

<div data-bbox="250 193 750 310" data-label="Section-Header"> <h2>Benthic biodiversity (α, β, and γ) & Benthic population processes</h2> </div> <div data-bbox="341 321 673 371" data-label="Text"> <p>Class 9: Tu September 30, 2008 Class 10: Th October 2, 2008</p> </div> <div data-bbox="532 493 789 537" data-label="Image"> </div>	<div data-bbox="820 130 1412 205" data-label="Section-Header"> <h3>Slide 1 Benthic biodiversity (α, β, and γ) & Benthic population processes</h3> </div> <div data-bbox="820 291 940 321" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="389 690 625 724" data-label="Section-Header"> <h2>Class schedule</h2> </div> <div data-bbox="431 737 579 760" data-label="Section-Header"> <h3>Order of topics</h3> </div> <div data-bbox="233 762 766 984" data-label="List-Group"> <ul style="list-style-type: none"> • Tuesday: overview of benthic community structure, with a start of benthic population processes <ul style="list-style-type: none"> • 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 <ul style="list-style-type: none"> • 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 and coexistence in marine intertidal deposit-feeding communities. J. Mar. Res. 38: 743-765. </div> <div data-bbox="532 1018 789 1062" data-label="Image"> </div>	<div data-bbox="820 657 1131 690" data-label="Section-Header"> <h3>Slide 2 Class schedule</h3> </div> <div data-bbox="820 779 940 810" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="289 1178 737 1243" data-label="Section-Header"> <h2>Required reading, community structure</h2> </div> <div data-bbox="232 1260 712 1304" data-label="Text"> <p>Chapter 5: Global Patterns of Benthic Community Structure Especially Deep-Sea Diversity</p> </div> <div data-bbox="232 1306 755 1362" data-label="Text"> <p>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</p> </div> <div data-bbox="232 1365 758 1467" data-label="Text"> <p>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]</p> </div> <div data-bbox="232 1470 747 1539" data-label="Text"> <p>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.</p> </div> <div data-bbox="532 1514 789 1556" data-label="Image"> </div>	<div data-bbox="820 1148 1343 1218" data-label="Section-Header"> <h3>Slide 3 Required reading, community structure</h3> </div> <div data-bbox="820 1306 940 1337" data-label="Text"> <p>NOTES:</p> </div>

<div data-bbox="303 161 721 228" data-label="Section-Header"> <h2>Required reading, Pollution effects</h2> </div> <div data-bbox="230 243 519 268" data-label="Section-Header"> <h3>Chapter 6: Benthic Pollution Biology</h3> </div> <div data-bbox="230 270 758 373" data-label="Text"> <p>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]</p> </div> <div data-bbox="230 403 742 476" data-label="Text"> <p>Rosenberg, R. 2001. Marine benthic faunal successional stages and related sedimentary activity. <i>Sci. Mar.</i> 65 (Suppl. 2): 107-119. [A broad insightful review of theories from Petersen to Thorson to Pearson & Rosenberg & Fauchald & Jumars]{1}</p> </div> <div data-bbox="532 493 787 535" data-label="Image"> </div>	<div data-bbox="820 130 1411 168" data-label="Section-Header"> <h2>Slide 4 Required reading, Pollution effects</h2> </div> <div data-bbox="820 254 940 287" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="295 678 704 795" data-label="Section-Header"> <h2>Tools of the trade: Describing community structure</h2> </div> <div data-bbox="332 808 686 837" data-label="Text"> <p>Alpha, Beta and Gamma diversity</p> </div> <div data-bbox="532 982 787 1024" data-label="Image"> </div>	<div data-bbox="820 619 1185 653" data-label="Section-Header"> <h2>Slide 5 Tools of the trade:</h2> </div> <div data-bbox="820 678 1240 716" data-label="Text"> <p>Describing community structure</p> </div> <div data-bbox="820 802 940 835" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="313 1142 711 1178" data-label="Section-Header"> <h2>Early Community Debates</h2> </div> <div data-bbox="397 1186 615 1211" data-label="Section-Header"> <h3>Clements vs. Gleason</h3> </div> <div data-bbox="238 1215 768 1486" data-label="List-Group"> <ul style="list-style-type: none"> • Clements (1916) <ul style="list-style-type: none"> ▸ Communities are like superorganisms ▸ <i>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.</i> • Gleason (1926) <ul style="list-style-type: none"> ▸ Communities are merely the juxtaposition of individuals ▸ <i>"... 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."</i> </div> <div data-bbox="532 982 787 1024" data-label="Image"> </div>	<div data-bbox="820 1106 1297 1144" data-label="Section-Header"> <h2>Slide 6 Early Community Debates</h2> </div> <div data-bbox="820 1230 940 1264" data-label="Text"> <p>NOTES:</p> </div>

Whittaker's environmental gradients

Clements: communities discrete; Gleason: continua of individual abundances

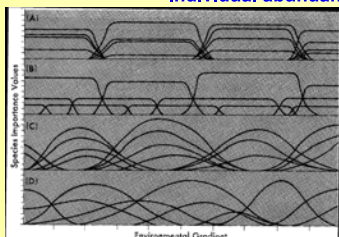


Figure 4.1. Four hypotheses on species distributions along environmental gradients. Each curve in each part of the figure represents one species population and the way it might be distributed along the environmental gradient.

Discrete
Community
Types

Continua

CANOCO now used to identify & describe these environmental gradients

Slide 7 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



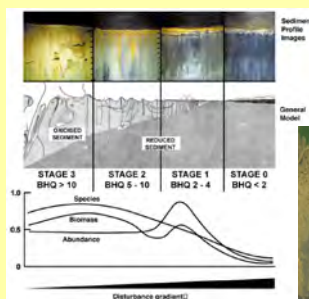
See Rosenberg (2001)

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

NOTES:

Pearson & Rosenberg model

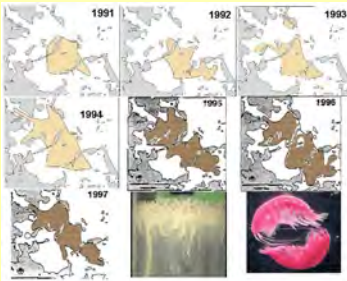
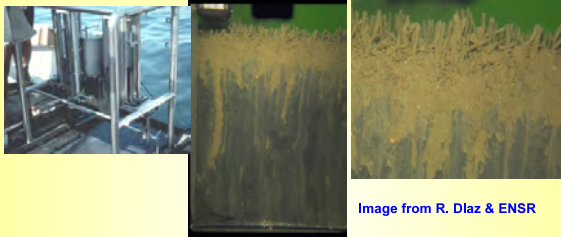
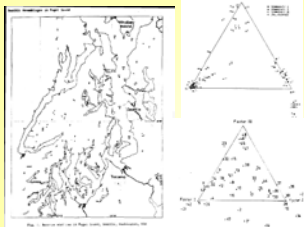
AND Rhoads et al. (1978)



Ampelisca abdita mats:
Stage 2

Slide 9 Pearson & Rosenberg model

NOTES:

<p>Ampelisca mats 1991-1997</p> <p>Oligochaete-spionid-Capitella → <i>Ampelisca-Polydora</i> → Corophiids & other amphipods</p>  <p><i>Ampelisca</i> are 'structure makers' in Goodall's terminology. The control local microclimate.</p> <p>Data from MWRA & ENSR (Bob Diaz)</p>	<p>Slide 10 Ampelisca mats 1991-1997</p> <p>NOTES:</p>
<p>The 90's <i>Ampelisca</i> mats</p> <p><i>Ampelisca</i> assemblage, Hull Bay (1997), Boston Harbor</p>  <p>Image from R. Diaz & ENSR</p>	<p>Slide 11 The 90's Ampelisca mats</p> <p>NOTES:</p>
<p>Continua vs. Discrete entities</p> <p>Ulf Lie's (1964, 1970, 1974) Puget Sound and WA shelf</p>  <p>WA shelf Distance in ternary plots proportional to change in community structure; Stations appear here as 3 Discrete entities</p> <p>Puget Sound Samples here appear distributed as Continua</p> <p>Ordination: ordering species abundances along gradients</p>	<p>Slide 12 Continua vs. Discrete entities</p> <p>NOTES:</p>

