 301(h) survey and before MWRA monitoring began in Fall 1991)
    - *Capitella*, the pollution indicator and a major prey of flounder, was dominant at many stations in 1982 but had largely disappeared by 1991
  - Species richness of benthic communities has doubled at many harbor stations
  - Organic enrichment in low-energy areas remains a major problem
- MA Bay biodiversity increased tremendously in the 1990s, prior to the outfall being moved offshore
- There is no indication of adverse outfall effects on MA Bay
- There are indications that long-term changes in biodiversity in the harbor are linked to MA Bay diversity

Slide 29 Conclusions on MA Bay

NOTES:

Why is MA Bay community structure changing?

- The perfect storm hypothesis: Infaunal communities recovering from severe storms in the early 1990s
- The climate-change hypothesis: MA Bay benthos experiencing a long-term climate-induced change. Perhaps due to the North Atlantic Oscillation, a large scale variation in the North Atlantic weather
- The productivity hypothesis: Long-term increase in organic matter supply to the benthos
- Changes in predation or disturbance (fishing intensity)
- Pollution reduction (LABs are excellent predictors of species richness)
- Chance or Hubbellian Ecological Drift
- Metodological differences, especially improvements in taxonomy

Slide 30 Why is MA Bay community structure changing?

NOTES:

Case Study 3: Keystone predation & intermediate disturbance in the Pacific Northwest Rocky Intertidal

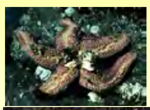
Paine (1966), Dayton (1971), Connell (1971)

Slide 31 Case Study 3: Keystone predation & intermediate disturbance in the Pacific Northwest Rocky Intertidal

NOTES:

Keystone Predation

Paine (1966), Dayton(1971), Connell (1971)

Slide 32 Keystone Predation

NOTES:

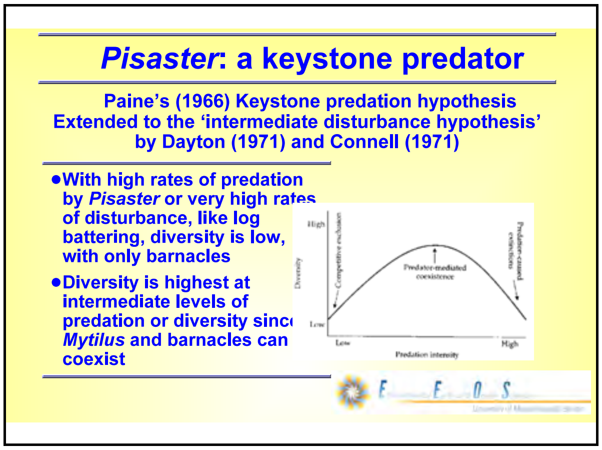
Keystone Predation

Paine (1966)

- The mussel *Mytilius californianus* is the dominant competitor for space in the Pacific Northwest Rocky intertidal
- In the absence of disturbance or predation, *Mytilus* will overgrow & crush other space-occupying species, especially barnacles.

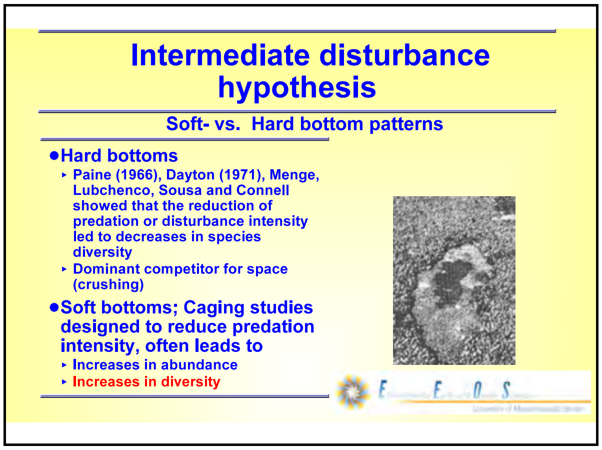
Slide 33 Keystone Predation

NOTES:



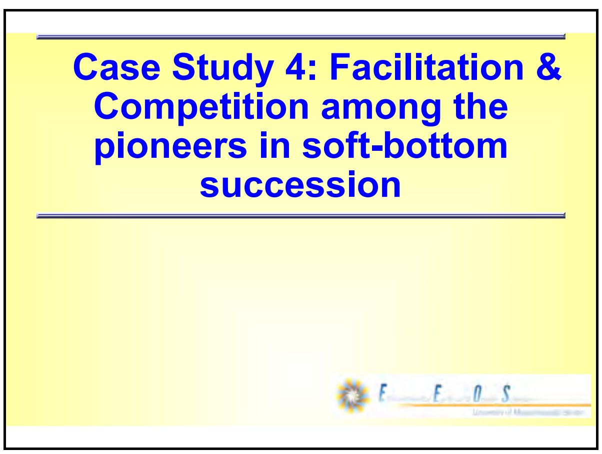
Slide 34 Pisaster: a keystone predator

NOTES:



Slide 35 Intermediate disturbance hypothesis

NOTES:



Slide 36 Case Study 4: Facilitation & Competition among the pioneers in soft-bottom succession

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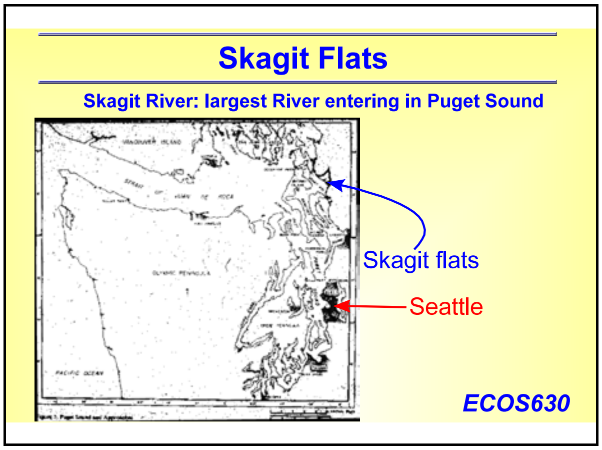

Slide 37 Skagit Flats

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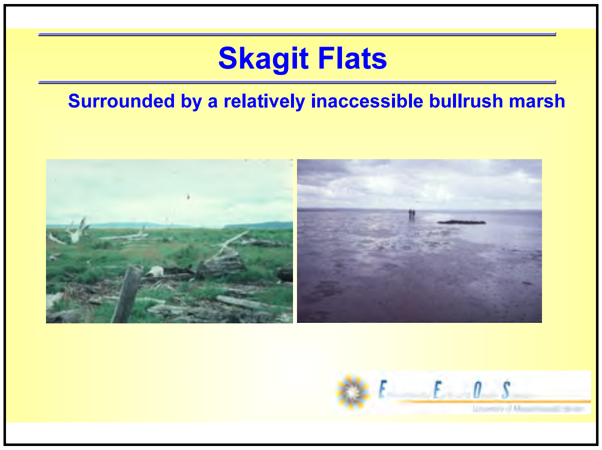
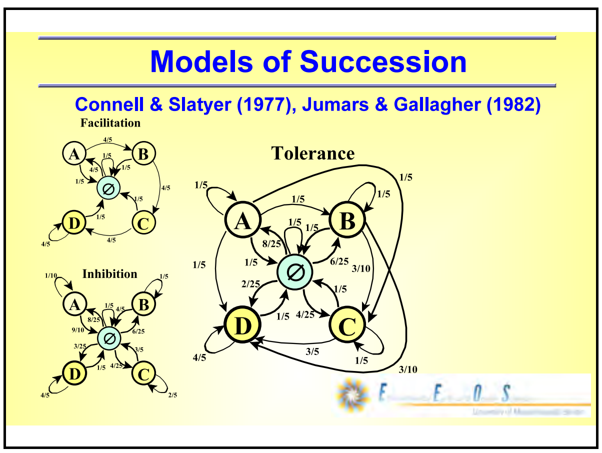