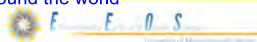
<div data-bbox="287 161 747 228" data-label="Section-Header"> <h2>Reconciliations of Clements v. Gleason</h2> </div> <div data-bbox="295 235 712 262" data-label="Text"> <p>Watt (1947, 1954), Mills (1969), Brown (1995)</p> </div> <div data-bbox="238 262 758 541" data-label="List-Group"> <ul style="list-style-type: none"> • Watt (1947, 1954): Communities = Spatio-temporal mosaics • Mills (1969) <ul style="list-style-type: none"> ➢ "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? <ul style="list-style-type: none"> ■ 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." </div>	<div data-bbox="820 130 1360 201" data-label="Section-Header"> <h2>Slide 13 Reconciliations of Clements v. Gleason</h2> </div> <div data-bbox="820 291 940 321" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="298 690 721 728" data-label="Section-Header"> <h2>Hubbell's (2001) community</h2> </div> <div data-bbox="232 743 758 1026" data-label="Text"> <p>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.</p> </div> <div data-bbox="531 1022 787 1064" data-label="Image"> </div>	<div data-bbox="820 657 1338 693" data-label="Section-Header"> <h2>Slide 14 Hubbell's (2001) community</h2> </div> <div data-bbox="820 779 940 810" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="328 1180 703 1218" data-label="Section-Header"> <h2>Components of diversity</h2> </div> <div data-bbox="303 1224 724 1251" data-label="Text"> <p>Whitaker's alpha, beta, and gamma diversity</p> </div> <div data-bbox="238 1253 747 1530" data-label="List-Group"> <ul style="list-style-type: none"> • Alpha (α) diversity <ul style="list-style-type: none"> ➢ The species diversity at a site, sometimes in a sample ➢ Consisting of: <ul style="list-style-type: none"> ■ Species richness ■ Species equitability or evenness • Beta (β) diversity <ul style="list-style-type: none"> ➢ 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 <ul style="list-style-type: none"> ➢ 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 </div>	<div data-bbox="820 1146 1284 1182" data-label="Section-Header"> <h2>Slide 15 Components of diversity</h2> </div> <div data-bbox="820 1268 940 1299" data-label="Text"> <p>NOTES:</p> </div>

Whittaker & Cody's definitions of gamma diversity

Gamma diversity [γ diversity] defined by Whittaker: a combination of α and β diversity. According to Cody (1986), gamma diversity is the change in species in similar habitat types over broad geographic areas.

Cody's definition is not the same as Whittaker's. Whittaker referred to Cody's gamma diversity as delta diversity.

Using Peterson and Thorson's benthic communities as an example, alpha diversity is the diversity within a given depth and sediment type, Beta diversity is the difference between different 'parallel level-bottom communities', and γ diversity is the replacement of members of the same genus but different species in different habitat types around the world



Slide 16 Whittaker & Cody's definitions of gamma diversity

NOTES:

MacArthur & Wilson's Island biogeography & Hubbell's Neutral model

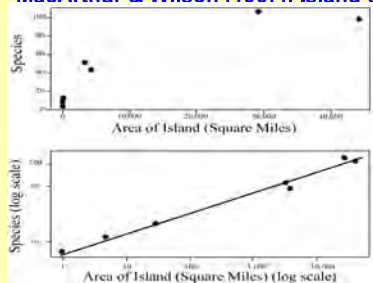


Slide 17 MacArthur & Wilson's Island biogeography & Hubbell's Neutral model

NOTES:

Island biogeography

MacArthur & Wilson (1967): Island-area effect

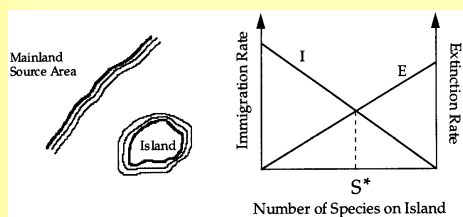


Slide 18 Island biogeography

NOTES:

Island biogeography

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



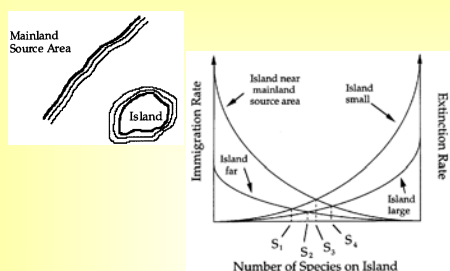
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Slide 19 Island biogeography

NOTES:

Effects of island distance & size

MacArthur & Wilson, Hubbell (2001) Fig. 1.3

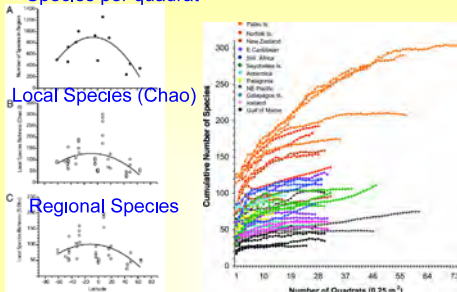


Slide 20 Effects of island distance & size

NOTES:

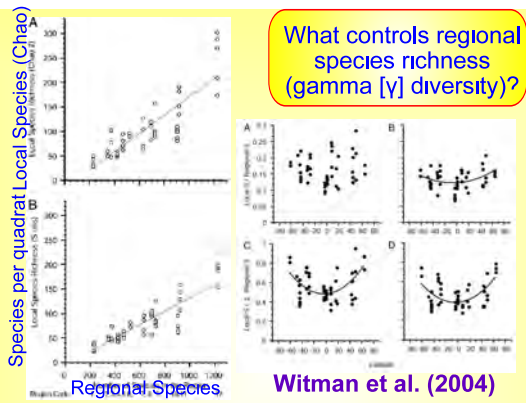
Hard substrate α diversity

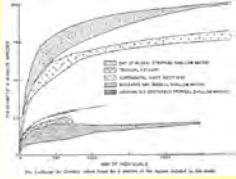
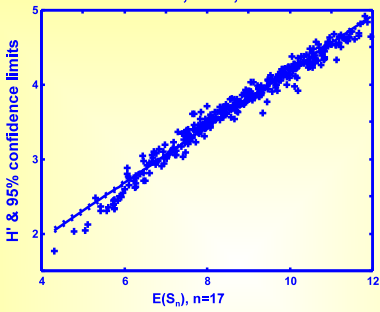
Witman et al. (2004): Regional species richness
Species per quadrat



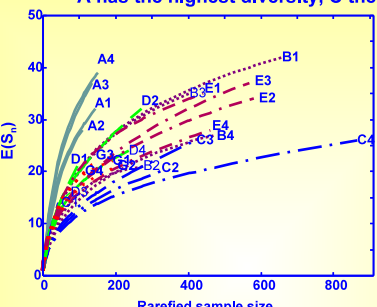

Slide 21 Hard substrate α diversity

NOTES:

<div data-bbox="215 149 737 548">  <p>What controls regional species richness (gamma [γ] diversity)?</p> <p>Witman et al. (2004)</p> </div>	<div data-bbox="824 132 935 163" data-label="Section-Header"> <h3>Slide 22</h3> </div> <div data-bbox="824 258 938 289" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="215 636 764 1056"> <h3>Conclusions from Witman et al. (2004)</h3> <p>"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.'"</p> </div>	<div data-bbox="824 619 1382 693" data-label="Section-Header"> <h3>Slide 23 Conclusions from Witman et al. (2004)</h3> </div> <div data-bbox="824 783 938 814" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="215 1161 764 1581"> <h3>Information Content Indices</h3> <p>Shannon's H' for populations & Brillouin's H for samples</p> $H' = - \sum_{i=1}^S p_i \log p_i$ <p>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.</p> <p>Brillouin's H = $\frac{1}{N} \log \left(\frac{N!}{N_1! N_2! \dots N_S!} \right)$</p> </div>	<div data-bbox="824 1144 1341 1176" data-label="Section-Header"> <h3>Slide 24 Information Content Indices</h3> </div> <div data-bbox="824 1266 938 1297" data-label="Text"> <p>NOTES:</p> </div>

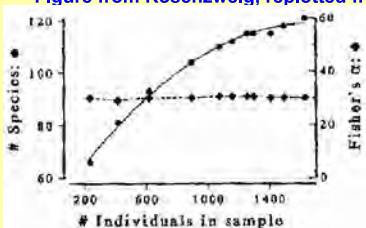
<div data-bbox="240 163 760 562"><h3>Sanders' rarefaction</h3><p>Sanders (1968)</p><ul style="list-style-type: none">Each sample is plotted as a rarefaction curve, with the end point being the actual number of species and individuals observedThe goal is to predict the expected number of species at a 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</div>	<div data-bbox="824 128 1412 170">Slide 25 Sanders' rarefaction</div> <div data-bbox="824 254 1412 296">NOTES:</div>
<div data-bbox="240 651 760 1029"><h3>Sanders-Hurlbert $E(S_n)$</h3><p>Sanders' (1968) idea but Hurlbert's (1971) equation</p>$E(S_m) = \sum_{k=1}^S 1 - \frac{\binom{N-N_k}{m}}{\binom{N}{m}}$<p>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.</p></div>	<div data-bbox="824 615 1412 657">Slide 26 Sanders-Hurlbert $E(S_n)$</div> <div data-bbox="824 741 1412 783">NOTES:</div>
<div data-bbox="240 1138 760 1537"><h3>H' and $E(S_{10})$ highly correlated</h3><p>Smith & Grassle, Peet, 1992-1997 MA Bay data</p></div>	<div data-bbox="824 1102 1412 1144">Slide 27 H' and $E(S_{10})$ highly correlated</div> <div data-bbox="824 1228 1412 1270">NOTES:</div>



<div data-bbox="240 159 766 548"><h3>GEEP Fjord gradient</h3><p>A has the highest diversity, C the lowest</p><p>Species per grab is a poor indicator of species richness!</p></div>	<div data-bbox="824 128 1416 180"><h3>Slide 28 GEEP Fjord gradient</h3></div> <div data-bbox="824 254 1416 569"><p>NOTES:</p></div>
<div data-bbox="240 653 766 1041"><h3>Fisher's log-series alpha</h3><p>Fisher, Corbet & Williams (1943); Only the number of species & individuals required; Fails 2 of Pielou's criteria</p>$S = -\alpha \ln(1-x)$<p>where, α = constant, dependent on diversity alone, and x = variable dependent on sample size.</p>$\frac{S}{N} = \left[\frac{(x-1)}{x} \right] \ln(1-x).$<p>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.</p></div>	<div data-bbox="824 621 1416 674"><h3>Slide 29 Fisher's log-series alpha</h3></div> <div data-bbox="824 737 1416 1062"><p>NOTES:</p></div>
<div data-bbox="240 1199 766 1545"><h3>End Lecture 9, Start Lecture 10</h3></div>	<div data-bbox="824 1115 1416 1167"><h3>Slide 30 End Lecture 9, Start Lecture 10</h3></div> <div data-bbox="824 1283 1416 1556"><p>NOTES:</p></div>

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'

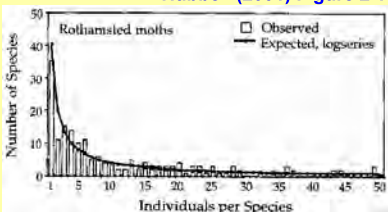
Bias $cf.$. The difference between the expected value and the true value of a parameter $cf.$, unbiased estimator

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

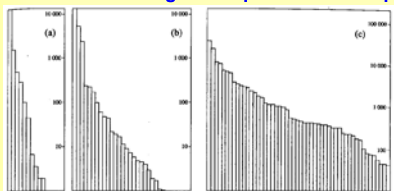


Figure 6.1 Fish catches (abundances) in (a) the Barents Sea, (b) the Indian Ocean, and (c) the Red Sea. Along the abscissa, species are arranged in order of decreasing frequencies. The ordinates of histograms are logarithmic. Adapted from Margalef (1974).

Slide 33 Fish species abundance patterns

NOTES:

Hubbell's (2001) neutral model

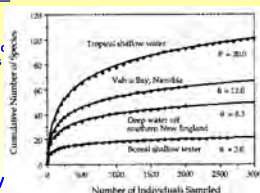
Fisher's $\alpha \approx \Theta = 2 J_M v$, Fundamental biodiversity No.

•Hubbell's (2001) unified neutral model argues that

- Local species frequencies can be modeled as a zero-sum game, 1 species increases at the expense 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 identical to Fisher's α

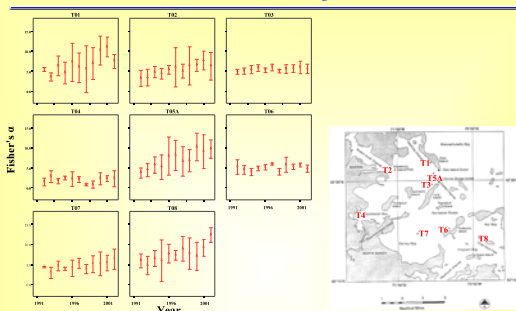


May (1975) Sanders' rarefaction curves nearly identical to log-series

Slide 34 Hubbell's (2001) neutral model

NOTES:

Fisher's α & Boston Harbor Recovery



Slide 35 Fisher's α & Boston Harbor Recovery

NOTES:

Species evenness

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

$$H' = - \sum_{i=1}^S p_i \log p_i$$

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 36 Species evenness

NOTES:

<div data-bbox="381 270 636 315" data-label="Section-Header"> <h2>Beta diversity</h2> </div> <div data-bbox="261 321 784 371" data-label="Text"> <p>Similarity & dissimilarity indices, Cluster analysis & ordination</p> </div> <div data-bbox="532 493 789 537" data-label="Image"> </div>	<div data-bbox="818 130 1141 168" data-label="Section-Header"> <h3>Slide 37 Beta diversity</h3> </div> <div data-bbox="818 254 941 287" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="266 646 764 676" data-label="Section-Header"> <h3>Quantitative analysis of the Hutchinsonian niche</h3> </div> <div data-bbox="393 684 609 714" data-label="Text"> <p>McGarigal et al. (2000)</p> </div> <div data-bbox="237 720 675 1024" data-label="Figure"> </div>	<div data-bbox="818 619 1328 690" data-label="Section-Header"> <h3>Slide 38 Quantitative analysis of the Hutchinsonian niche</h3> </div> <div data-bbox="818 779 941 812" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="253 1163 553 1556" data-label="Figure"> </div> <div data-bbox="573 1188 769 1545" data-label="Text"> <p>Ter Braak's canonical methods (Canonical Correspondence Analysis [CCA] & Redundancy Analysis [RA]) are much more general and flexible than McGarigal's use of discriminant analysis</p> </div>	<div data-bbox="818 1146 937 1180" data-label="Section-Header"> <h3>Slide 39</h3> </div> <div data-bbox="818 1268 941 1302" data-label="Text"> <p>NOTES:</p> </div>

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)?

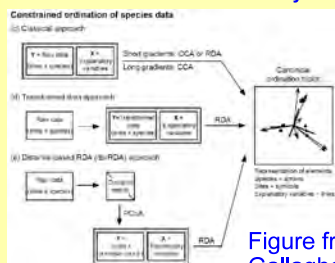
- To explain rather than describe patterns
 - What variables are really linearly associated with the major changes in community composition?
 - What are the patterns of covariation among species and pollutant variables?
- To test hypotheses about group differences (treatment groups can be set as dummy variables)
 - Exxon 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?

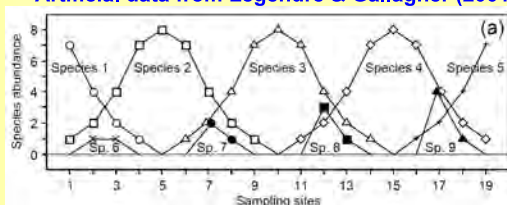
Figure from Legendre & Gallagher (2001)

Slide 42 Constrained Ordination

NOTES:

Coenocline, species change along an environmental gradient

Artificial data from Legendre & Gallagher (2001)



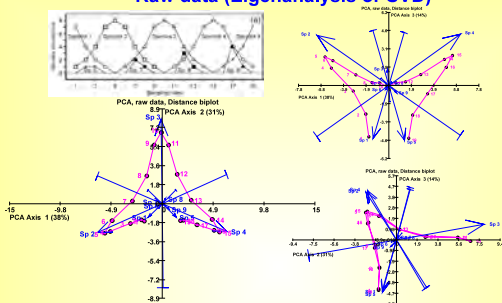
Benthic environmental gradient could be depth, grain size, salinity, organic carbon or other pollutant concentration

Slide 43 Coenocline, species change along an environmental gradient

NOTES:

Principal Components Analysis

Raw data (Eigenanalysis or SVD)

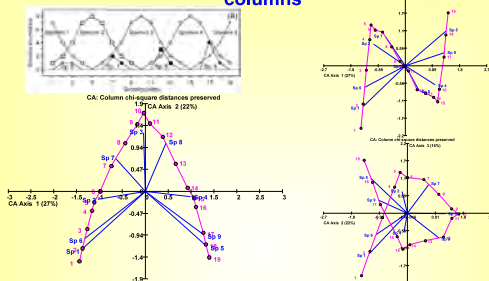


Slide 44 Principal Components Analysis

NOTES:

Correspondence Analysis

Displays the Chi-square distances among rows or columns



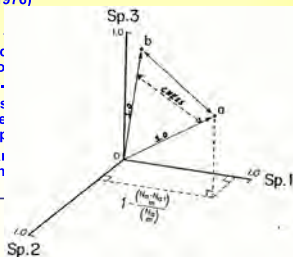
Slide 45 Correspondence Analysis

NOTES:

CNESS Geometry

Chord distance, 1 unit from the origin, 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 would randomly selected with a random of m individuals from a sample.
- Each sample can be plotted in s space. If there are just 3 species sample (a and b) is a point in s space.
- The chord distance is the distance between samples 1 unit from the origin.

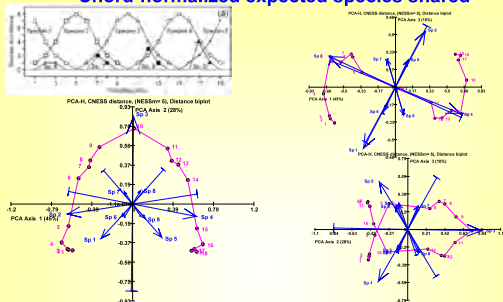


Slide 46 CNESS Geometry

NOTES:

CNESS & PCA-H

Chord-normalized expected species shared



Slide 47 CNESS & PCA-H

NOTES:

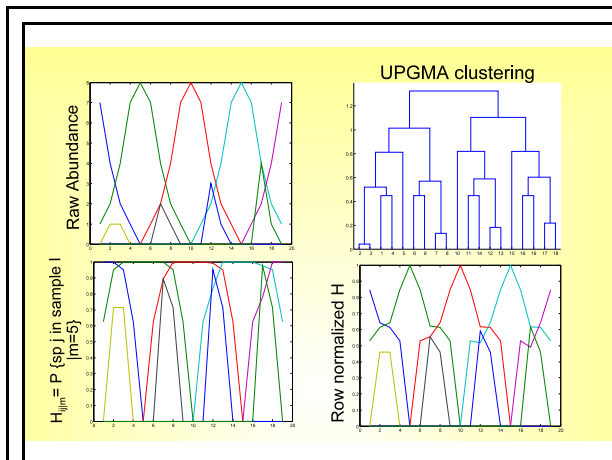
Advantages of CNESS & PCA-H

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

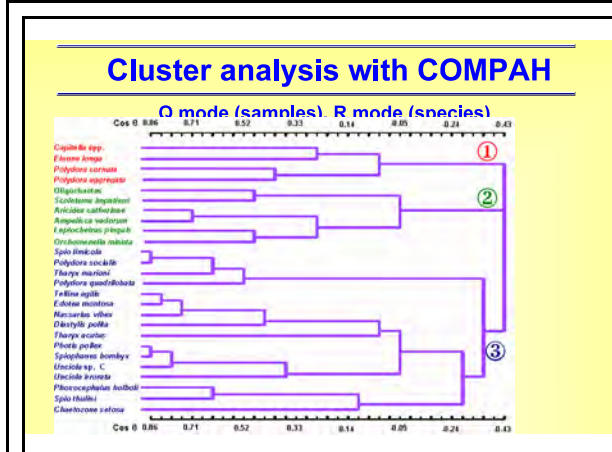
Slide 48 Advantages of CNESS & PCA-H

NOTES:



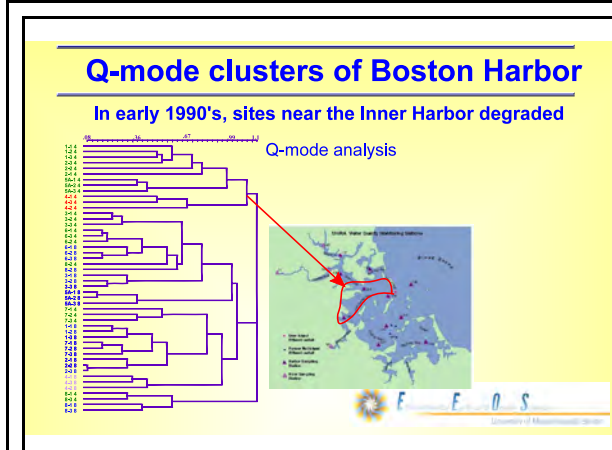
Slide 49

NOTES:



Slide 50 Cluster analysis with COMPAH

NOTES:



Slide 51 Q-mode clusters of Boston Harbor

NOTES:

Biplots & triplots

Graphically display species & environmental variables

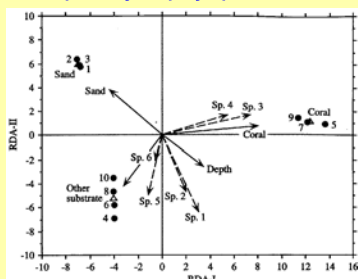


Figure from
Legendre &
Legendre,
Numerical
Ecology

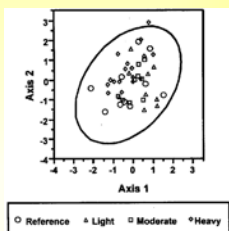
Slide 52 Biplots & triplots

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

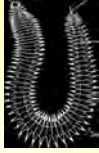


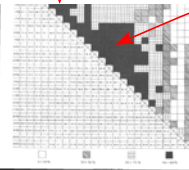
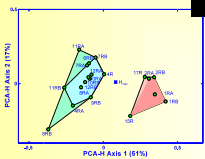
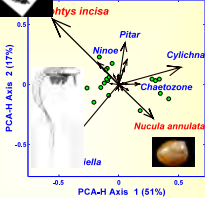
NOTES:

Benthic Communities and Populations

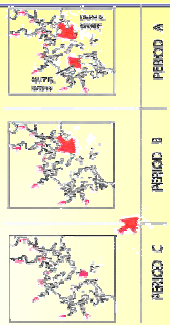
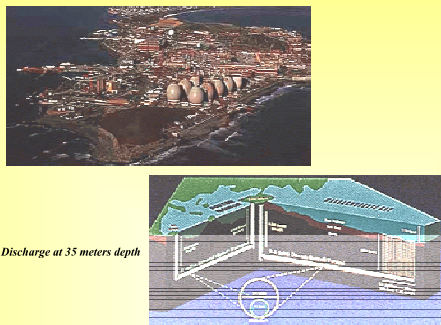
- Case 1: Sanders' Buzzards Bay St. R
- Case 2: Massachusetts Bay
- Case 3: Pacific NW Intertidal
- Case 4: Skagit Intertidal
- Case 5: Deep-Sea & Hydrothermal Vents
- Case 6: Boston Harbor


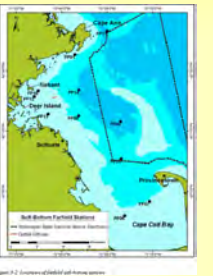

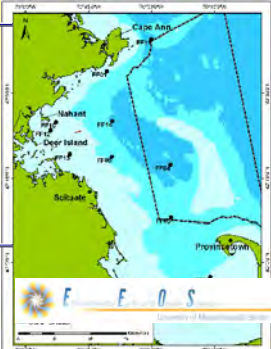
Slide 54 Benthic Communities and Populations

NOTES:

<p style="text-align: center;">Sanders (1960)</p> <p style="text-align: center;"><i>Buzzards Bay Station R, south of New Bedford Harbor</i></p> <ul style="list-style-type: none"> • 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 <i>Nephtys incisa</i> & the protobranch bivalve <i>Nucula annulata</i>. • Described the community as being remarkably stable • Resampled by Boyer & Whitlatch 20 y later – little changed <div style="display: flex; justify-content: space-around; align-items: center;">   </div> <div style="display: flex; justify-content: space-around; align-items: center;"> <p><i>Nephtys incisa</i></p> <p><i>Nucula annulata</i></p> </div> 	<p style="text-align: center;">Slide 55 Sanders (1960)</p> <hr/> <p>NOTES:</p> <hr/> <hr/> <hr/> <hr/> <hr/> <hr/> <hr/> <hr/>
<p style="text-align: center;">Sanders' (1960): Buzzards Bay</p> <p style="text-align: center;">07. Similarity & a trellis diagram</p> <p>Q-mode Similarity = Sanders (1960) Dissimilarity Affinity:</p> $d_{ij} = \sum_{k=1}^S \ln \left(\frac{n_{ij}}{n_i + n_j - n_{ij}} \right)$ <p>where, n_{ij} = Abundance of species in triangle i, S = Number of species</p> <p style="text-align: right;">Similar samples</p>  <p>Is the Buzzards Bay community Gleasonian or Clementsian? Can't really tell here. Also, samples taken over 2 years.</p>	<p style="text-align: center;">Slide 56 Sanders' (1960): Buzzards Bay</p> <hr/> <p>NOTES:</p> <hr/> <hr/> <hr/> <hr/> <hr/> <hr/> <hr/> <hr/>
<p style="text-align: center;">Sanders (1960): Buzzards Bay</p> <p style="text-align: center;"><i>Nephtys incisa</i>-<i>Nucula</i> community over 2 years: Two discrete clusters, or distinct community types, produced by Q-mode cluster analysis, shown as convex hulls below</p> <div style="display: flex; justify-content: space-around; align-items: center;">   </div>	<p style="text-align: center;">Slide 57 Sanders (1960): Buzzards Bay</p> <hr/> <p>NOTES:</p> <hr/> <hr/> <hr/> <hr/> <hr/> <hr/> <hr/> <hr/>

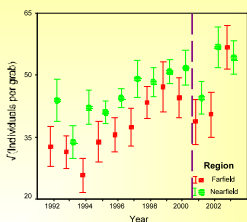
<div data-bbox="259 203 761 275" data-label="Section-Header"> <p>Case Study 2: Did the Massachusetts sewage effluent outfall affect the soft-bottom benthos? Yes, but the effects are not significant for management</p> </div> <div data-bbox="251 333 747 432" data-label="Text"> <p>ED Gallagher, Environmental, Earth & Ocean Sciences, UMASS Boston; NJ Maciolek & JA Blake, ENSR; RJ Diaz, VIMS; R Kropp, Battelle; and KE Keay MWRA.</p> </div> <div data-bbox="532 493 789 537" data-label="Image"> </div>	<div data-bbox="820 130 1380 317" data-label="Section-Header"> <p>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</p> </div> <div data-bbox="820 401 941 436" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="240 808 636 1129" data-label="Figure"> </div> <div data-bbox="532 1129 789 1173" data-label="Image"> </div>	<div data-bbox="820 768 1364 840" data-label="Section-Header"> <p>Slide 59 Boston Harbor & the Western Gulf of Maine</p> </div> <div data-bbox="820 926 941 961" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="373 1329 626 1356" data-label="Section-Header"> <p>Boston Harbor in the 1980s</p> </div> <div data-bbox="243 1409 516 1673" data-label="List-Group"> <ul style="list-style-type: none"> • 250-500 mgd sewage effluent, only primary treated, discharged at Deer & Nut Islands • 20 tons sludge daily released in Presidents Roads • >90% <i>Capitella</i> in Inner Harbor & Deer Island Sediments • Few <i>Ampelisca</i> • 17% of winter flounder with liver cancer • Cleanup began under court order in 1984 </div> <div data-bbox="524 1432 774 1633" data-label="Figure"> </div> <div data-bbox="532 1656 789 1701" data-label="Image"> </div>	<div data-bbox="820 1293 1326 1331" data-label="Section-Header"> <p>Slide 60 Boston Harbor in the 1980s</p> </div> <div data-bbox="820 1417 941 1451" data-label="Text"> <p>NOTES:</p> </div>

<p><i>The \$4 billion MWRA cleanup of Boston Harbor</i></p> <ul style="list-style-type: none"> 1991 Sludge dumping ended 1991 & 1992 Monitoring of Harbor & Bay began 1996 New primary treatment facility at Deer Island 1997-2001 Upgrade to secondary treatment at Deer Island 1998 Period B. Inter-island transfer tunnel to Deer Island September 2000 Period C. Offshore 15 km outfall began discharging effluent to MA Bay 	<p>Slide 61 The \$4 billion MWRA cleanup of Boston Harbor</p> <p>NOTES:</p>
 <p>Discharge at 35 meters depth</p> <p>E F O S University of Massachusetts - Boston</p>	<p>Slide 62 The Deer Island Treatment Facility & Tunnels</p> <p>NOTES:</p>
<p><i>Models for assessing outfall effects</i></p> <ul style="list-style-type: none"> NPDES permit & OMSAP thresholds within weeks of final sorting <ul style="list-style-type: none"> Response variables: Total abundance, Total species, Fisher's alpha, Shannon's H', & Pielou's J' and opportunistic taxa (<i>Sireblospio benedicti</i>, <i>Polydora cornuta</i> & <i>Capitella</i> spp.) No caution or warning triggers in the post-outfall period BACI (Before-After Control Impact) Design <ul style="list-style-type: none"> Contrast Near- & Farfield regions in the pre- (1992-2000) & post-outfall (2001-2003) periods Account for site-to-site & year-to-year variation with a hierarchical 2-factor ANOVA <ul style="list-style-type: none"> Site-to-site variation is nested within region & year-to-year variability nested within pre- and post-outfall periods Years assessed as indicator variables 	<p>Slide 63 Models for assessing outfall effects</p> <p>NOTES:</p>

<p>Assessing MA Bay biodiversity</p> <p>Is the outfall having an effect on Bay biodiversity?</p> <p>Nearfield</p>  <p>Farfield</p> 	<p>Slide 64 Assessing MA Bay biodiversity</p> <p>NOTES:</p>
<p>23 Nearfield stations</p> <ul style="list-style-type: none"> Sampled (August) for <ul style="list-style-type: none"> Species composition Grain size Organic carbon Effluent tracers (<i>Clostridium perfringens</i> spores) Contaminants: all EPA pollutants and molecular tracers for sewage Sediment profile images Benthic infauna <ul style="list-style-type: none"> 0.04-m² Y-Van Veen 300-µm mesh Same team of taxonomists since 1991, now led by Blake & Maciolek 	<p>Slide 65 23 Nearfield stations</p> <p>NOTES:</p>
<p>8 Farfield Stations used as impact reference stations</p> <ul style="list-style-type: none"> 8 Farfield stations (3 stations nearest Boston Harbor are regarded as 'nearfield') Sampled every August with same set of environmental variables as nearfield 	<p>Slide 66 8 Farfield Stations used as impact reference stations</p> <p>NOTES:</p>

60% increase in infaunal abundance, 4x since 1993

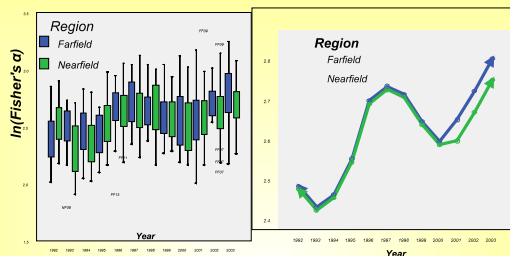
- Strong evidence that abundance higher
 - in the nearfield ($P(F_{1,653} \geq 51.7) < 10^{-6}$)
 - in the post-outfall period ($P(F_{1,653} \geq 63.7) < 10^{-6}$).
- Little evidence for an outfall effect (Region x period interaction: $P(F_{1,653} \geq 0.49) = 0.48$).



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

NOTES:

Large increases in species richness from 1992-2003

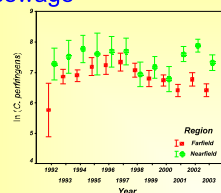


Little effect of the outfall (outfall effect $p \approx 0.10$)

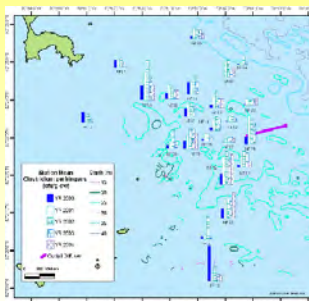
Slide 68

NOTES:

Clostridium perfringens spores, an indicator of human sewage

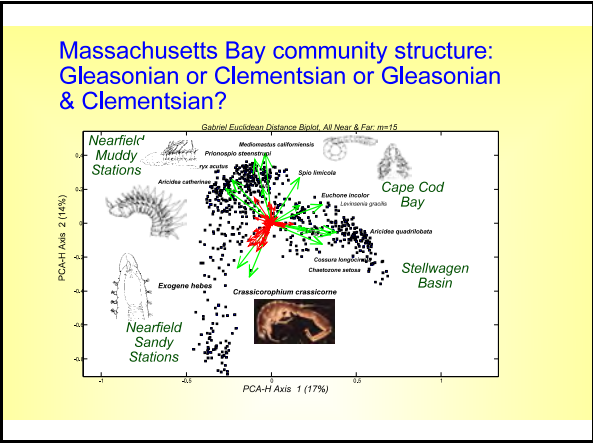


Exceptionally strong evidence that *C. perfringens* spores more abundant in nearfield ($P(F_{1,512} \geq 132) < 10^{-6}$) & very strong evidence that near-far difference greater in the post-outfall period (Interaction: $P(F_{1,512} \geq 19.6) < 10^{-4}$).



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

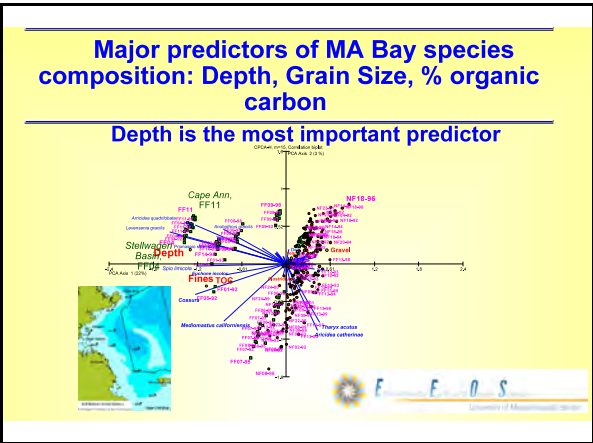
NOTES:



Slide 70 Community structure in MA Bay:

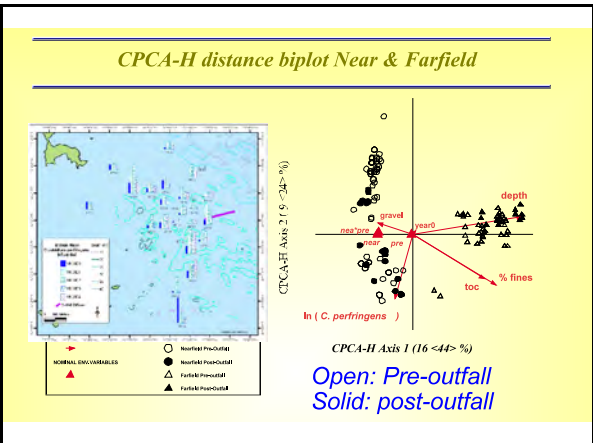
PCA-H, ordination of CNESS

NOTES:



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

NOTES:

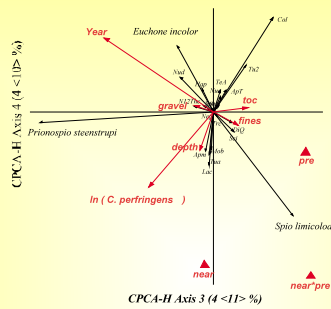


Slide 72 CPCA-H distance biplot Near &
Farfield

NOTES:

Slide 73 Long-term changes in numerical dominants

There are long-term temporal changes in community structure: Succession

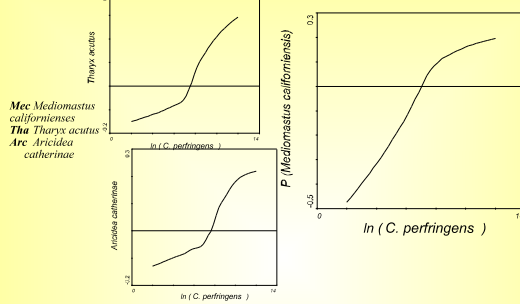


NOTES:

Slide 74 Canonical C-PCAH correlation plot

Canonical C-PCA-H correlation plot

3 species are ecological indicators for sewage input



NOTES:


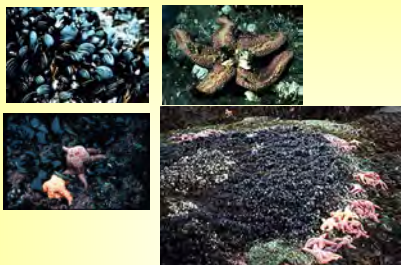



Why has MA Bay species richness increased?

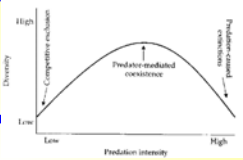

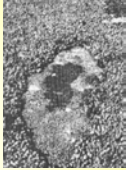


- **The Perfect storm hypothesis:** *The infaunal communities are recovering from disturbance by storms in October-November 1991.*
- **The NAO hypothesis:** *Massachusetts Bay benthos is exhibiting a long-term pattern of change, with 1993 and 2000-2001 minima associated with negative NAO events in 1988 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:

<p>Case Study 3: Keystone predation & intermediate disturbance in the Rocky Intertidal</p> <p><i>Paine (1966), Dayton (1971), Connell (1971)</i></p> 	<p>Slide 76 Case Study 3: Keystone predation & intermediate disturbance in the Rocky Intertidal</p> <p>NOTES:</p>
<p>Keystone Predation</p> <p><i>Paine (1966), Dayton(1971), Connell (1971)</i></p>  	<p>Slide 77 Keystone Predation</p> <p>NOTES:</p>
<p>Keystone Predation</p> <p><i>Paine (1966)</i></p> <ul style="list-style-type: none"> •The mussel <i>Mytilus californianus</i> is the dominant competitor for space in the Pacific Northwest Rocky intertidal •In the absence of disturbance or predation, <i>Mytilus</i> will overgrow & crush other space-occupying species, especially barnacles.  	<p>Slide 78 Keystone Predation</p> <p>NOTES:</p>

<p>Pisaster: a keystone predator</p> <p>Paine's (1966) Keystone predation hypothesis Extended to the 'intermediate disturbance hypothesis' by Dayton (1971) and Connell (1971)</p> <ul style="list-style-type: none"> With high rates of predation by <i>Pisaster</i> or very high rates of disturbance, like log battering, diversity is low, with only barnacles Diversity is highest at intermediate levels of predation or diversity since <i>Mytilus</i> and barnacles can coexist  	<p>Slide 79 Pisaster: a keystone predator</p> <p>NOTES:</p>
<p>Intermediate disturbance hypothesis</p> <p>Soft- vs. Hard bottom patterns</p> <ul style="list-style-type: none"> Hard bottoms <ul style="list-style-type: none"> Paine (1966), Dayton (1971), Menge, Lubchenco, Sousa and Connell showed that the reduction of predation or disturbance intensity led to decreases in species diversity Dominant competitor for space (crushing) Soft bottoms; Caging studies designed to reduce predation intensity, often leads to <ul style="list-style-type: none"> Increases in abundance Increases in diversity  	<p>Slide 80 Intermediate disturbance hypothesis</p> <p>NOTES:</p>
<p>Case Study 4: Facilitation & Competition among the pioneers in soft-bottom succession</p> 	<p>Slide 81 Case Study 4: Facilitation & Competition among the pioneers in soft-bottom succession</p> <p>NOTES:</p>

Skagit Flats

Skagit River: largest River entering in Puget Sound



Skagit flats

Seattle



ECOS630

Slide 82 Skagit Flats

NOTES:

Skagit Flats

Surrounded by a relatively inaccessible bullrush marsh



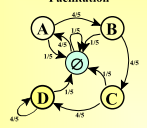
Slide 83 Skagit Flats

NOTES:

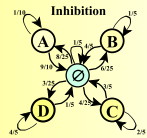
Models of Succession

Connell & Slatyer (1977), Jumars & Gallagher (1982)

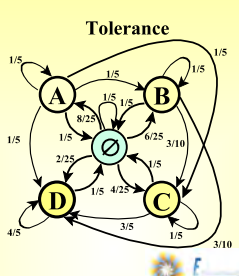
Facilitation




Inhibition



Tolerance





Slide 84 Models of Succession

NOTES:

Testing Succession Models

Connell & Slatyer (1977), Gallagher et al. (1983)

- **Enhancement experiment:** Enhance the abundance of an early succession species
 - **Facilitation** if later succession species increased relative to control
 - **Inhibition** if later succession species decreased relative to control
 - **Tolerance** if no difference (the null model)
- **Removal experiment:** Reduce the abundance of an early succession species
 - **Facilitation** if later succession species reduced
 - **Inhibition** if later succession species increased

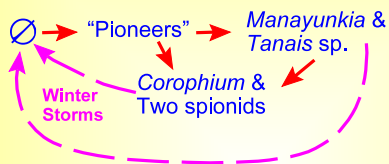


Slide 85 Testing Succession Models

NOTES:

Seasonal Skagit Succession

Reset by winter storms each year, continual disturbance by dabbling ducks

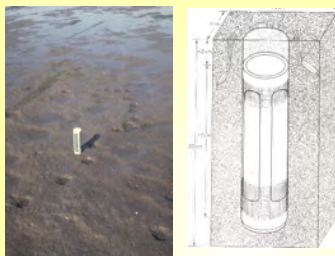


Slide 86 Seasonal Skagit Succession

NOTES:

Dabbling duck disturbance


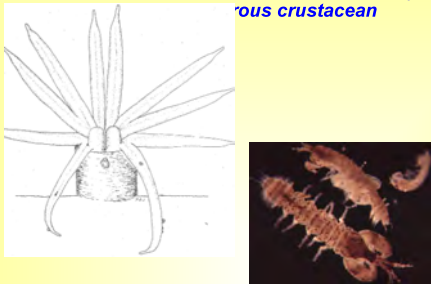
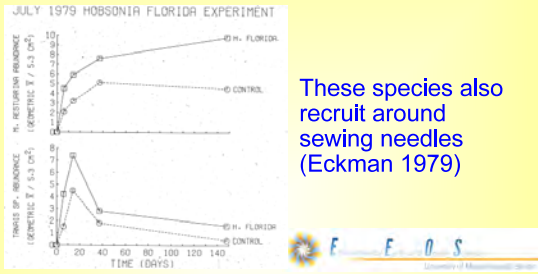
Smith (1980): about 30% of the area affected each month!



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Slide 87 Dabbling duck disturbance

NOTES:

<p>Controlled field experiments</p> <p>Enhancement experiments, Gallagher et al. (1983)</p> 	<p>Slide 88 Controlled field experiments</p> <p>NOTES:</p>
<p>Manayunkia aestuarina & Tanaids</p> <p>Meiofaunal sized feather-duster worm (Sabellid) & Tanaid crustacean</p> 	<p>Slide 89 Manayunkia aestuarina & Tanaids</p> <p>NOTES:</p>
<p>Facilitation of Manayunkia aestuarina & Tanaid recruitment</p> <p>Gallagher et al. (1983)</p> 	<p>Slide 90 Facilitation of Manayunkia aestuarina & Tanaid recruitment</p> <p>NOTES:</p>

Facilitation is a major soft-bottom successional mechanism

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

MANIPULATIONS	EFFECTS							
	N. Benthos	S. Benthos	T. Benthos	M. Benthos	M. Macroalgae	O. Organisms	S. Macroalgae	S. FISHES
N. Benthos	○	+	+	+	+	+	+	○
S. Benthos	○	○	+	○	○	○	○	○
T. Benthos	○	○	+	○	○	○	○	○
M. Benthos	+	○	+	○	○	○	○	○
Control Tubes	○	○	+	○	○	○	○	○

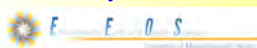


Slide 91 Facilitation is a major soft-bottom successional mechanism

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



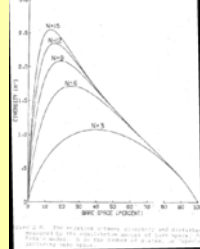
Slide 93 Caging in the soft-bottom benthos

NOTES:

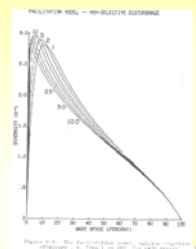
Effects of Succession model in intermediate disturbance

Quinn (1979) Ph.D.

Tolerance model



Facilitation model



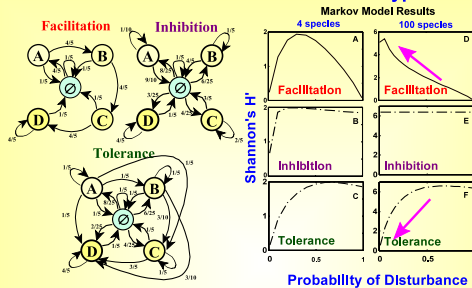
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Slide 94 Effects of Succession model in intermediate disturbance

NOTES:

Successional models

And the intermediate disturbance hypothesis



Slide 95 Successional models

NOTES:

A controlled removal experiment

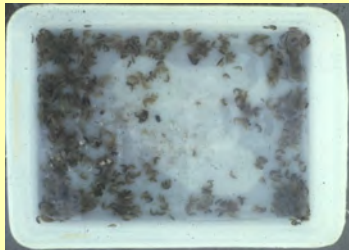



Eogammarus to play to role of Neill's (1975) Alosa



Eogammarus confervicolus,
an epifaunal omnivore

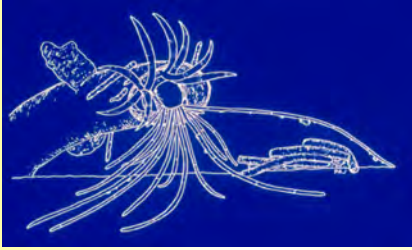
Slide 96 A controlled removal experiment

NOTES:

<p><i>Eogammarus</i> is an omnivore</p> <p>900 <i>Eogammarus</i> in a 1-liter plastic container</p>  	<p>Slide 97 <i>Eogammarus</i> is an omnivore</p> <p>NOTES:</p>
<p>Natural sediment enclosed in cut-away 5-gal buckets for 3 days; <i>Eogammarus</i> added to 2 buckets</p> 	<p>Slide 98 Natural sediment enclosed in cut-away 5-gal buckets for 3 days; <i>Eogammarus</i> added to 2 buckets</p> <p>NOTES:</p>
<p>Buckets enclosed with 1-mm mesh to retain <i>Eogammarus</i></p> <p><i>Eogammarus</i>, the predator, removed after 3 days</p> 	<p>Slide 99 Buckets enclosed with 1-mm mesh to retain <i>Eogammarus</i></p> <p>NOTES:</p>

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

Tentaculate surface deposit feeder

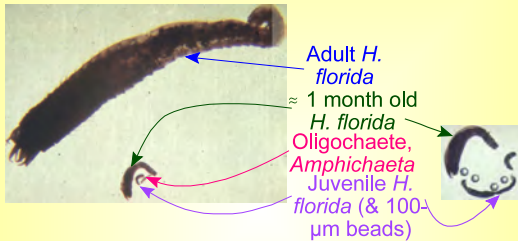


Slide 100 *Hobsonia florida*, an ampharetid polychaete worm, the major prey

NOTES:

In May, most of the *H. florida* were very small

90% pass through a 250- μ m mesh sieve

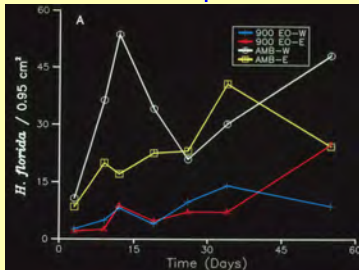


Slide 101 In May, most of the *H. Florida* were very small

NOTES:

Eogammarus* reduced day 3 abundances of *H. florida

Differences persisted for 55 days

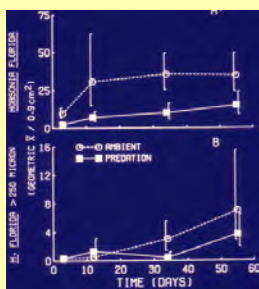


Slide 102 *Eogammarus* reduced day 3 abundances of *H. Florida*

NOTES:

Only juvenile *H. florida* affected

Juveniles, < 250- μ m width, reduced by *Eogammarus*



E F O S
University of Massachusetts-Dartmouth

Slide 103 Only juvenile *H. florida* affected

NOTES:

Asexually reproducing naidid oligochaete: *Amphichaeta leidigii*

Oligochaetes similar in size to *H. florida* juveniles

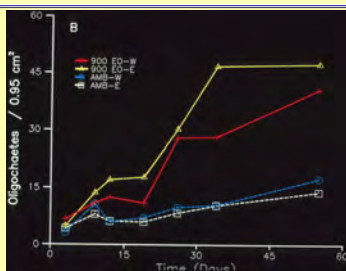


E F O S
University of Massachusetts-Dartmouth

Slide 104 Asexually reproducing naidid oligochaete: *Amphichaeta leidigii*

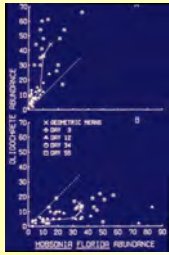



NOTES:

Oligochaetes exhibited 'logistic' growth in predator treatments with low *H. florida* abundances



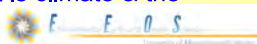
Slide 105 Oligochaetes exhibited 'logistic' growth in predator treatments with low *H. florida* abundances

NOTES:

<h3>Two distinct population growth trajectories</h3> <p>In predator treatment, oligochaetes > <i>H. florida</i> In natural community, <i>H. florida</i> > Oligochaetes</p>  	<h3>Slide 106 Two distinct population growth trajectories</h3> <p>NOTES:</p>
<h3>What is competition?</h3> <ul style="list-style-type: none"> • 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." <ul style="list-style-type: none"> ▶ "intraspecific competition occurs if increasing density of the population leads to a decrease in the per capita ▶ Density dependence 	<h3>Slide 107 What is competition?</h3> <p>NOTES:</p>
<h3>Types of competition</h3> <p>Exploitative ('scramble') vs. Interference</p> <p>In exploitative, or scramble competition, the effects of competition are caused by the consumption of the shared resource.</p> <p>In interference competition, one individual or group of individuals prevents another individual or group of individuals from gaining access to the resource.</p> 	<h3>Slide 108 Types of competition</h3> <p>NOTES:</p>

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, α = Interspecific competition coefficient.
 K = Carrying capacity.
 r = maximum per capita growth rate.



Slide 110 Lotka-Volterra competition

NOTES:

Model Estimates

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

Taxon	Doubling Time	Carrying Capacity	Competition Coefficient (α_{ij})
<i>Oligochaetes</i>	5.8 Days	57	1.005
<i>Nobesia Florida</i>	2.8 Days	45	0.857

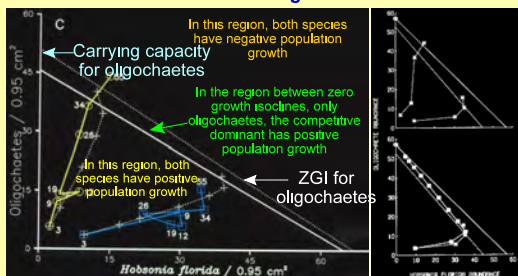


Slide 111 Model Estimates

NOTES:

Trajectories fit by Lotka-Volterra model

A race to the zero-growth isoclines

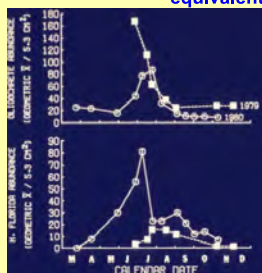


Slide 112 Trajectories fit by Lotka-Volterra model

NOTES:

Ambient community: 1979 v. 1980

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



Slide 113 Ambient community: 1979 v. 1980

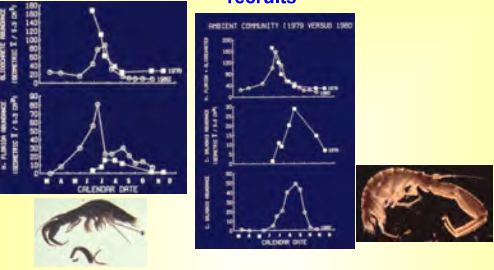
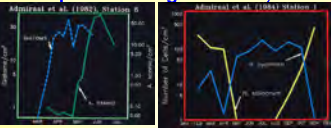
NOTES:

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:

<div data-bbox="240 163 766 541"><p>Ambient community: 1979 v. 1980</p><p>Oligochaetes & <i>H. florida</i> appear to be competitively equivalent species & both crash as <i>C. salmonis</i> recruits</p></div>	<div data-bbox="824 128 1416 212"><p>Slide 115 Ambient community: 1979 v. 1980</p></div> <div data-bbox="824 352 1416 401"><p>NOTES:</p></div>
<div data-bbox="240 688 766 1066"><p>What is the limiting resource for oligochaetes & juvenile <i>H. florida</i>? Small benthic diatoms</p><p>The juvenile stage is a competitive bottleneck for the deposit-feeding <i>H. florida</i>; see Hentschel & Jumars</p></div> <p>Admiraal et al. (1984): <i>Amphichaeta sanna</i> blooms follow the diatom blooms on Dutch mudflats; <i>N. pygmaea</i>, a diatom resistant to digestion, takes over the diatom community</p>	<div data-bbox="824 657 1416 779"><p>Slide 116 What is the limiting resource for oligochaetes & juvenile <i>H. Florida</i>? Small benthic diatoms</p></div> <div data-bbox="824 856 1416 905"><p>NOTES:</p></div>