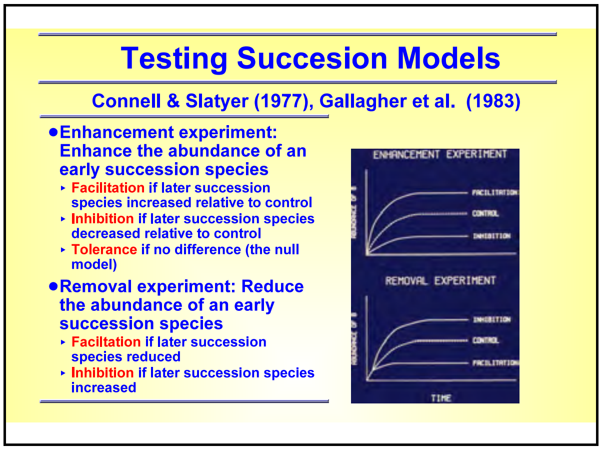
Slide 38 Skagit Flats

NOTES:



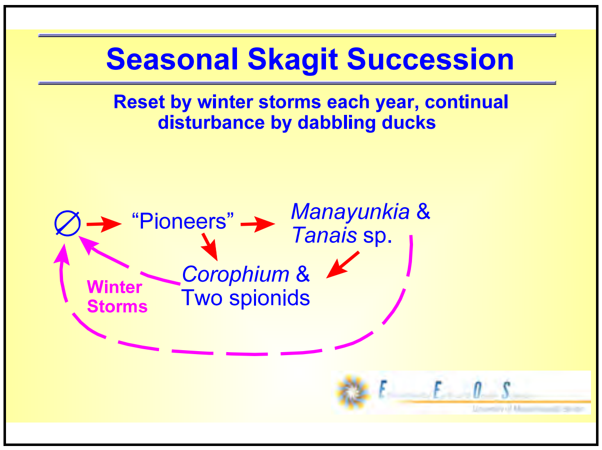
Slide 39 Models of Succession

NOTES:



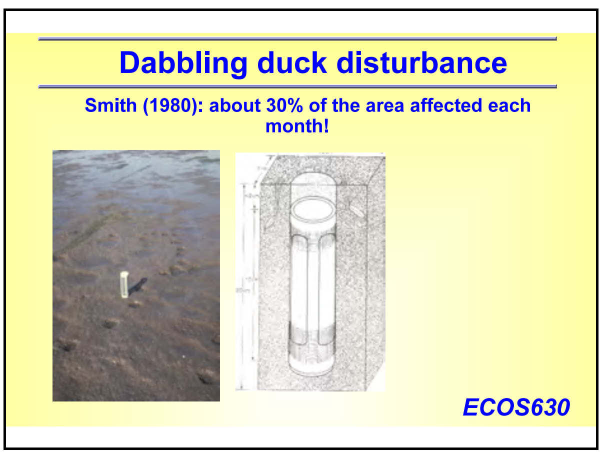
Slide 40 Testing Succesion Models

NOTES:



Slide 41 Seasonal Skagit Succession

NOTES:

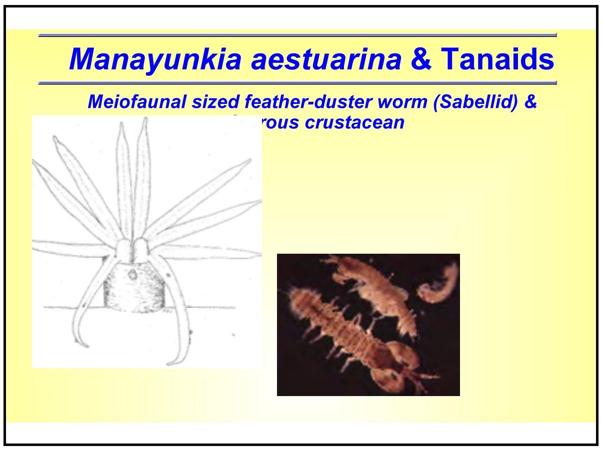


Slide 42 Dabbling duck disturbance

NOTES:

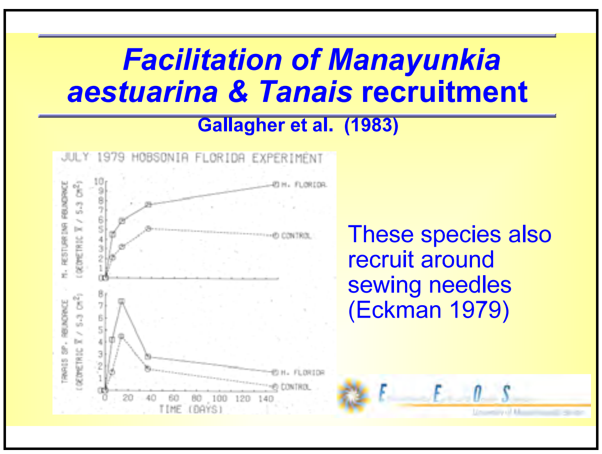
Slide 43 Controlled field experiments

NOTES:



Slide 44 Manayunkia aestuarina & Tanaids

NOTES:

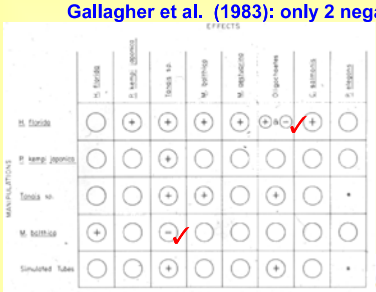


Slide 45 Facilitation of Manayunkia aestuarina & Tanais recruitment

NOTES:

Facilitation is a major soft-bottom successional mechanism

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



Slide 46 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 in soft bottoms
  - 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 in soft-bottom benthos

Slide 47 Predation & Soft bottom benthos

NOTES:

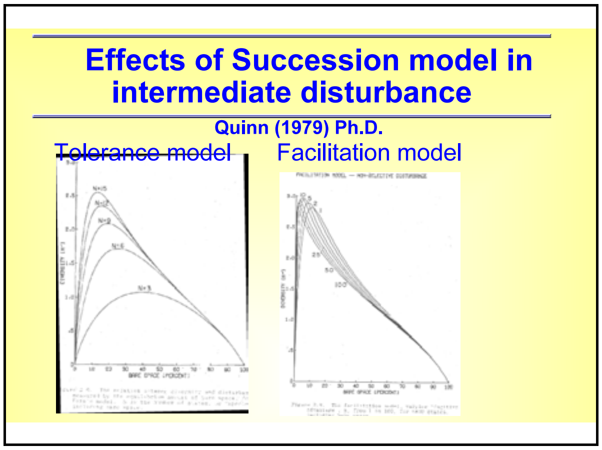
Caging in the soft-bottom benthos

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

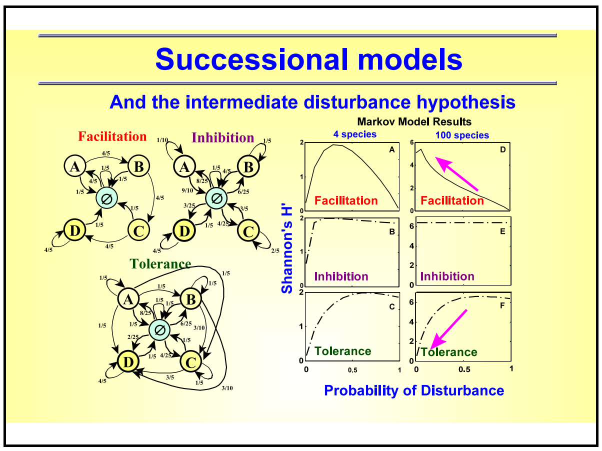
Slide 48 Caging in the soft-bottom benthos

NOTES:



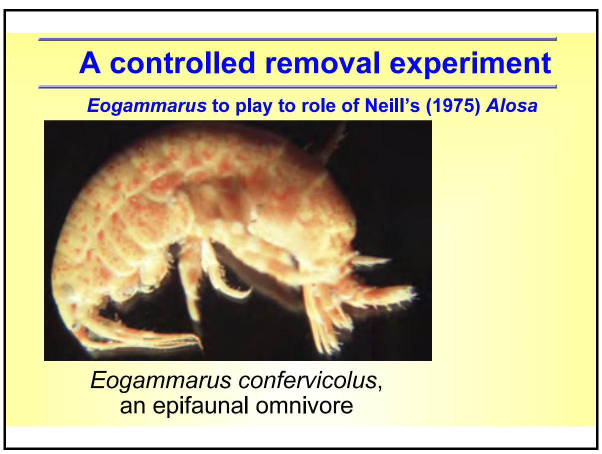
Slide 49 Effects of Succession model in intermediate disturbance

NOTES:



Slide 50 Successional models

NOTES:

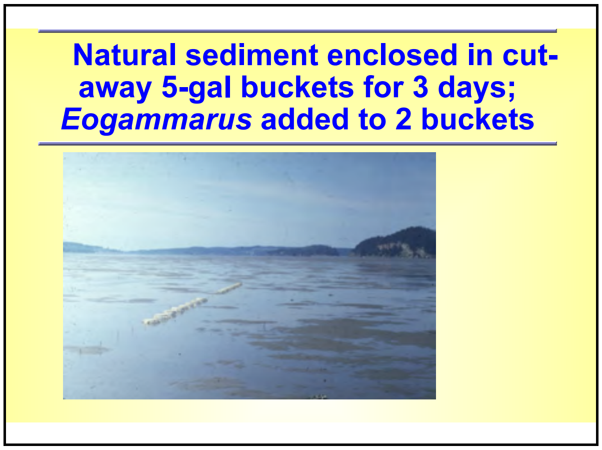


Slide 51 A controlled removal experiment

NOTES:

Slide 52 Eogammarus is an omnivore

NOTES:

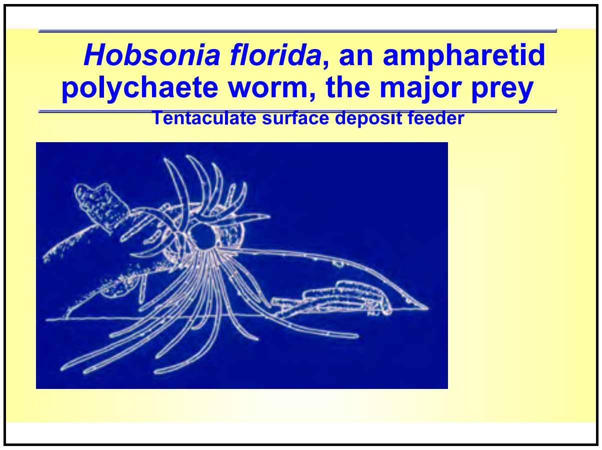


Slide 53 Natural sediment enclosed in cut-away 5-gal buckets for 3 days; Eogammarus added to 2 buckets

NOTES:

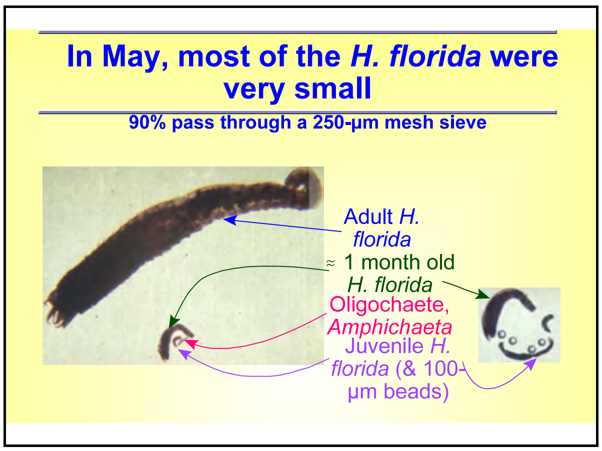
Slide 54 Buckets enclosed with 1-mm mesh to retain Eogammarus

NOTES:



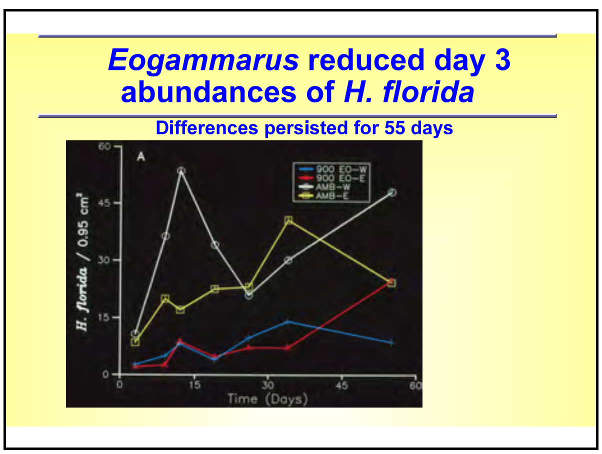
Slide 55 Hobsonia florida, an ampharetid polychaete worm, the major prey

NOTES:



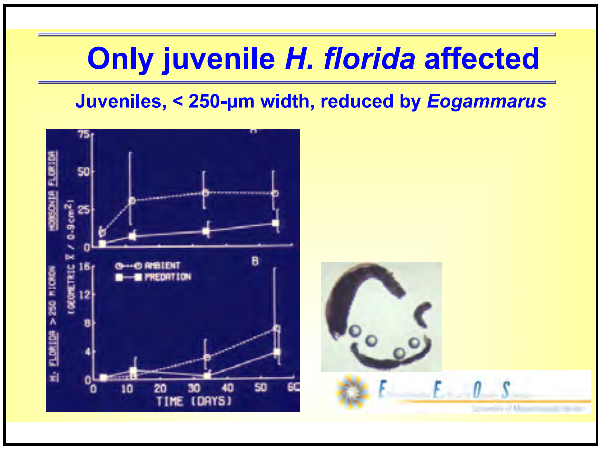
Slide 56 In May, most of the H. Florida were very small

NOTES:



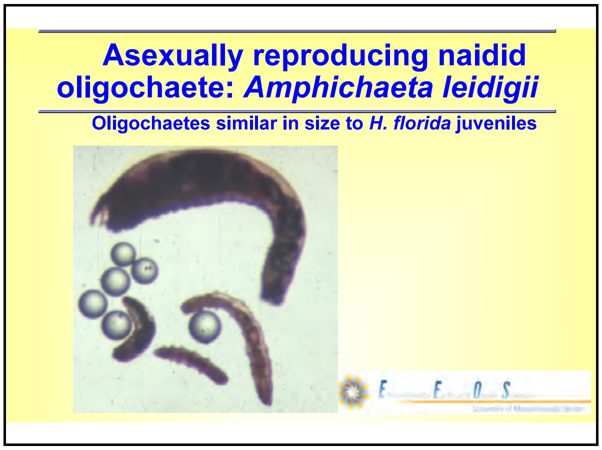
Slide 57 Eogammarus reduced day 3 abundances of H. Florida

NOTES:



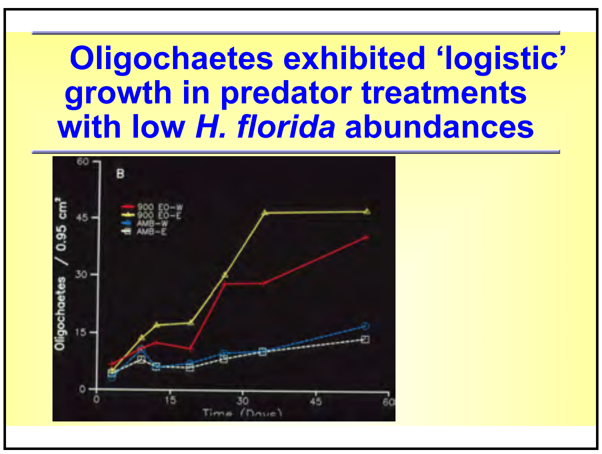
Slide 58 Only juvenile H. Florida affected

NOTES:



Slide 59 Asexually reproducing naidid oligochaete: Amphichaeta leidigii

NOTES:

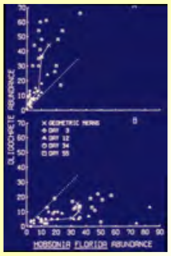


Slide 60 Oligochaetes exhibited 'logistic' growth in predator treatments with low H. Florida abundances

NOTES:

Two distinct population growth trajectories

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



Slide 61 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 62 What is competition?

NOTES:

Types of competition

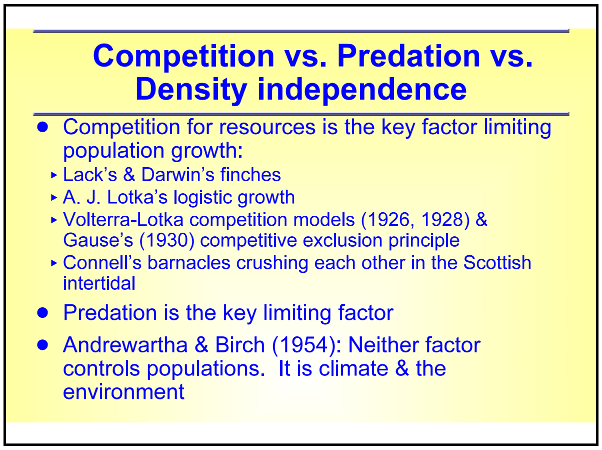
Exploitative ('scramble') vs. Interference

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.

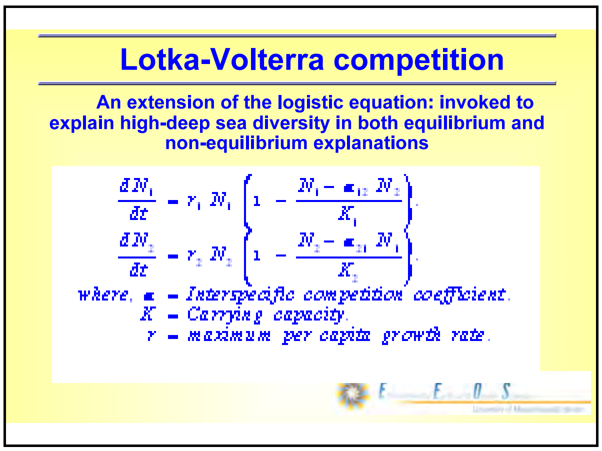
Slide 63 Types of competition

NOTES:



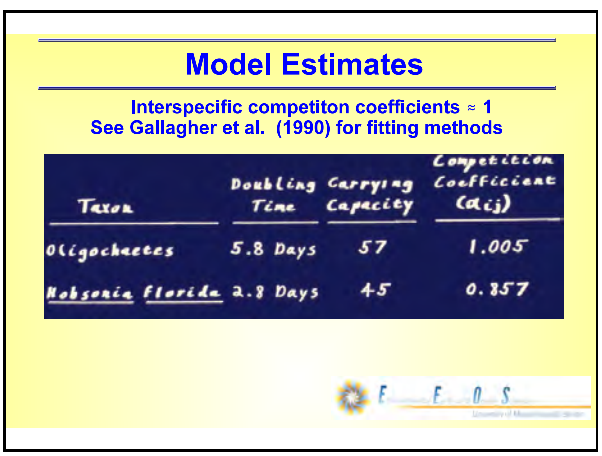
Slide 64 Competition vs. Predation vs. Density independence

NOTES:



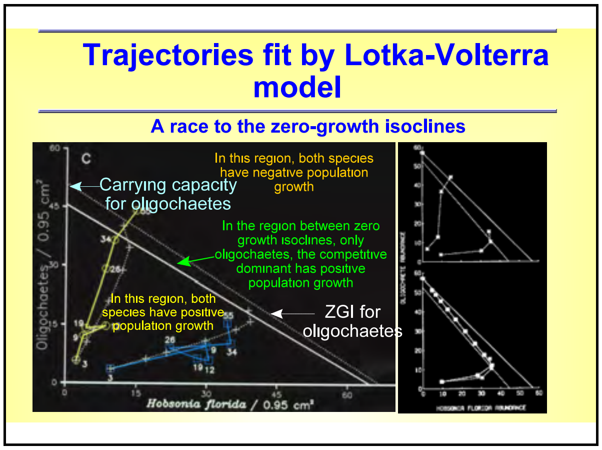
Slide 65 Lotka-Volterra competition

NOTES:



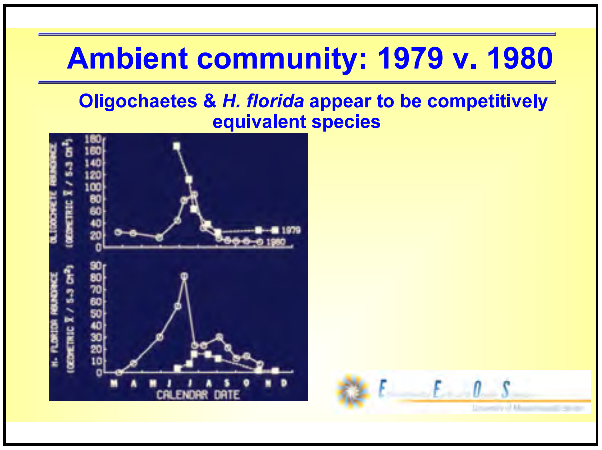
Slide 66 Model Estimates

NOTES:



Slide 67 Trajectories fit by Lotka-Volterra model

NOTES:

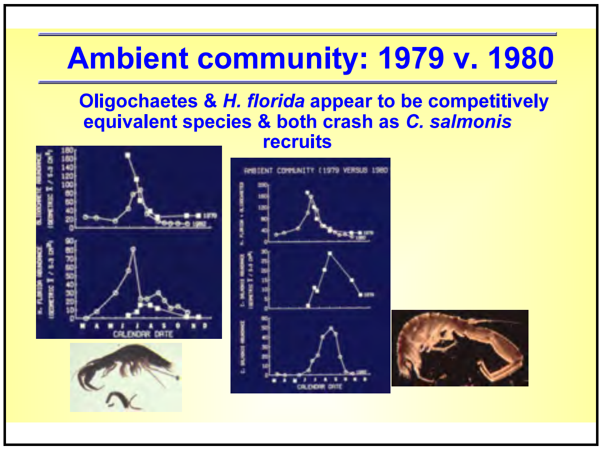


Slide 68 Ambient community: 1979 v. 1980

NOTES:

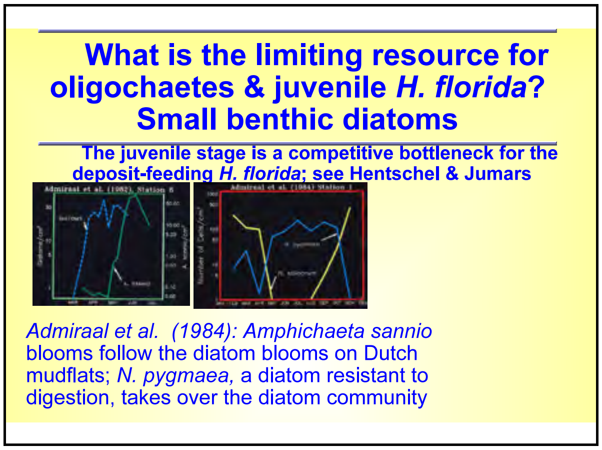
Slide 69 Corophium salmonis, a large interface feeder, recruits to the sandflat each July AS ADULTS

NOTES:



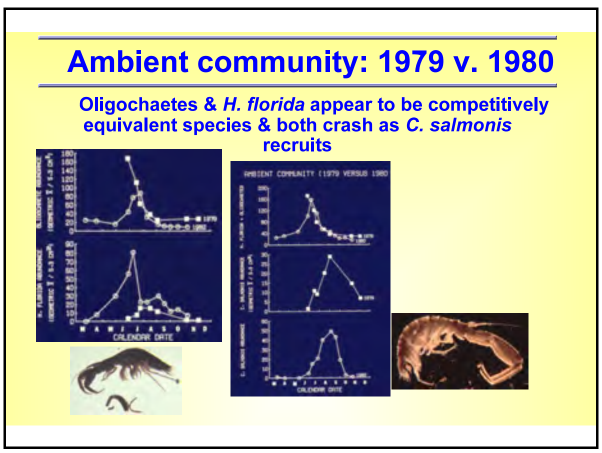
Slide 70 Ambient community: 1979 v. 1980

NOTES:



Slide 71 Ambient community: 1979 v. 1980

NOTES:



Slide 72 What is the limiting resource for oligochaetes & juvenile H. Florida? Small benthic diatoms

NOTES:

Case Study 5: High deep-sea diversity

See Jumars & Gallagher (1982) & Etter & Mullineaux

Slide 73 Case Study 5: High deep-sea diversity

NOTES:

Milestones in deep-sea diversity

Documenting High Deep-Sea diversity

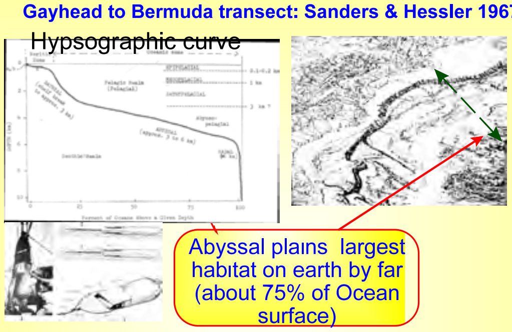
- 1846 Forbes dredged shells from the abyss, indicating that there is life in the deep sea.
- 1873-1876 Challenger expedition
  - Dredged animals from 5500 m1880
  - Thomas: The deep sea fauna is stable and ancient, containing the ancestral forms of many shallow water taxa.
- 1967 Hessler and Sanders
  - First quantitative demonstration of high deep-sea diversity.
  - Gayhead MA to Bermuda transect.

Slide 74 Milestones in deep-sea diversity

NOTES:

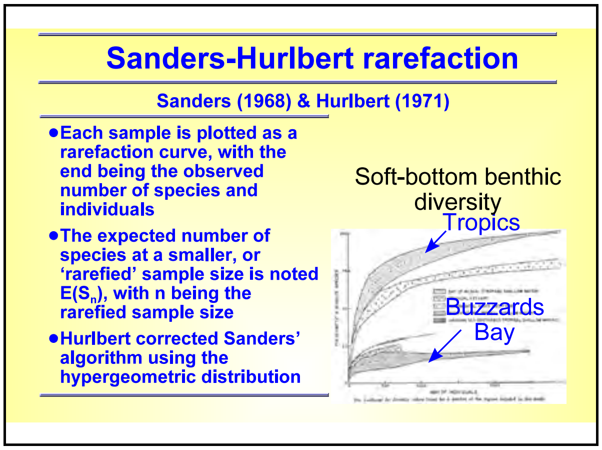
High deep-sea diversity

Gayhead to Bermuda transect: Sanders & Hessler 1967



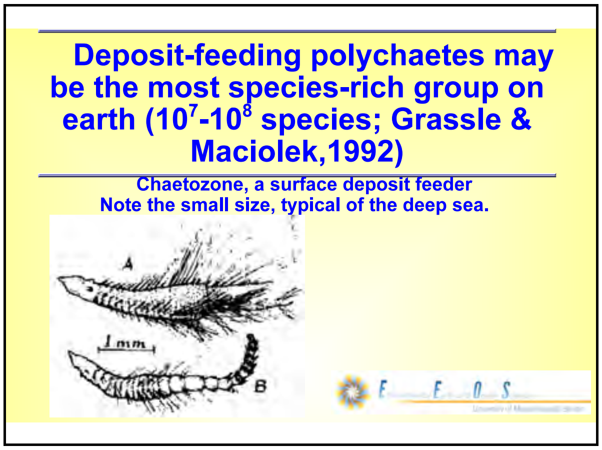
Slide 75 High deep-sea diversity

NOTES:



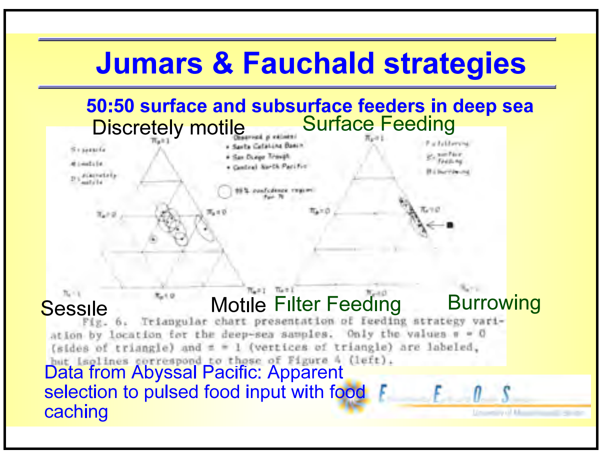
Slide 76 Sanders-Hurlbert rarefaction

NOTES:



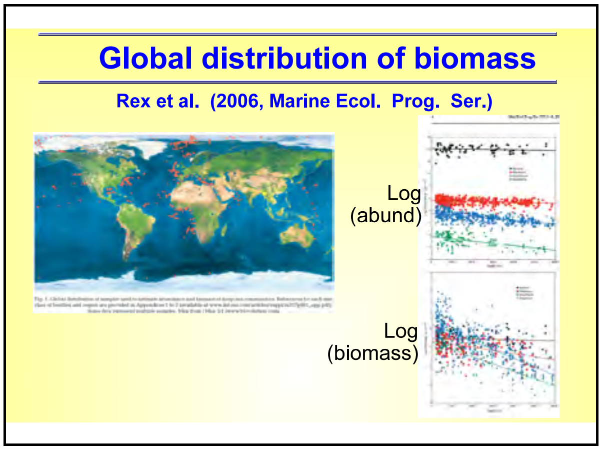
Slide 77 Deposit-feeding polychaetes may be the most species-rich group on earth (107-108 species; Grassle & Maciolek,1992)

NOTES:



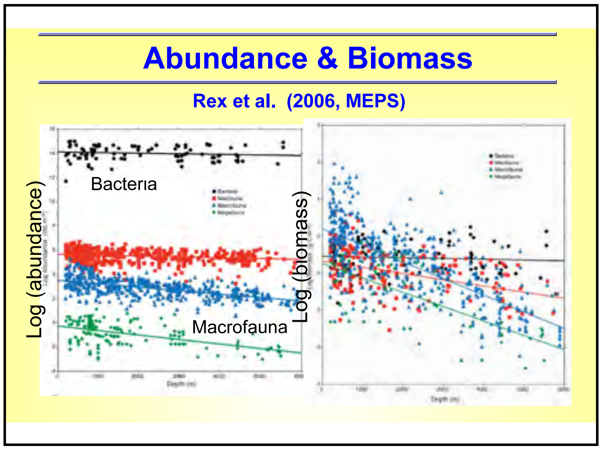
Slide 78 Jumars & Fauchald strategies

NOTES:



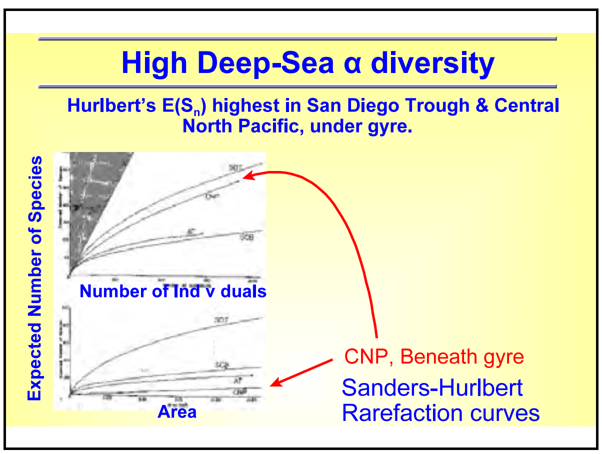
Slide 79 Global distribution of biomass

NOTES:



Slide 80 Abundance & Biomass

NOTES:



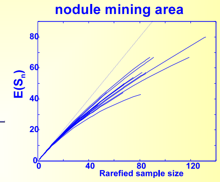
Slide 81 High Deep-Sea α diversity

NOTES:

High deep-sea diversity

Grassle & Maciolek (1992)

- Analysis of the rate at which new species being added along a transect in the North Atlantic deep sea: 1 species every 0.5 m^2
- 10^9 species globally estimated based on beta diversity in the North Atlantic
- Since, abundances lower in the abyssal Pacific, lowered estimate to 10^8 species
  - But note that beta diversity appears to be much higher in the Pacific than in the Atlantic Ocean
- Far higher species richness than any other biome on earth



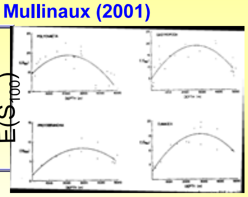
Slide 82 High deep-sea diversity

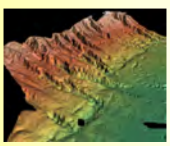
NOTES:

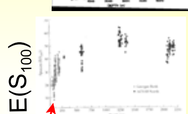
Slope & rise diversity> abyss

Rex (1973); Etter & Mullinaux (2001)

- Deep-sea diversity is highest at intermediate depths
  - Maximum at lower slope and continental rise
  - declining into the abyss.
- $E(S_{100})=14.6+0.004\ Z-0.000001\ Z^2$
  - r=0.68







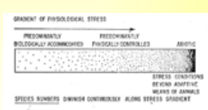
Slide 83 Slope & rise diversity> abyss

NOTES:

Sanders' Stability-time hypothesis

Proposed in 1968 American Naturalist

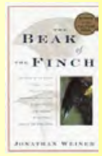
- The deep sea is 10's of millions of years old in the N. Atlantic and older still in the Pacific.
- Deep sea is the most stable environment on earth
- Animals evolve adaptations to the finest dimensions of the niche, allowing coexistence
- *"We might expect stenotopy, complex behavior of rather specific and stereotyped kinds, and the possibility of specialization to specific foods, hiding places, hunting methods, and environmental periodicities – in short to the details of the most significant parts of the environment."*



Slide 84 Sanders' Stability-time hypothesis

NOTES:

Sanders (1968): adaptative radiation to the finest dimensions of the niche, like Darwin's finches



Slide 85 Sanders (1968): adaptative radiation to the finest dimensions of the niche, like Darwin's finches

NOTES:

The cropper hypothesis

Dayton & Hessler (1972) based on the rocky intertidal paradigm

- ***"...high species diversity in the deep sea is more a result of continued biological disturbance than of highly specialized competitive niche diversification ... most animals would consume living particles as well as dead. We call this dominant life-style `cropping'."***
- ***If resource partitioning occurred, it would be unlikely to occur on the basis of space or time because of the high physical homogeneity, both temporally and spatially, of the deep-sea environment.***

Slide 86 The cropper hypothesis

NOTES:

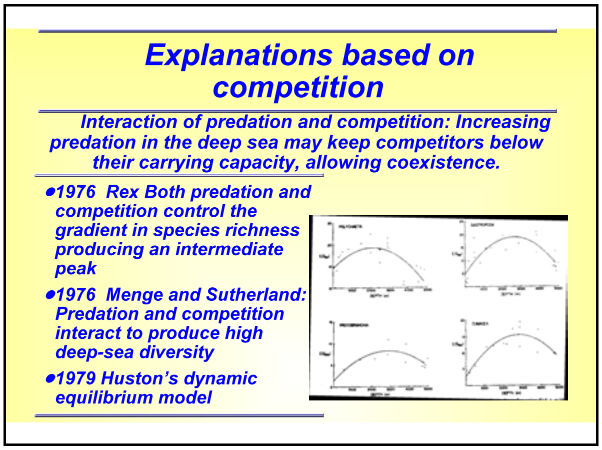
Spatial heterogeneity

Grassle & Sanders (1973), Jumars (1975 a & b, 1976)

- *Written as a rebuttal to Dayton & Hessler's (1972) cropper hypothesis based on predation and disturbance*
- *Grassle & Sanders (1973): little evidence for 'cropping' in the deep-sea*
- ***Habitat specialization, aided by deep-sea spatial heterogeneity** may be the key to maintaining high deep-sea diversity*
- *Jumars (1975a & b, 1976, Jumars & Eckman 1980): Deep sea may be the most spatially heterogeneous environment on earth.*

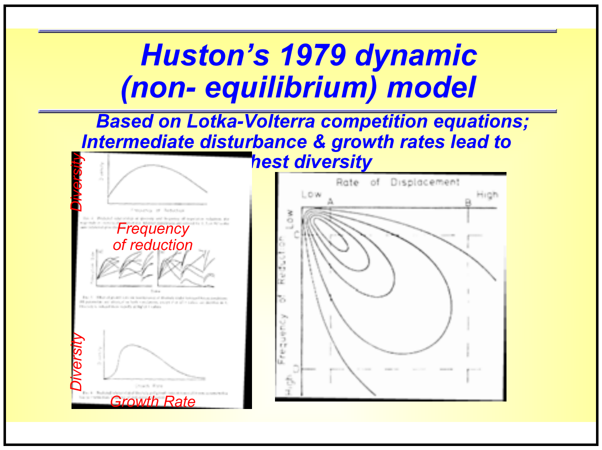
Slide 87 Spatial heterogeneity

NOTES:



Slide 88 Explanations based on competition

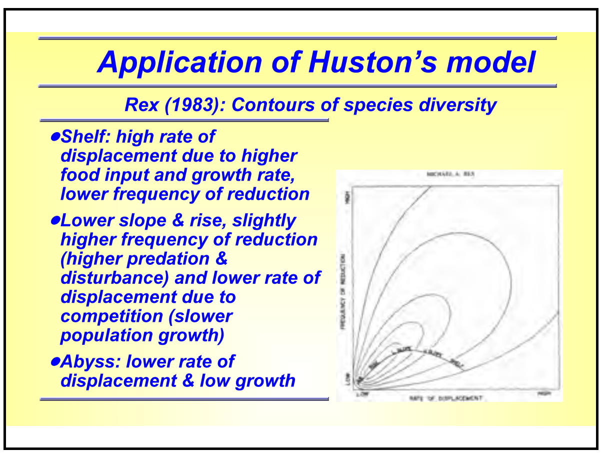
NOTES:



Slide 89 Huston's 1979 dynamic

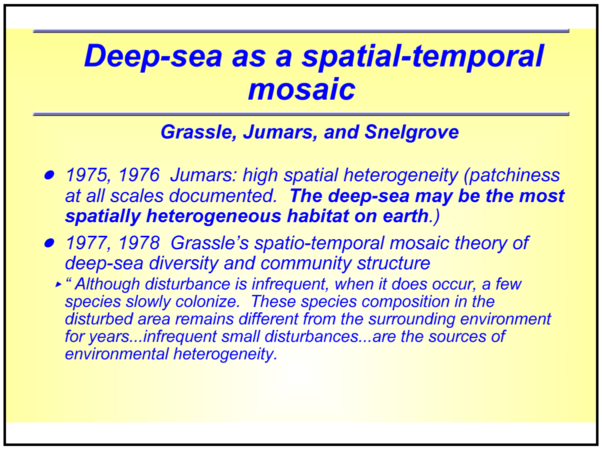
(non- equilibrium) model

NOTES:



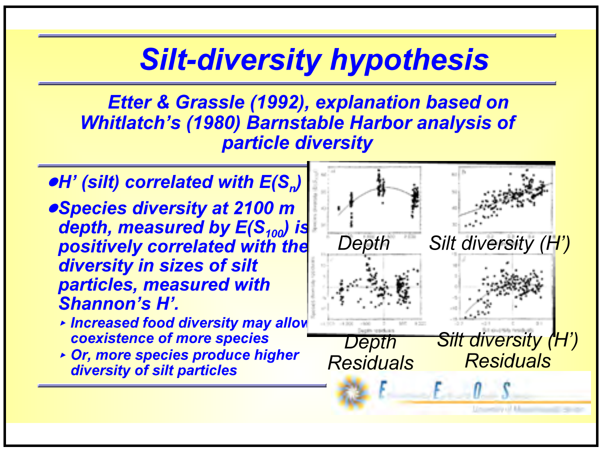
Slide 90 Application of Huston's model

NOTES:



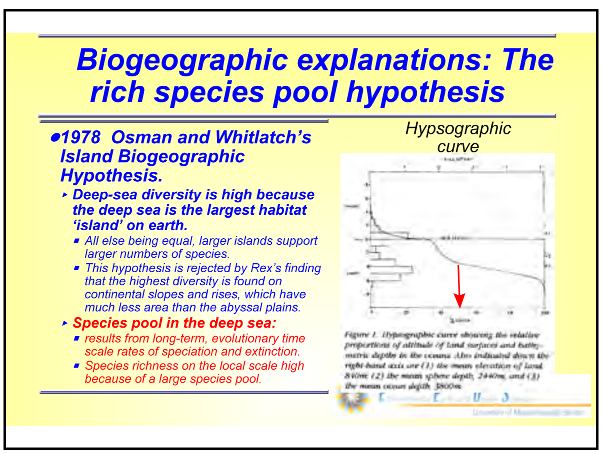
Slide 91 Deep-sea as a spatial-temporal mosaic

NOTES:



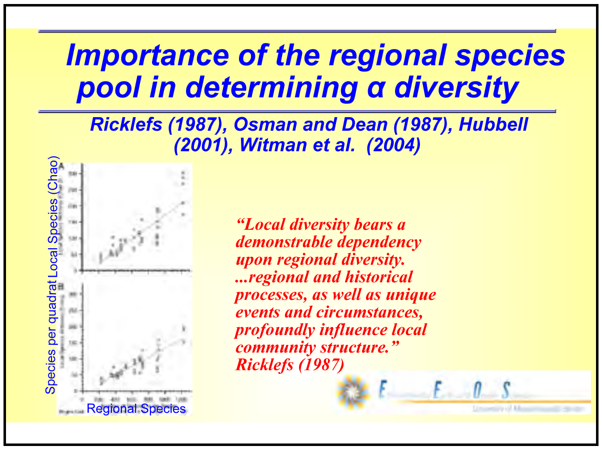
Slide 92 Silt-diversity hypothesis

NOTES:



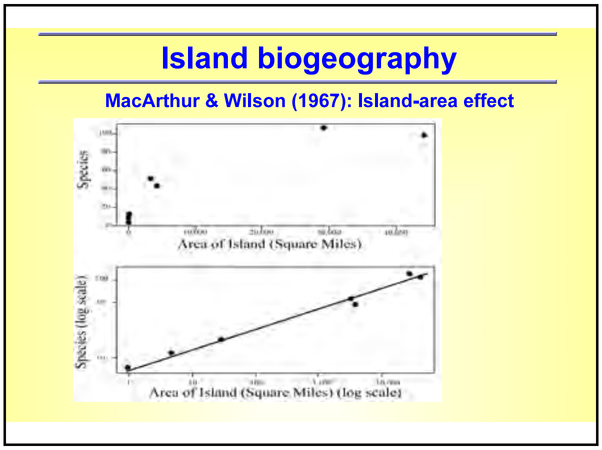
Slide 93 Biogeographic explanations: The rich species pool hypothesis

NOTES:



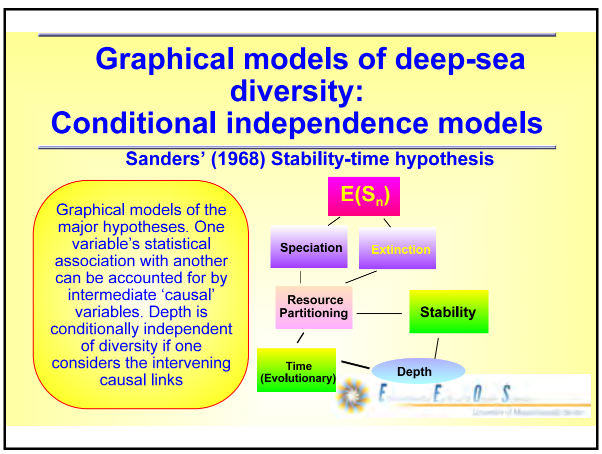
Slide 94 Importance of the regional species pool in determining α diversity

NOTES:



Slide 95 Island biogeography

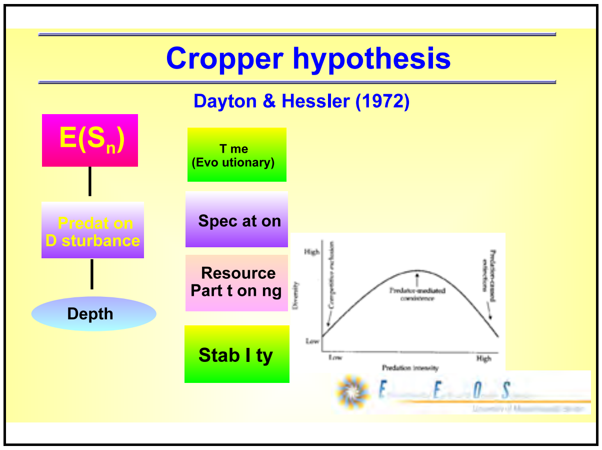
NOTES:



Slide 96 Graphical models of deep-sea diversity:

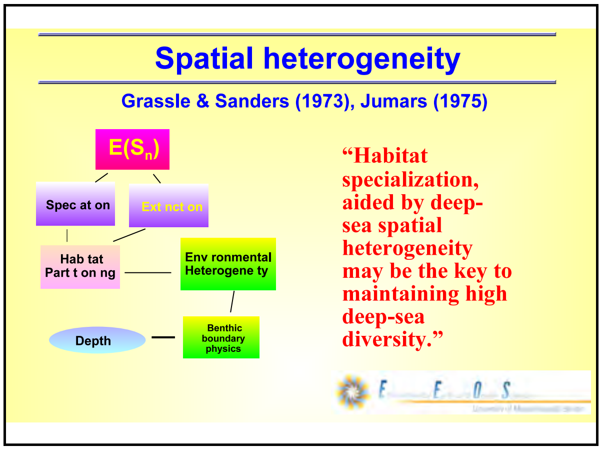
Conditional independence models

NOTES:



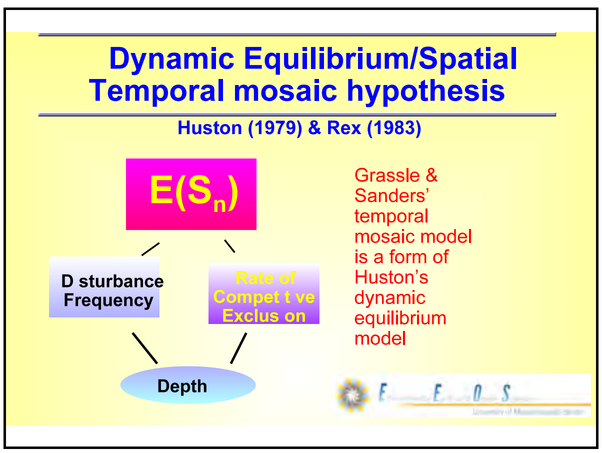
Slide 97 Cropper hypothesis

NOTES:



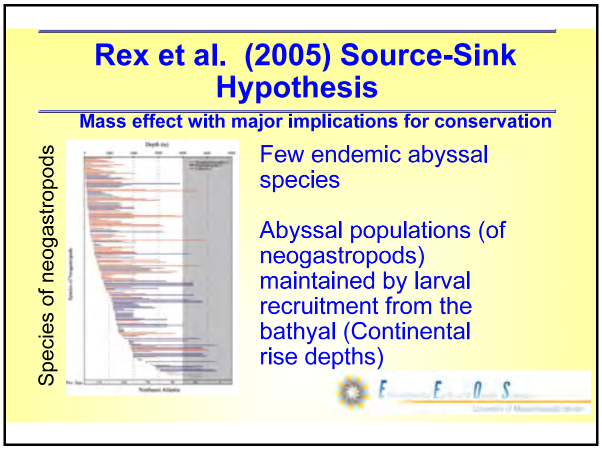
Slide 98 Spatial heterogeneity

NOTES:



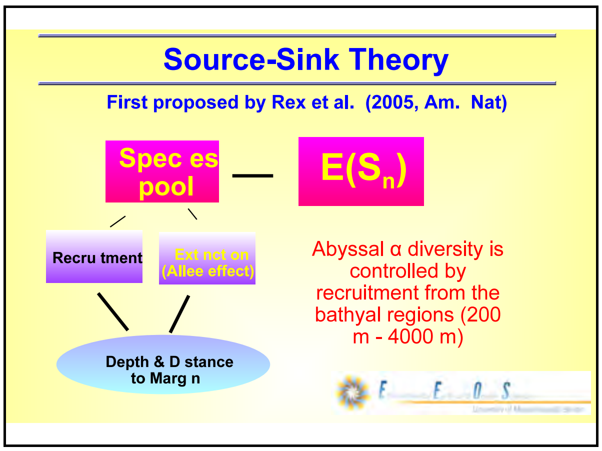
Slide 99 Dynamic Equilibrium/Spatial Temporal mosaic hypothesis

NOTES:



Slide 100 Rex et al. (2005) Source-Sink Hypothesis

NOTES:



Slide 101 Source-Sink Theory

NOTES: