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Chapter 5
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GLOBAL PATTERNS OF BENTHIC COMMUNITY STRUCTURE ESPECIALLY DEEP-SEA DIVERSITY

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Assignment

Required

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Snelgrove, P. V. R. and C. R. Smith. 2002. A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. Oceanography and Marine Biology: an annual review *40*: 311-342. *[A nice review of theories of deep-sea diversity, especially the temporal mosaic model]*

Trueblood, D. D., E. D. Gallagher, and D. M. Gould. 1994. Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. Limnol. Oceanogr. *39*: 1440-1454. *[The introduction of **CNESS** and **PCA-H**]*

Witman, J. D., Ron J. Etter, and F. Smith. 2004. The relationship between regional and local species diversity in marine benthic communities: A global perspective. Proc. Natl. Acad. Sci. USA *101*: 15664-15660. *[“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.’]{**48**, **76**}*

Comments on the papers

> *“The belief that science proceeds from observation to theory is so widely and so firmly held that my denial of it is often met with incredulity . . . But in fact the belief that we can start with pure observation alone, without anything in the nature of a theory is absurd; as may be illustrated by the story of the man who dedicated his life to natural science, wrote down everything he could observe, and bequeathed his priceless observations to the Royal Society to be used as inductive evidence. This story should show us that though beetles may profitably be collected, observations may not.”* ***Popper (1965)***

The above quote from Popper's "Conjectures and Refutations" indicates the central role that theory plays in science. Community ecology is in the doldrums right now. While there is an abundance of theory to explain the distribution and abundance of populations in nature, community theory has lagged far behind theory at the levels of the individual and population (see **Jumars (1993)** for a critique of modern community ecology theory). **Hubbell's (2001)** unified neutral model of succession is a new theory of marine biodiversity and, in my opinion, has rejuvenated the theory of community structure.

One of the areas where community theory is most exciting and challenging involves deep-sea community structure. **Hessler & Sanders (1967)** documented very high rates of species diversity in the deep sea, along the Gay Head MA to Bermuda transect. **Sanders (1968)** in a monumental paper introduced a new statistical method, rarefaction, to describe the patterns in diversity. He also proposed his stability-time hypothesis to explain the increase in diversity from the shelf to the continental slope, rise and abyss.

What is a community?

Continua vs. discrete entities

Mills (1969) provides an excellent review of the community concept in benthic ecology. There has been a fierce debate about the meaning of the term community. Clements in his papers on succession (*e.g.*, **1916**, **1928**) argued that the community could be viewed as a 'superorganism', and succession was analogous to the ontogeny of this organism. The first line of **Clements' (1916)** monograph on succession clearly stated his superorganism view of the community and succession:

> *"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."*

To Clements, succession was a predictable orderly process leading to a stable assemblage of species, whose composition was largely set by allogenic environmental factors. This final stage of succession was the climax community. Clements ideas were bitterly opposed by Henry Gleason, who argued that populations are distributed according to their own niche requirements. **Gleason (1926)** argued that there was no unifying feature to communities; plant associations were merely "fortuitous juxtaposition of plant individuals." He concluded his attack against the Clementsian view of the community with:

> *"In conclusion, it may be said that 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. Its disseminules migrate everywhere, and grow*

> *wherever they find favorable conditions. The species disappears from areas where the environment is not longer endurable. It grows in company with any other species of similar environmental requirements, irrespective of their normal association affiliations. The behavior of the plant offered in itself no reason at all for the segregation of definite communities. A rigid definition of the scope or extent of the association is impossible, and a logical classification of associations into larger groups, or into succession series has not yet been achieved."*

Since each species was distributed according to its own habitat requirements, there could be no distinct boundary between community types. Populations, distributed as single entities, continually grade into each other. **Gleason's (1926)** views have come to be called the 'individualistic hypothesis ' or the continuum view of community structure.

Few ecologists today adhere to the Clementsian 'superorganism' view of communities, but there remains a kernel of the old Clementsian-Gleasonian debate left. This debate hinges on whether communities are distributed as 'continua' or as 'discrete entities.' This is an important question, and the answer is that some communities are distributed as discrete entities and some as continua. If there is a distinct break in a controlling external environmental factor, then there will be a distinct break in community structure. Also, if some key species can effectively control the microenvironment of an area, then these 'structure making' species can set the boundaries of community structure. Other species, 'the hangers on', will be distributed only in areas which have a microenvironment controlled by the 'structure maker.' Goodall was responsible for introducing the idea that species in a community could be divided into 'structure makers' and 'hangers on.'

Mills (1969) proposed a definition of community which fits both the 'continua' and 'discrete entity' view of community structure:

> *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.*

The techniques that can be used to separate such groups include cluster analysis, which works well in separating groups of species that are distributed as discrete entities and ordination analysis which can separate groups of species which are distributed either as discrete entities or continua.

Community structure

Community structure includes most of the things that can be measured from a set of samples. The basic unit of analysis of community structure is the sample by species matrix of abundances. With this data matrix, then all of the standard measures of community structure can be determined. These are:

- Total abundance
- Numerically dominant taxa
- Spatial heterogeneity (*e.g.*, variance to mean ratios of taxa, Moran's I & Geary's c autocorrelation)
- Species Diversity (Richness & evenness)
- Faunal similarity/dissimilarity among samples

Biomass is another important indicator of community structure, but it is relatively difficult to get good biomass estimates for all of the species in a community. One of the drawbacks of obtaining accurate biomass measurements is that many, if not all, of the animals must be destroyed. Other descriptions of community structure might include the feeding guild membership of the species (*e.g.*, is the benthic community composed mainly of surface deposit feeders?). Fauchald & Jumars' polychaete feeding guilds are the standard method for describing the trophic composition of benthic communities.

With a standard sample × species matrix, the spatial heterogeneity in species composition can be determined. A much better description of the spatial pattern in the community can be obtained if the x-,y- coordinates of the samples are known. Then, the spatial autocorrelation and spatial cross-correlations among the species in the community can be determined. **Wartenberg's (1985)** multivariate spatial correlation is an excellent way to determine the spatial patterns in a complex data set. I have written MATLAB™ versions of Wartenberg's algorithms.

There has been considerable interest in examining the static statistical patterns in food-web patterns within communities. These would include descriptions of the number of 'basal species' (*e.g.*, primary producers, detritivores), intermediate, and top-predators. Also, food-web theorists tabulate the ratios of prey to predators, basal: intermediate species, intermediate: top predators, the average number of trophic links between species. All of these trophic links could be considered part of 'community structure'.

Some authors include descriptions of the predator-prey interactions in the community in descriptions of community structure, but these are probably better included in an assessment of community function.

Community function

I personally don’t care for the term community function. I believe it is teleological to refer to the “function” of a community. Individuals have a function: to produce young that will in turn reproduce. Most ecologists and evolutionary theorists believe strongly that communities are **not** the units on which natural selection acts. Clements believed that communities were an important unit for studying evolutionary processes, and in the 80 years since Clements proposed his ideas, there are occasional papers describing communities and ecosystems as being subject to natural selection. Ramon **Margalef (1968, p. 81)**, Spain’s most famous ecologist and an important contributor to our understanding of phytoplankton succession, describes the view that succession is a driving force behind natural selection:

> *“Evolution cannot be understood except in the frame of ecosystems. By the natural process of succession, which is inherent in every ecosystem, the evolution of species is pushed - or sucked- in the direction taken by succession, in what has been called increasing maturity. The implication is that in general the process of evolution should conform to the same trends manifest in succession. Succession is in progress everywhere and evolution follows, encased in succession’s frame.”*

What is Margalef saying? At one level, he seems to be making the statement that evolution recapitulates succession. I suppose that there is an element of truth in this statement. The fitness of individuals can be increased or reduced by changes in the activities of other individuals in the community and changes in the environment. Both changes in species frequencies and changes in the local microenvironment are part of succession, so that one could say that successional change drives evolutionary change. It would be an error though to assume that successional processes act to alter the phenotypes of early succession species to more closely resemble later succession species. For example, in soft-bottom benthic succession small surface and subsurface deposit feeders with rapid development, such as *Capitella sp. I* and *Streblospio benedicti*, are replaced by larger deposit feeders capable of ingesting sediments deeper within the sediments. I don’t see that this succession reveals anything about the selective forces acting on *Capitella sp. I* and *S. benedicti*. For example, I find it highly unlikely that natural selection mirrors succession in selecting for larger & later reproducing individuals of the early opportunists.

Features of communities that are often described as part of community function include the biological interactions among species and the interactions among the populations and biogeochemical cycles. Early succession species are often regarded has having low rates of nutrient recycling and being unstable. Later succession communities are regarded as having high rates of nutrient recycling and being relatively stable. **Eugene P. Odum (1969)** provided a list of these community attributes in one of the most widely cited papers of all times. He listed 24 attributes of both the structure and function of communities that change during the process of succession, shown in Table 1.

Table 1. 24 Ecosystem attributes that change during succession (**Odum 1969**)

ECOSYSTEM ATTRIBUTES			DEVELOPMENTAL STAGES	MATURE STAGES
Energetics	1	Production/Respiration (P/R)	>1	Approaches 1
	2	Production/Biomass (P:B Ratio)	High	Low
	3	Biomass supported per unit energy flow (B/E)	Low	High
	4	Net community production	High	Low
	5	Food chains	Linear (grazing)	Web Like
Community Structure	6	Total Organic matter	Small	Large
	7	Inorganic nutrients	Extrabiotic	Intrabiotic
	8	Species richness	Low	High
	9	Species equatability	Low	High
	10	Biochemical diversity	Low	High
	11	Stratification & spatial heterogeneity	Poorly organized	Well organized
Life History	12	Niche specialization	Broad	Narrow
	13	Size of organisms	Small	Large
	14	Life cycles	Short, simple	Long, complex
Nutrient Cycling	15	Mineral cycles	Open	Closed
	16	Nutrient exchange between organisms and environment	Rapid	Slow
	17	Role of detritus in nutrient regeneration	Unimportant	Important
Selection Pressure	18	Growth form	For rapid growth (r selection)	For feedback control (K-selection)
	19	Production	Quantity	Quality
Overall Homeostasis	20	Internal symbiosis	Undeveloped	Well developed
	21	Nutrient conservation	Poor	Good
	22	Stability (resistance to perturbations)	Poor	Good
	23	Entropy	High	Low
	24	Information	Low	High

Odum's (1969) 24 attributes of community structure and function have been widely criticized, but nevertheless he has summarized features that **are** associated with a wide variety of terrestrial and marine communities. One can quibble about a few of the attributes, indeed, **Peters (1976)**

argued that many of the attributes of community development were mere tautologies: they were either logical consequences of the definition of early *vs.* mature successional changes. **Peters (1976)** also attacks Sanders' stability-time hypothesis as suffering from tautology.

Rhoads *et al.* (1978), **Rhoads & Boyer (1982)**, and **Rhoads & Germano (1986)** argue that soft-bottom benthic communities undergo changes in community function very similar to those described by **Odum (1969)**. Table 1 from **Rhoads *et al.* (1978)** adapts Odum's strategies for ecosystem development to the soft-bottom benthos, listing eight attributes that change as soft-bottom benthic succession proceeds.

Table 2. Soft-bottom benthic community attributes that change during the course of succession (**Rhoads *et al.* 1978**).

ECOSYSTEM ATTRIBUTES		EARLY STAGES	MATURE STAGES
1	Organism Size	Small	Large
2	Life cycles of species	Short	Long
3	Growth of individuals and populations	Rapid	Slow
4	Gross production to standing stock	High	Low
5	Feeding mode or strategy	Suspension feeding and surface deposit feeding	Subsurface deposit feeding
6	Utilization of buried detritus	More important	Less important
7	Symbiosis within the system	Undeveloped	Developed
8	Nutrient conservation	Poor	Good

Rhoads *et al.* (1978), **Rhoads & Boyer (1982)**, and **Rhoads & Germano (1986)** have adapted this successional paradigm as a method for determining the effects of disturbance and organic enrichment on benthic communities. The early stages of succession, dominated by suspension and surface deposit feeders are called Type I communities, and the assemblages dominated by larger subsurface deposit feeders are called Type III assemblages. Rhoads has argued that most shallow water benthic assemblages undergo a transition from Type I ➜ Type III as soft-bottom benthic succession proceeds. **Rhoads & Young (1970)** provided one mechanism for this successional transition: trophic group amensalism. Amensalism describes an interaction between organisms that harms one but does not affect the other. Subsurface deposit feeders may interfere with the feeding activities of suspension feeders. Trophic group amensalism might provide a mechanism for the replacement of early succession suspension feeders by subsurface deposit feeders, however the evidence is weak. There isn't a clear causal necessity for trophic group amensalism between subsurface deposit and suspension feeders. **Rhoads & Young's (1971)** photographs of the sediment-water interface in Cape Cod Bay (Massachusetts) show that the mounds of the conveyor-belt feeder *Molpadia oolitica* are colonized by the suspension-feeding *Euchone incolor*.

This successional paradigm has recently been refined by **Rosenberg (2001)**, who provides a visual display of the succession (Fig. 1). Classifying communities, not by their species composition, but by their physical appearance is called physiognomy, and Pearson & Rosenberg's and Rhoads' succesional models are analogues to the physiognomic models of plant succcession:

> *"The physiognomic approach classifies community by structure - generally by the dominant growth-form of the uppermost stratum or the stratum of highest coverage in the community. A major kind of community characterized by physiognomy (and environment) is a* ***formation*** *or* ***biome****."* ***Whittaker (1975, p. 126)***

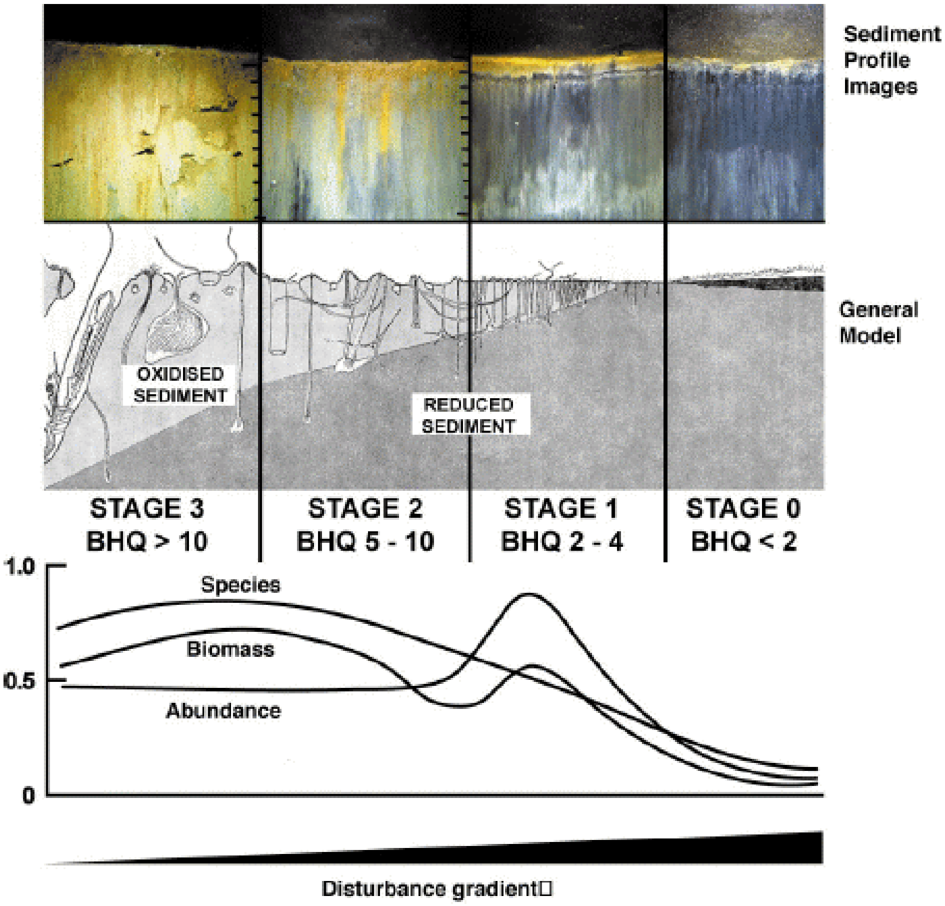

FIG. 2. – General model of distribution of benthic infaunal successional stages along a gradient of increased environmental disturbance from left to right (after Pearson and Rosenberg 1978) and the associated Benthic Habitat Quality (BHQ) index (Nilsson and Rosenberg 1997). Sediment profile images assigned to a successional stage are mounted above the general model (colours are digitally enhanced), where oxidised sediment is rust-brown and reduced sediment is grey or black. In the bottom of the figure the generalised species (S), abundance (A), biomass (B) diagram are illustrated (after Nilsson and Rosenberg 2000).

Figure 1. General model of distribution of benthic infaunal successional stages along a gradient of increased environmental disturbance from left to right (after **Pearson & Rosenberg 1978**) and the associated Benthic Habitat Quality (BHQ) index... Sediment profile images assigned to a successional stage are mounted above the general model, where oxidized sediment is rust-brown and reduced sediment is grey or black. In the bottom of the figure the generalized species (S), abundance (A), biomass (B) diagram are illustrated. Fig. 2 from **Rosenberg (2001)**

Rice & Rhoads (1989) provide a causal hypothesis for the successional patterns described in Table 2 above. **Rice & Rhoads (1989)** argue that the transition from suspension feeding and surface deposit feeding to subsurface deposit feeding is controlled by the flux of organic matter to the sediments. That is, soft-bottom benthic succession is largely controlled by allogenic processes. If the organic input to the benthos is high, organic-rich and variable, the community will be dominated by surface deposit feeders. If the organic input is low or constant, then the community will be dominated by larger subsurface deposit feeders.

Parallel-level bottom communities

Petersen (1918) carried out an extensive survey of Danish soft-bottom benthic communities to determine the areal extent of 'fish food.' In analyzing the patterns in his data, he concluded that there were seven basic community types in Danish coastal waters. Each community could be described by naming one or two of the dominant species in the community. **Stephenson *et al.* (1972)** reanalyzed Petersen's data, finding that Petersen's communities were readily distinguished using modern multivariate statistical methods. They also found that **Petersen (1918)** favored naming biomass dominants rather than numerically dominant taxa. Petersen stated that the community composition was determined by depth and grain size. All shallow water muddy-sand sites should be dominated by the bivalve *Macoma balthica*. Petersen's views of the benthic community meshed perfectly with Clements' climax theory of plant vegetation. **Clements & Shelford (1939)** devoted a chapter to the climax theory of soft-bottom benthic communities, and documented the occurrence of Petersen's *Macoma* community or biome on the northwest coast of the United States. **Mills (1969)** would later describe their classification of marine & terrestrial biomes as nearly meaningless:

> *"The system is strongly synthetic and is based on large, conspicuous plants and animals across large geographic areas. It assumes the concreteness and organismic unity of communities, listing 10 biomes for Puget Sound and North Atlantic areas, requires intermediate groupings ("faciations" governed by "subclimates") to maintain coherence. After the passage of 20 years, this attempt at classification now appears an almost meaningless oversimplification. Incomplete faunal and floral lists were forced into a theoretical framework of succession, climax and organismic unity, ideas which are not supported by any kind of evidence."*

Gunnar Thorson, another Dane, published a series of papers from 1950 to 1971 in which he argued that Petersen's seven community types had parallels around the world. He further argued that sediments of the same type (*e.g.*, sand, silty clay) at the same depth are dominated by members of the same genus but different species worldwide. Thorson (**1956**, **1957**) thought that all shallow muddy-sand environments should be dominated by members of the genus *Macoma*, but that the northern temperate *Macoma balthica* would be replaced by different *Macoma* species in different biogeographic regions.

The parallel level bottom community concept was highly influential. Howard Sanders Ph.D. studies of Long Island Sound (**Sanders 1956**), and his first field research on Buzzards Bay after joining the Woods Hole Oceanographic Institution (Sanders **1958**, **1960**) are based on the Petersen-Thorson view of community structure. Communities, according to Petersen and Thorson, should be named by one or two characteristic species that must be both abundant and conspicuous. The adjective conspicuous generally meant large. **Sanders (1956)** named Long Island Sound as a *Nephtys incisa-Yoldia limatula* community and Buzzards Bay as a *Nephtys incisa-Nucula* community. *Nephtys incisa* is a large omnivorous polychaete which can be both the biomass and numerical dominant in Buzzards Bay and *Yoldia limatula* and *Nucula* are subsurface deposit feeding protobranch bivalves. By the way, *Yoldia* does not “replace” *Nucula*. Both are abundant in Long Island Sound and Buzzards Bay.

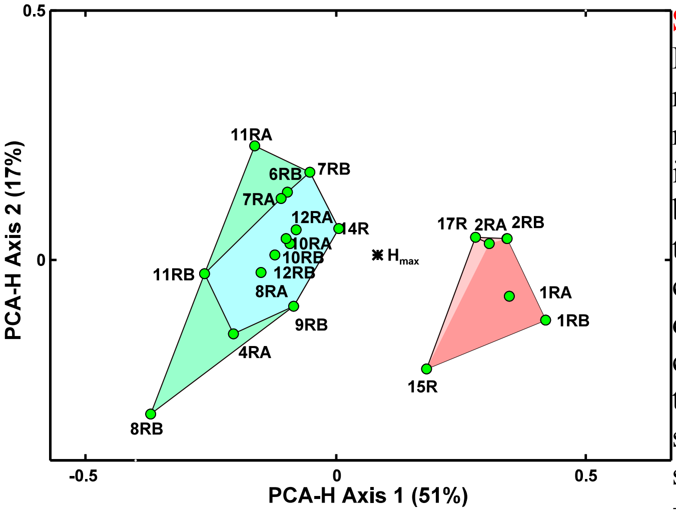

Figure 2. A metric scaling of Sander’s Station R data, using PCA-H ordination of CNESS (m=7) as described in Trueblood *et al.* (1994). The sampling period (1➞17) and replicate number are indicated. The results of a cluster analysis of the same CNESS matrix is superimposed on the ordination. The point where a sample with equal abundances of all species, H_{max}, is also shown.

Sanders (1960) published the Buzzards Bay Station R data in an Appendix. I have carried out a reanalysis of the data with my PCA-H ordination method (**Trueblood *et al.* 1994**). Sanders introduced quantitative analytic methods to US soft-bottom benthic ecology, but his decision to name the Buzzards Bay community a *Nephtys-Nucula* community was subjective. The PCA-H method determines the major sources of variation in a set of community structure data and plots the stations and the species that account for the variance. Figure 2 shows the metric scaling of stations. I have superimposed the results of a cluster analysis on the figure. The twenty samples taken over a three-year period form two distinct assemblages. This metric scaling doesn’t reveal which species account for the differences in community structure.

The species that account for most of the variation in **CNESS** are shown in Figure 3, which is called a Gabriel Euclidean distance biplot. The length of the arrows in this plot indicates the importance of species in accounting for differences in community structure. *Nephtys incisa* is the most important species accounting for differences in community structure among samples. It became abundant during the middle period of Sanders' three years of sampling. The protobranch bivalve *Nucula annulata* was also a good choice. It was the characteristic taxon during the early and late periods of Sanders' sampling. It didn't tent to co-occur in high numbers with *Nephtys incisa*. Other species that Sanders might have chosen as indicators of the Buzzards Bay community are the crustacean *Hutchinsoniella*, a group that Sanders discovered and named after his Yale thesis advisor G. E. Hutchinson, and the small gastropod *Cylichna*.

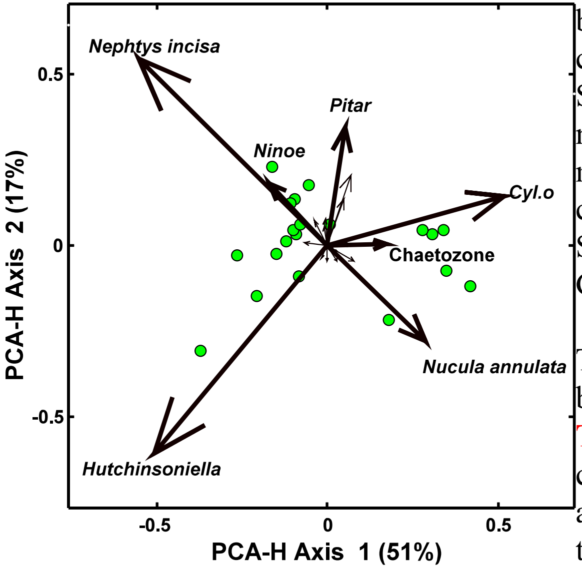

Figure 3. A metric scaling of Sander's Station R data, using PCA-H ordination of CNESS (m=7) as described in Trueblood *et al.* (1994). The results of a cluster analysis of the same CNESS matrix is superimposed on the ordination. The point where a sample with equal abundances of all species, H_{max}, is also shown.

The 'parallel level bottom community concept' has never been properly refuted. In his last book "Life in the Sea," **Thorson (1971)** continued to tout the parallel level-bottom community concept. In that final book, **Thorson (1971)** acknowledged those samples from the deep-sea and from the tropics revealed unexpectedly high species richness and species equatability. The parallel level bottom community concept failed because Thorson could not name the community based on one or two characteristic species if those species made up only a few percent of the abundance or biomass of the total communities. The next section describes the statistical procedures that have developed to replace the Petersen-Thorson scheme of describing communities by one or two biomass dominants.

Diversity

Measuring richness and evenness

Diversity is a key component of any description of community structure. There are dozens of different diversity indices that have been used to describe the diversity of a sample and community. Diversity has two components: species richness and species equatability or evenness. A variety of different indices have been developed to assess these two components of diversity.

General principles

If the goal of a diversity calculation is to determine the diversity of the community, every diversity index calculation is based on the assumption that a random sample of the population was taken. This turns out to be a fairly big assumption. **Jumars (1975a)** introduced the heterogeneity χ-square statistic to test whether replicate samples could be regarded as random draws of individuals from the same multinomial assemblage (*i.e.*, the same community). I programmed the heterogeneity χ-square statistic in MATLAB™ about four years ago and since then have checked dozens of different data sets, collected from the intertidal to the deep sea. Every data set has shown violations of the assumption that samples are drawn from the same underlying multinomial population. It turns out that this assumption doesn't limit the use of diversity indices. It turns out that spatial variability can never be ignored when determining the diversity of any set of samples.

Pielou (1969), based on arguments from **Shannon & Weaver (1949)**, proposed the following three criteria that any diversity index should meet:

- For a given S (*i.e.*, number of species) - maximum when all species have equal proportions
- For a give evenness, maximum when S is maximum
- Hierarchical

The third criterion is met by only a few diversity indices. Pielou describes how the variation in a diversity index can be apportioned into hierarchical components. For example, after calculating the diversity of a sample based on the relative abundance of species, one might wish to determine how much of this variation is due to generic diversity and how much to diversity of species within genera:

$$H'(all\ species) = H'(genera) + mean\ H'(species\ within\ genus). \qquad \textbf{(1)}$$

Pielou (1969) stated that only the two information theory indices, **Shannon's H'** (**Shannon & Weaver 1949**) and **Brillouin's (1951) H**, meet her hierarchical criterion. Rao (1984) and **Smith (1989)** have shown that forms of **Simpson's diversity**, and other indices which Rao terms quadratic entropy measures can also be hierarchical. He showed that the Expected Species Shared index is hierarchical, but that **Hurlbert's E(S_n)** is not. Rao introduced a fourth criterion for a diversity measure:

- The diversity of a mixture of populations should not be smaller than the average of the diversities within the individual populations.

Rao (1984) showed that Shannon's H' met this fourth criterion as well.

Simpson's diversity

There are a variety of older diversity indices. One of the best is Simpson's (1949) unbiased diversity estimator:

$$\begin{aligned} Simpson's\ D &= 1 - \sum_{j=1}^{S} \frac{N_j\,(N_j - 1)}{N\,(N-1)}. \\ where,\ N_j &= abundance\ of\ species\ j. \\ N &= sample\ total. \\ S &= number\ of\ species. \end{aligned} \qquad \textbf{(2)}$$

The biased form of **Simpson's diversity index,** also called the Gini-Simpson index is :

$$Gini\text{-}Simpson's\ D = 1 - \sum_{j=1}^{S} \left(\frac{N_j}{N} \right)^2 . \qquad \textbf{(3)}$$

Both formulas calculate the probability of sampling different species when two individuals are drawn from a sample. In the unbiased formula, the probability is calculated without replacement. So that a pair of individuals are drawn simultaneously or 1 individual is drawn and then another. In the second formula, sampling without replacement. So that one individual is drawn and its removal does not affect the probability that the same species will be selected when the second individual is sampled.

Bias refers to 'statistical bias'. A diversity statistic is a measure of some property of the underlying statistical population of individuals in the community. If there is a true 'population' parameter value, an unbiased estimator has an expected value that equals the 'true' value. If the value of the diversity index is a function of how many individuals are sampled, then the statistic is biased. Simply tallying the total number of species in a sample is an obvious example of a 'biased statistic'. The total number of species sampled will be a strong function of the number of individuals sampled. Simpson's unbiased diversity estimator provides an estimate of diversity which is not a function of sample size. It may vary as a function of the number of individuals sampled, but will eventually converge on the 'true' population diversity. Both the biased and unbiased forms of Simpson's diversity have direct analogues in population genetics, where the index is referred to as either Gini's (1912) diversity ($1-\sum p_i^2$) or gene heterozygosity ($_\pi$ being the allele frequency). Simpson's unbiased diversity index is mathematically identical to one minus the Sanders-Hurlbert expected number of species, $E(S_n)$, with n=2. This unbiased estimator predicts the expected number of species from a random draw of two individuals from a community. It is no suprise that there is a relationship between the indices, since Simpson's unbiased diversity estimator is the probability that two individuals drawn at random from a community will be the same species.

The main problems with Simpson's diversity index are that it is insensitive to singleton species in the community (*i.e.*, species represented by single individuals).

Information content indices

There are two major diversity indices based on information theory: Shannon's H' (**Shannon & Weaver 1949**) and **Brillouin's H**. Shannon's H' is defined in terms of the population frequency of individuals, not the sample frequency:

$$
\begin{aligned}
H' &= -\,C \sum_{i=1}^{S} \pi_i \,\log \pi_i.\\
\textit{where},\ \pi_i &= \textit{population (not sample) frequency of species } i.\\
S &= \textit{Number of species}.\\
C &= \textit{A constant, usually set to } 1.
\end{aligned}
\qquad \textbf{(4)}
$$

Any logarithm can be used to calculate H', but $\log_2$ is the most common. The index works well only if given an infinite population size and is strictly applicable only to an infinite population. There is no unbiased estimator for Shannon's H', but **Peet (1974)** provides a bias correction for H'. Although Shannon's H' is defined for population frequencies only, it is usually used with sample frequencies:

$$
\begin{aligned}
\hat{H}' &= -\sum_{i}^{S} p_i \log p_i\ ,\\
&\textit{where},\\
p_i &= \textit{frequency of species } i \textit{ in sample}.\\
p_i &= \frac{N_i}{N}.\\
N_i &= \textit{Number of individuals of species } i.\\
N &= \textit{Total individuals in sample}.\\
S &= \textit{Number of species}.\\
\log &\ \textit{could be base } 2,\ 10,\ \textit{or natural } \log.\\
\hat{H}_{\max} &= -\sum_{1}^{S} \frac{1}{S} \log\left(\frac{1}{S}\right) = \log\ s.
\end{aligned}
\qquad \textbf{(5)}
$$

Pielou (1969) recommends using Brillouin's H for finite populations, like the individuals taken from a grab sample or a quadrat sample. Brillouin's H looks complicated but is easily calculated with MATLAB™.

$$\begin{aligned} Brillouin's\ H &= \frac{1}{N} * \ln\left(\frac{N!}{N_1!\ N_2!\ \ldots\ N_s!}\right). \\ &= \frac{1}{N} * \ln\left(\frac{N!}{\prod_{k=1}^{S} N_k!}\right). \\ where,\ N &= Sample\ total. \\ N_k &= Abundance\ of\ species\ k. \\ \frac{N!}{N_1!N_2!\ \ldots\ N_s!} &= No.\ distinguishable\ permutations\ with\ the\ N_i's. \end{aligned} \qquad \textbf{(6)}$$

Shannon's H' and Brillouin's H are strongly biased at small sample sizes. Whenever a finite sample is taken, Brillouin's measure should be used. Shannon's H is defined only in terms of the theoretical population frequencies, and as such it can only be estimated. Brillouin's index is designed to determine the information content of finite samples, and as such **Pielou (1969)** states that it is determined not estimated. Brillouin's H hasn't been used much because it was more difficult to calculate than H'. I've programmed both Shannon's H' and Brillouin's H in MATLAB™ . In practice, the correlation between the two indices nearly always approaches 1.0. If all of the population abundances are very large, Brillouin's index converges to **Shannon's H'**.

Sanders rarefaction and Hurlbert's E(S_n)

Sanders (1968) described a new method for analyzing the species diversity of a sample and area: rarefaction. Instead of relyi8ng on a single number, such as H' or H, Sanders showed both the richness and equatability portions of diversity by plotting each sample as a curve on a graph in which the abscissa is the number of individuals and the ordinate is the expected number of species.

Sanders' (1968) method for calculating the rarefaction curve was wrong, and this error was corrected by **Hurlbert (1971)**. Here is the equation that can be used to calculate the expected number of species from a sample, at sample sizes m less than the number of individuals actually sampled:

$$
\begin{array}{rrcl}
 & E(S_m) & = & \sum_{k=1}^{S} 1 - \frac{\binom{N-N_k}{m}}{\binom{N}{m}}. \\
\textit{where,} & m & = & \textit{random sample size.} \\
 & \binom{N}{m} & = & \textit{binomial coefficient.} \\
 & & = & \textit{Number of different ways of sampling } N \textit{ objects, } m \textit{ at a time.} \\
 & & = & \frac{N!}{(N-m)! * m!} \\
 & N & = & \textit{Total individuals in sample.} \\
 & N_k & = & \textit{Individuals of species } k. \\
 & S & = & \textit{Number of species.}
\end{array}
\qquad \textbf{(7)}
$$

Smith & Grassle (1977) documented the sampling properties of Hurlbert's $E(S_n)$. They showed that $E(S_n)$ was an unbiased estimator of diversity, if the underlying populations were randomly Poisson distributed. They also produced formulae to calculate the variance of $E(S_n)$.

Hurlbert's $E(S_n)$ is a family of diversity measures. At a random sample size of 2, $E(S_n)$ is mathematically identical to 1 + **Simpson's unbiased diversity**. At a sample size of 10, $E(S_n)$ produces diversities for a set of shallow-water samples that are directly linearly related to either the **Shannon H'** or **Brillouin H** diversity. This relationship does not hold for deep-sea samples, due to the high frequency of sparsely represented species.

The major advantage of **$E(S_n)$** over **H** or **H'** is it is less biased. For samples that have drastically different numbers of individuals, $E(S_n)$ provides a relatively unbiased indication of whether the samples could have been drawn from the same population of species. H, H', and most other diversity indices are biased so that the value increases with increasing numbers of individuals sampled. In the deep sea, where the number of individuals drops off exponentially with depth, it is important that an index assess species diversity and not the number of individuals sampled in a grab. Another advantage of $E(S_n)$ is that it is easier to understand and relate to ecological processes. H' and H have units of bits per individual. The ecological meaning of this measure of information content is far from clear. Hurlbert's $E(S_n)$ has a direct ecological meaning. If a predator were to consume 10 individuals at random from a community, $E(S_{10})$ would provide the expected number of different species that it could expect to encounter.

Evenness estimators for H' and H

Species diversity has two major components, species richness, the number of species in a population and species equatability, the distribution of individuals among species. Both H' and H have associated evenness indices, called J' and E. These are calculated by dividing the observed H' or H by the maximum H' or H that could be expected if all species observed were equally abundant. While J' and E are sensitive only to evenness, H' and H are not strictly measures of species richness. Indeed, both H’ and H are sensitive to both the evenness and richness portions of diversity.

Table 3 Three hypothetical communities, I, II, and III, showing the ambiguous nature of diversity.

		Sample Abundances		
		I	***II***	***III***
Species	**A**	150	293	150
	B	100	4	150
	C	50	2	0
	D	0	1	0
		Sample Diversity (& Ranks)		
Diversity Estimator	**Number of species**	3 (2)	4 (1)	2 (3)
	H' ($\log_2$)	1.5 (1)	.2 (3)	1.0 (2)
	H	0.99 (1)	0.12 (3)	0.68 (2)
	$J'=H'/H_{max}$ Pielou’s evenness	0.9 (2)	0.1 (3)	1.0 (1)
	$E=H/H_{max}$	0.9 (2)	0.1 (3)	1.0 (1)
	Hurlbert’s $E(S_{150})$	3.0 (2)	3.2 (1)	2.0 (3)
	Simpson’s unbiased diversity ($=E(S_2)-1$)	0.6 (1)	.05 (3)	.5 (2)

Table 3 demonstrates that diversity indices attach different weights to the two components of diversity: richness and equatability. Community II contains the largest number of species, but the distribution of individuals among species is the least equitable, estimated by Pielou’s evenness. Community III is the most even, but the least species rich, and Community I has neither the greatest evenness nor the highest species richness but would be regarded as the most diverse using **Shannon’s H’**. Many of the samples taken from Massachusetts Bay resemble Community III in Table 1 in having high species richness but low equatability, *i.e.,* many species are present but one or two species make up the vast majority of individuals.

Classification and ordination

Sanders' (1960) study of Buzzards Bay community structure is a landmark paper in benthic ecology. Sanders, borrowing methods recently introduced in plant ecology, moved quantitative benthic ecology past the descriptive Petersen-Thorson stage. He assessed the faunal similarity among stations in Buzzards Bay over a three year period using a quantitative faunal similarity index. He used an ordination procedure to describe the spatial and temporal patterns in community structure in the Bay.

Sanders (1960) used a faunal similarity index, which we now call the % similarity index to assess community structure. Sanders' % similarity, which he called dominance affinity, is one of 30 faunal similarity or dissimilarity indices that are available on the COMPAH clustering package, which is available on my web site (**http://alpha.es.umb.edu/faculty/edg/files/edgwebp.htm#COMPAH**). After calculating the faunal similarity among all pairs of samples, Sanders arranged them in a trellis diagram to show the variation in community structure. In this trellis diagram, Sanders showed that Buzzards Bay community structure had features of both the continua or 'individualistic' pattern of community structure. There were also features of the 'discrete entity' of community structure.

Since **Sanders' 1960** study, there have been literally hundreds of multivariate analyses of benthic community structure and dozens of multivariate statistical procedures proposed to analyze benthic community structure. There are two large classes of multivariate procedures: cluster analysis and ordination. In BIO640, I devote about 6 weeks of the class to these multivariate procedures, but I'll just quickly summarize the major techniques here.

Cluster analysis takes a faunal similarity index or dissimilarity index and creates a cluster diagram from it. The standard cluster method used in community ecology is called combinatorial polythetic agglomerative hierarchical clustering. The mathematical algorithm for carrying out this cluster analysis was developed by **Lance & Williams (1967a)**. There are dozens of different faunal similarity or dissimilarity indices that have been developed to describe the similarity between pairs of samples. Similarity indices have values approaching zero for nearly identical samples and increase in value as samples become more dissimilar in species composition. Dissimilarity indices usually have a value of zero for identical samples and increase as samples become more dissimilar. The term metric is used often in ecology and science, but the term has a strict meaning. A metric is a distance measure which meets 4 axioms, including the triangular inequality (see Terms and Concepts above). Many of the dissimilarity measures used by ecologists in their ordination and cluster analyses violate the triangular inequality. There are metric equivalents for most of the dissimilarity or similarity indices used by ecologists (summarized in my COMPAH documentation, available on my web site, or stop by for a copy).

In benthic ecology, % similarity and **Bray-Curtis similarity** are used more than any other index. These indices are often only sensitive to the most abundant species in a community. It has now become standard, particularly in Europe to subject species abundance data with a 4th-root transform prior to calculating the Bray-Curtis similarity to make the index more sensitive to the rarer species.

Grassle & Smith (1976) introduced the NESS similarity index, which can be made increasingly sensitive to the rare species in a community by increasing the sample size.

Factors controlling benthic community structure

Gallagher & Keay (1998) listed a hierarchy of factors that can control soft-bottom benthic community structure in Boston Harbor. These same factors apply to most benthic communities:

- Biogeography
- Salinity & temperature
- Depth & light
- Organic carbon concentration
- Sediment grain size
- Larval supply rates
- Toxicity/anoxia
- Biological interactions

Biogeography

Biogeography is a term describing the historical factors that have produced the regional species pool. Before focusing on whether biological interactions or pollution have affected local community structure, consider the effects of biogeography. Boston Harbor and Massachusetts Bay have a very low species richness compared to similar communities on the West Coast of the United States. There might be three species of maldanid polychaetes in shallow depths in Massachusetts Bay, while at similar depths in Puget Sound there are over twenty.

Salinity and temperature

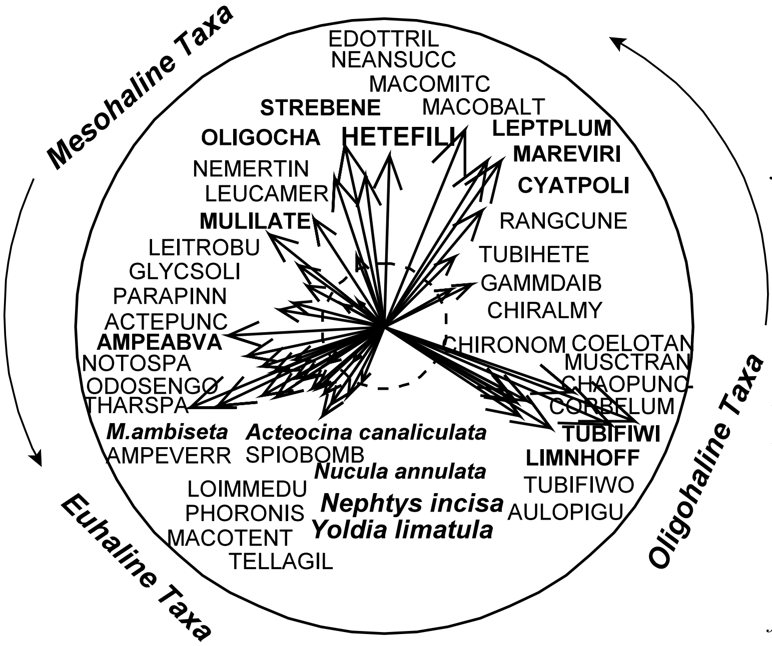

Figure 4 The salinity clock for the US East Coast. The cosine of the angle among species vectors (“arrows”) indicates the probability that species will co-occur. Salinity is the major factor controlling the distribution of species in the neritic zone. Abbreviations: **ACTECANA** (*Acteocina canaliculata*), **AMPEABVA** (*Ampelisca abdita* & *A. vadorum*), CYATPOLI (Cyathura polita), **HETEFILI** (*Heteromastus filiformis*), **LEPTPLUM** (*Leptocheirus plumulosa*), **LIMNHOFF** (Limnodrilus hoffmeisteri), **MAREVIRI** (*Marenzelleria viridis*), **MEDIAMBI** (*Mediomastus ambiseta*), **MULILATE** (*Mulinia lateralis*), **NEPHINCI** (*Nephtys incisa*), **NUCUANNU** (*Nucula annulata*), **OLIGOCHA** (Oligochaetes), **STREBENE** (*Streblospio benedicti*), **TUBIFIWI** (Tubificid oligochaetes w. cap. setae), **YOLDLIMA** (*Yoldia limatula*)

Figure 4 shows the effects of salinity on species groupings in the EPA’s Virginian Province EMAP data. Nearly 2000 benthic samples were taken over a 4-year period from areas just south of Chesapeake Bay to Martha’s Vineyard and Nantucket. About ⅓ of the samples were taken from salinities less than 15 ‰. Salinity is by far the most important factor controlling community structure in the Virginian Province. This poses severe problems for assessing the effects of pollution because many of the species that thrive in polluted and disturbed environments are the typical dominants in mesohaline regions. These species include *Streblospio benedicti*, *Heteromastus filiformis*, and *Mulinia lateralis*. Oligohaline (< 5 ‰) and mesohaline (<18 ‰) environments also have very low species richness. Pollution indices which focus on “pollution indicating” taxa and sites with low species richness would flag many non-polluted low-salinity environments as being degraded.

The ranges for the species shown in Figure 4 are the result of biogeographic factors. Chance events can play a key role in biogeography. One of the species indicating low mesohaline conditions is the bivalve *Rangea cuneata* (**RANGECUN**). **Carlton & Geller (1993)** document that this species is a recent introduction to the Virginian Province, being introduced to New York Harbor in 1991. The spionid polychaete *Marenzelleria viridis*, perhaps the premier indicator of mesohaline conditions was introduced via ballast water to Germany in 1983.

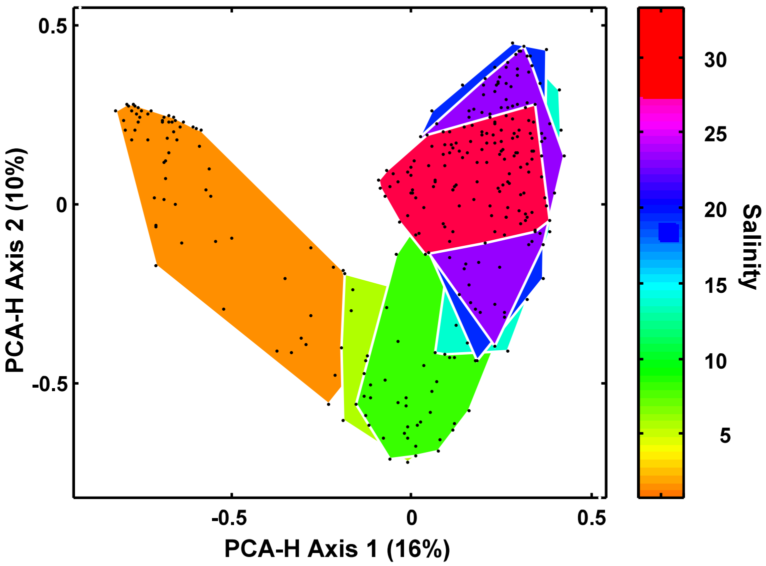

Figure 5. An ordination of sample sites using PCA-H and CNESS (random sample size = 20). Samples within 5 psu salinity ranges are surrounded with convex hulls.

Figure 5 shows an ordination of the sample sites in the EMAP data. The distances among samples are directly related to the similarity of species composition. In Figure 5, I have surrounded samples taken from different salinity ranges with hulls to show the overwhelming importance of salinity in controlling community structure. Some of the strong difference in community structure between samples from 0to 5 ‰ and higher salinities is real and some is due to sampling artefact. The EPA EMAP program sent the oligohaline samples to a different group of taxonomists, who identified insects and oligochaetes. Insects and oligochaetes from higher salinity environments were lumped at the Class level. The usual solution to problems like this is to examine the animals and to use a consistent level of identification. Unfortunately, the EMAP samples were destroyed to estimate biomass..

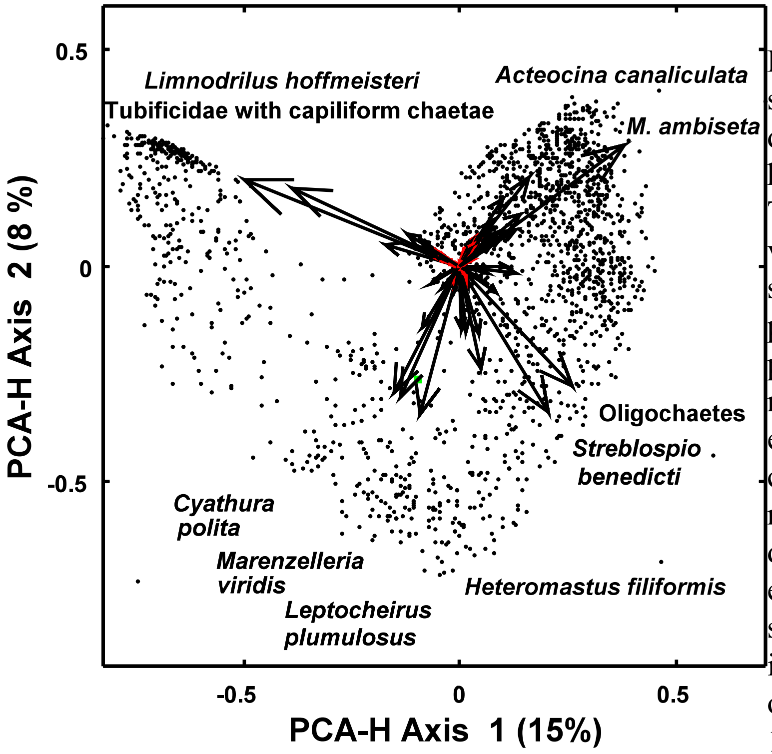

Figure 6 An ordination of the 1918 EMAP Virginian Province samples with CNESS (random sample size = 20). The dominant pattern in community structure is salinity. This pattern is confounded somewhat because the EMAP program used different taxonomic resolution for samples taken in less than 5 psu environments.

Figure 6 shows a Q-mode ordination of 1918 samples in the EMAP data set. In this Q-mode display, the distance among samples indicate how similar they are in species composition. The species which account for most of the variation in species composition among samples are shown as vectors. The spionid polychaete *S. benedicti* is often used as a pollution indicator, but this species is the most abundant taxon in mesohaline environments, from pristine to polluted. The capitellid polychaete *M. ambiseta* is the most abundant taxon in the entire EMAP data set. It tends to be found in euhaline environments (> 25 ‰). This species is sometimes regarded as being a pollution indicator. It was the species that became the overwhelming numerical dominant after the 1969 West Falmouth oilspill (**Grassle & Smith 1976**, **Sanders 1978**, **Sanders *et al.* 1980**). However, this species is often the numerical dominant in unpolluted silt-clay environments in the Virginian Province.

One of the strongest biogeographic patterns that I know of is the mysterious termination of the range of *M. ambiseta* at Cape Cod. *Mediomastus ambiseta* is usually the numerical dominant in Buzzards Bay, attaining abundances of over 8×10^5 m^{-2}. This species has a long planktonic dispersal stage, several weeks at least, but *M. ambiseta* is never found North of Cape Cod. There is a slightly larger Mediomastus species in Cape Cod, Massachusetts Bay, and Boston Harbor called *Mediomastus californiensis*. This species is almost never found south of Cape Cod. This species reappears South of Chesapeake Bay, where it can again become the numerical dominant. We'll get back to the mystery of *Mediomastus* in the final lecture.

The Intermediate Disturbance Hypothesis

The intermediate disturbance hypothesis has now achieved the status of a well-verified theory. **Paine (1966)** proposed that predation and disturbance were major factors leading to higher local species diversity in nature. He had performed controlled field experiments in the rocky intertidal showing:

- Space is the limiting resource for many rocky intertidal species like barnacles and mussels
- In the absence of predation by the generalist predatory starfish *Pisaster*, the mussel *Mytilus californianus* overgrows and crushes other space-occupying species. Species diversity declines.
- *Pisaster* is an apostatic generalist, feeding on the high quality prey that are most abundant. *Pisaster* is highly selective for mussels when they are abundant.
- With increasing predation, space is opened up for competitively inferior species, and species diversity increases.
    - Dayton (**1971**, **1975**) showed that at high levels of disturbance, like logs battering the intertidal, diversity again declines.
- *Pisaster*, because it produces a cascade of effects on community structure far in excess of its abundance or biomass, is a "keystone species"

The intermediate disturbance hypothesis has been applied to a number of benthic communities. **Dayton & Hessler (1972)**, Rex (**1976**, **1981**), and **Huston (1979)** used the intermediate disturbance hypothesis to explain high deep-sea diversity. **Rhoads *et al.* (1978)** argued that disturbance from pollution produced an intermediate peak in benthic species diversity along gradients of increasing pollution and disturbance.

In rocky intertidal benthic ecology, demonstrations of the importance of predation on community structure has been clear-cut. Rocky intertidal ecology went through two major transitions. First, European intertidal ecology, most notably TA Stevenson, argued that intertidal zonation patterns were set by physical factors. Then, there was a strong shift in attitude towards the hypothesis that competition controlled the zonation of intertidal species. The key papers fostering this view were Joe Connell's studies of barnacle distributions in Scotland conducting for his Ph.D. research. In the late 1960s and early 1970s, there had been a major paradigm shift, led by Connell and Bob Paine. Both did studies in the rocky intertidal in the 60s and 70s showing that predation was a major process controlling the distribution of rocky intertidal species. **Connell (1975)** and **Paine (1977)** published key review papers arguing that:

- Predation was the most important biological interaction controlling rocky intertidal distributions
- The importance of biological interactions could only be determined through controlled field experiments.

Dayton & Hessler (1972) immediately applied the rocky intertidal paradigm of predation control of community structure to explain patterns of diversity in the soft-bottom benthos. They combined the general rocky intertidal paradigm with **Thorson's (1966)** view of predation on settling larvae to argue that the deep sea benthos is diverse because of intense cropping of the juvenile stages of the benthic infauna. **Rex (1976)** argued that predation increased in relative importance from shallow water to the deep sea. Craig Smith documented that the benthic community near experimentally placed mounds, designed to mimic those produced by deep-sea animals, had higher diversity in intermediate stages of recovery. His was the first direct demonstration of the intermediate disturbance hypothesis in the deep sea.

Soft-bottom benthic ecologists rushed to repeat the successes of the rocky intertidal paradigm in the soft-bottom benthos, but with little success. Cages set up to exclude predators in the soft-bottom benthos produced artificial results. The cages impeded the near-bed flow, resulting in altered sedimentation rates. Not only did fine sediments accumulate beneath cages, but so too did the larvae of benthic invertebrates. During the late 70s and early 80s the benthic literature was replete with Rube-Goldberg-like cage controls, which tried to control for the hydrodynamic effect of cages. **Virnstein (1977)** produced one of the few really convincing caging studies during this period, showing that blue crabs in Chesapeake Bay probably do control the distribution and abundance of the opportunistic bivalve *Mulinia lateralis*. This study was later criticized by **Hurlbert (1984)** for using an improper ANOVA design, but a close reading of the paper shows that the results are so clear-cut that the ANOVA significance tests were not really crucial to the major results. Karsten Reise (**1977**, **1978**, **1979**, 1985 **a** & **b**) conducted an extensive set of controlled experiments on a German mudflat, concluding that epibenthic predation was only of minor importance in controlling the distribution and abundance of the benthic infauna. While epibenthic predators consume infauna, their predation rates are insufficient to significantly affect the abundance of the infauna. Based on the results of Reise and **Virnstein (1977)**, **Gray (1981)** concluded that predation was relatively unimportant in controlling soft-bottom benthic community structure, affecting mainly the recruitment of bivalve spat.

Peterson (1979b) reviewed a decade or more of caging studies in the soft-bottom benthos. While acknowledging the problems with caging artefacts, he concluded that soft-bottom benthic communities are structured differently from rocky intertidal communities. In the rocky intertidal, predation exerts its strongest effects when it falls differentially on the competitively dominant species. In the Northwest US intertidal, the dominant competitor for space is the mussel *Mytilus californianus*. **Paine (1966)** showed that in the absence of starfish predation, mussels competitively excluded other space-occupying intertidal species like barnacles. Starfish are generalist feeders, which Paine calls apostatic generalists. They feed on high quality prey that are most abundant. Because of their importance in determining community structure, Paine called starfish “keystone” species. **Paine (1966)** argued that species diversity increases with increasing predation intensity. **Dayton (1971)**, a student of Paine’s, showed that disturbance can mimic the effects of predation, opening space for competitively inferior species and increasing overall species diversity. Dayton also showed that at high rates of disturbance or predation, that diversity again declines, with the community being dominated by species with high recruitment rates. **Peterson (1979b)** argued that the soft-bottom benthos differs from the rocky intertidal in that crushing and overgrowth, the mechanisms used by one intertidal species to exclude another from a rock surface, are rare in the soft-bottom benthos. With reduced predation intensity in the soft-bottom benthos, the species diversity of the community often increases.

There may not be as much difference between the soft-bottom and hard-bottom benthos as **Peterson (1979b)** indicates. **Peterson (1979b)** stressed that the three-dimensional and soft structure of mud and sand communities limited the possibilities for crushing and overgrowth, the major mechanism of competitive displacement in the rocky intertidal. However, this three-dimensional structure also occurs in the rocky intertidal. Suchanek (1979) showed that the low-diversity *Mytilus californianus* community in the Northwest intertidal is only low-diversity if the space-occupying species attached to the rock are enumerated. If all of the critters that live in the byssal threads and that are attached to the mussels are counted, the dense *M. californianus* assemblages harbor a very high diversity assemblage.

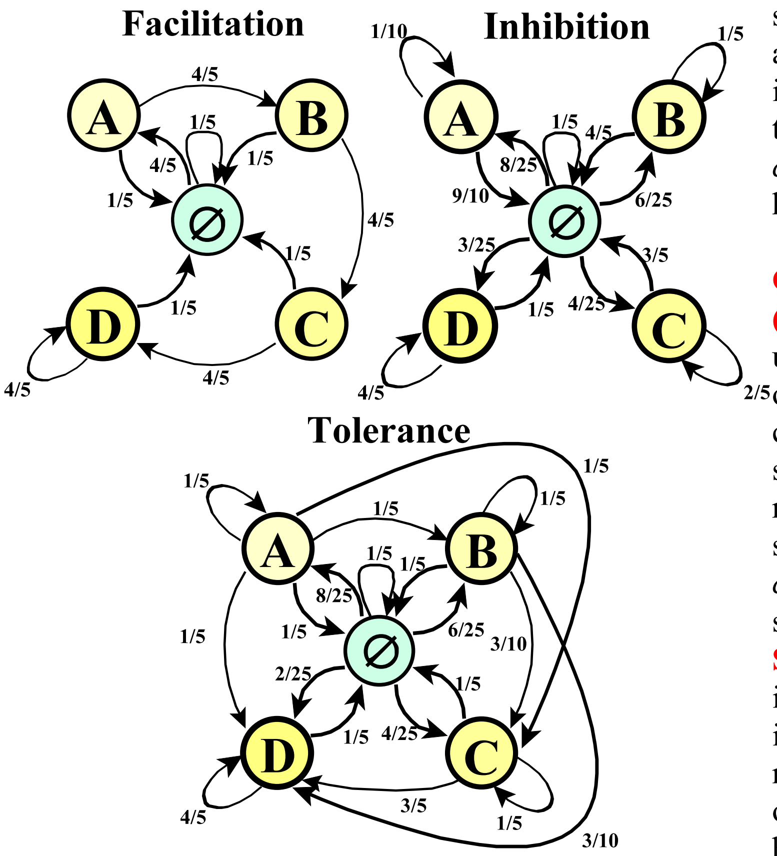

Figure 7. Flow diagrams showing how Connell & Slatyer’s (1977) facilitation, inhibition and tolerance models can be viewed as Markov processes. ∅ indicates empty space. The probabilities that one state (*e.g.*, a patch of mud or rock) will change to another in a given time unit are shown.

Quinn (1979) and **Jumars & Gallagher (1982)** argued that there is a general theory underlying the different effects of predation on soft-bottom and rocky intertidal communities. In the rocky intertidal, early species occupy space inhibiting the recruitment of later species. Later succession species, like the mussel *Mytilus californianus* overgrow and crush early space-occupying colonists**. Connell & Slatyer (1977)** referred to this as the inhibition model if the early colonists impeded the later colonists and the tolerance model if the early colonists had little effect on the later colonists. In the soft-bottom benthos, early species may be more likely to modify the environment paving the way for later succession species. **Connell & Slatyer (1977)** referred to this type of succession as the facilitation model. **Gallagher *et al.***

(1983) found that the facilitation model appeared to account for the effects of early successional tube-building species on later succession species on an intertidal sandflat. **Quinn (1979)** and **Jumars & Gallagher (1982)** following an earlier model by **Horn (1975)**, showed that predation or disturbance has very different effects on communities in which facilitation dominates over the tolerance or inhibition models. Figure 7, modified from **Jumars & Gallagher (1982)**, shows the Markov chain models for **Connell & Slatyer's (1977)** facilitation, inhibition & tolerance models. The facilitation model is based on Clements' original theory of succession: early species must pave the way for later succession species. In the tolerance model, early species neither inhibit nor facilitate the recruitment of later succession species, but there are still strong differences in recruitment ability and longevity which drive the succession from early to late succession species. The transition probabilities shown in Fig. 7 are based on a model where recruitment decreases and longevity increases linearly from the first to last colonists. A Markov chain succession model assumes that the transitions from one species to the next are controlled only by the species present now, not the species present at previous time periods. If the process is allowed to continue with the same transition probabilities, the community will converge on a steady-state assemblage.

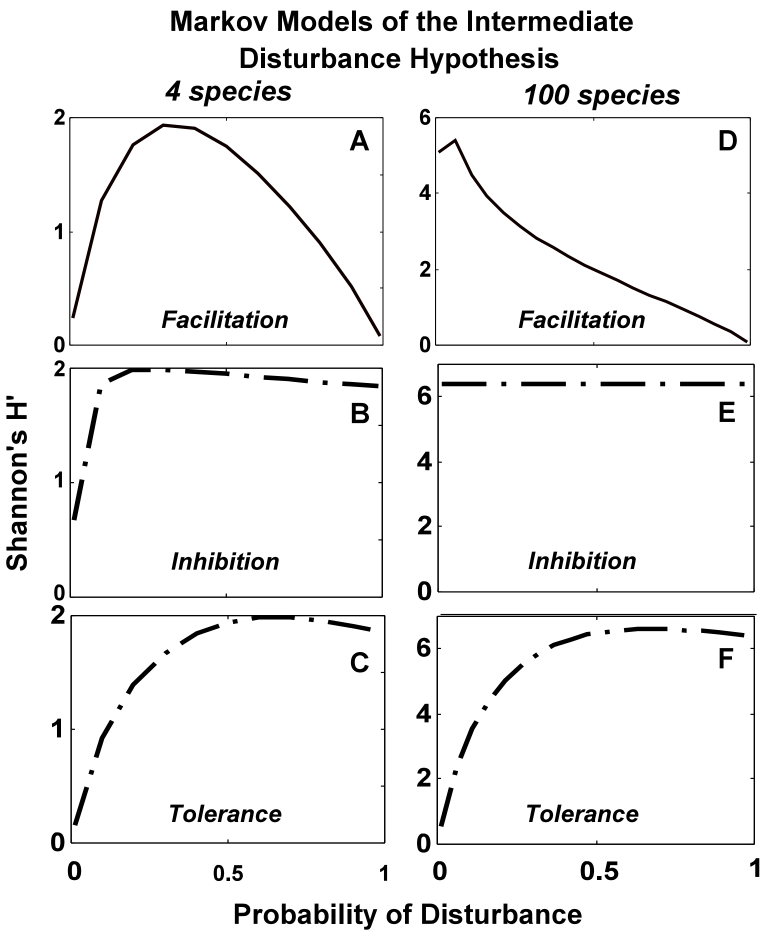

Figure 8. Shannon's H' diversity (log$_2$) for the facilitation (**A & D**), inhibition (**B & E**) and tolerance models (**C & F**). The transition probabilities for **A-C** at a disturbance probability of 0.2 are shown in Fig. 7. Note the change in ordinate scale for the 100-species model. No matter what the underlying model of succession, the size of the local species pool is always a major determinant of species diversity.

Figure 8 shows the diversity (using Shannon's H') for the steady state communities corresponding to the Markov succession sequences shown in Figure 8. The intermediate peak in diversity is shifted to the left in the facilitation model relative to the tolerance model. In the inhibition model, there is relatively little effect of disturbance on species diversity if the number of species is large. Note the different scale on panels **A-C** *vs.* **D-E**. No matter the nature of biological interactions, the species pool in the region is always a major determinant of species diversity.

In Figure 9, note that if the underlying succession is dominated by facilitation, reducing the amount of predation or disturbance will generally increase species diversity. This is exactly the opposite of **Paine's (1966)** result for the rocky intertidal, where the removal of *Pisaster* led to a low-diversity mussel community. **Peterson's (1979b)** review of caging studies in the soft-bottom benthos indicates that predator reduction tends to lead to increased soft-bottom benthic diversity. Note also that if the pure inhibition model is operating, the effects of disturbance or predation on species diversity will be slight. **Sale (1977)** described succession in coral reef fish communities with a model similar to the inhibition model shown in Fig. 8. Territorial fish occupy holes in the coral, holding off other fish. The initial colonist tends to persist. Sale called this type of succession a lottery since chance rather than intrinsic competitive ability determined whether a fish would be able to obtain the scarce habitat resource. In such a system, disturbance would have little effect on species diversity.

Why are there so many species in the deep sea?

Grassle & Maciolek (1992) described the number of species observed at 2100 m depth on the continental slope of the East Coast of North America. In 233 30-cm x 30-cm samples, they observed 798 species in 171 families and 14 phyla. New species were being added regionally at the rate of 25 species per 0.5-m^2 additional area sampled. Along the transect, 1 species was being added per km sampled. If this rate of new species addition were extrapolated to 1 new species per km^2, they calculated that the total number of deep-sea species would exceed **10^9**. They argued that the abundance of deep-sea individuals was much lower in the abyssal Pacific and reduced this number of expected deep-sea species to **10^8**. This number of species far exceeds the number of species calculated for the tropics or any other major biome on earth.

More recent analysis of the rate of species turnover in the abyssal Pacific by Buz Wilson (see **Poore & Wilson (1993)**) indicates much higher rates of species replacement (β diversity) among peracarid crustaceans (especially amphipods & iosopods) in the Pacific abyss than in **Grassle & Maciolek's (1992)** outer Atlantic continental shelf transect. Wilson estimates that the number of species may be greater than the 10^8 estimate. In the following section, I'll list some of the major ideas and hypotheses that have been invoked to account for high deep-sea diversity.

Basic patterns in deep-sea communities

Jumars & Gallagher (1982) document many of the striking features of deep-sea communities. The two most striking features are the small size of most deep-sea deposit feeders, relative to their shallow-water analogues and the exponential decline in benthic abundance, biomass and respiration with depth. Rowe (1983) documented the exponential decline in biomass with depth:

$$\log_{10} biomass\ [\ g\ m{-2}\ ] = 1.25 - 0.00039 * depth. \qquad \textbf{(8)}$$

Smith (1983) found that depth alone accounted for 83% of the variation in oxygen utilization rates in sediments. These exponential declines with depth in infaunal abundance, biomass and metabolism are due to the exponential decline in organic matter flux to the sediments. Pace *et al.* (1987) used ^{14}C primary production estimates under trace-metal clean conditions with sediment traps suspended at depth to determine the flux of organic matter at depth and its relationship to overlying water column production:

$$\begin{aligned} POC\ flux &= 3.523 * z^{-0.374} * PP*1.00. \\ PON\ flux &= 0.432 * z^{-0.843} * PP*1.123. \\ where,\ PP &= Primary\ production. \\ z\ is\ between\ 2000m\ and\ base\ of\ euphitoc\ zone. \end{aligned} \qquad \textbf{(9)}$$

The amount of organic matter reaching the deep-sea benthos declines exponentially with depth. Since Pace did their study, additional work has shown that the deep-sea benthos in the North Atlantic receives a relatively large pulse of phytodetritus from the spring bloom. This bloom material, in the form of fast-sinking flocs sometimes called marine snow, can be traced throughout 4000 m water columns as it sediments to the benthos. This phytodetritus fall would not be observed in the central north Pacific nor in the subarctic Pacific. Many deep-sea populations appear to be adapted to utilize this periodic food input.

Table 4 from Jumars & Gallagher (1982) indicates the sharp decline in animal abundance with depth and dominance of polychaetes from some deep-sea benthic communities in the Pacific.

Table 4 Some characteristics of four Pacific deep-sea communities (**Jumars & Gallagher 1982**)

Locality	**SCB Santa Catalina Basin**	**SDT San Diego Trough**	**CNP Central North Pacific**	**AT Aleutian Trench**
Depth (m)	1130	1230	5500-5800	7298
Total macrofaunal abundance Numbers / m^2	1880	2251	115	1272
Most abundant species	*Paraonis*	*Tharyx*	*Chaetozone*	*Chaetozone*
Abundance	350	142	15	184
% polychaetes	77	76	55	49
% tanaids	3.8	3.7	18.4	6.1
% gastropods	0.4	1	0.4	0.7
% carnivores	2	13	12	7

List of ideas on deep-sea diversity

Table 5 is a chronological list of the major theories proposed to explain high deep-sea soft-bottom benthic diversity.

Table 5. A list of key dates and ideas in the study of deep-sea diversity. Many of these ideas are reviewed in **Jumars & Gallagher (1982)**, **Rex (1983)**, and **Grassle (1989)**.

Year	Author	Description
1846	Forbes	Dredged shells from the abyss, indicating that there is life in the deep sea.
1873-1876	Challenger expedition	Dredged animals from 5500 m. The recorded species lists, (see **Sverdrup et al. 1942**), appear relatively species-rich
1880	Thomas	The deep sea fauna is stable and ancient, containing the ancestral forms of many shallow water taxa.
1967	**Hessler & Sanders**	**First quantitative demonstration of high deep-sea diversity**. Samples were taken by anchor dredge on the Gayhead MA to Bermuda transect.
1968	**Sanders**	**Stability-time hypothesis.** The deep sea is an ancient environment, 10's of millions of years old in the North Atlantic and older still in the Pacific. The deep sea is also the most stable environment on earth allowing animals to evolve adaptations to the finest dimensions of the niche, allowing coexistence of many species. **Rex (1983)** calls this the competitive niche partitioning hypothesis: *"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."*

Table 5. A list of key dates and ideas in the study of deep-sea diversity. Many of these ideas are reviewed in **Jumars & Gallagher (1982)**, **Rex (1983)**, and **Grassle (1989)**.

Year	Author	Description
1972	**Dayton & Hessler**	**The cropper hypothesis** (Biological disturbance) This hypothesis attacked the view that deep-sea communities are structured by competition. Dayton & Hessler, using the paradigm developed by **Paine (1966)** for the intertidal, argued that the high relative disturbance and predation rates could account for high deep-sea diversity. Much of this predation could be caused by deposit feeders cropping the juvenile stages of other deposit feeders. *“**The maintenance of high species diversity in the deep sea is more a result of continued biological disturbance than of highly specialized competitive niche diversification. Detrital food is the primary resource...most animals would consume living particles as well as dead. We call this dominant life-style `cropping’. [emphasis added]** 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**. Documentation of catholic tastes would support the view that predation was relatively more important.”*
1973	**Rex**	**Deep-sea diversity is highest at intermediate depths** (slope and rise depths), declining into the abyss.
1973	**Grassle & Sanders**	The contemporaneous disequilibrium hypothesis. 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.
1975a, 1975b, 1976	Jumars	High spatial heterogeneity, with patchiness at all scales documented. **The deep-sea may be the most spatially heterogeneous environment on earth**.
1976	**Rex (1976)**	**Both predation and competition**, mediated by reduced productivity with depth, may account for the parabolic increase in diversity at intermediate depths from shalow water to the abyss.

Table 5. A list of key dates and ideas in the study of deep-sea diversity. Many of these ideas are reviewed in **Jumars & Gallagher (1982)**, **Rex (1983)**, and **Grassle (1989)**.

Year	Author	Description
1976	Menge & Sutherland (1976)	**Predation and competition** Increasing predation in the deep sea may keep competitors below their carrying capacity, allowing coexistence.
1977	**Grassle (1977)**	Slow recolonization rates of the deep-sea benthos documented. This is the key to Grassle's mosaic theory of deep-sea diversity and community structure.
1978	**Grassle (1978)**	**The deep sea is a spatial-temporal mosaic**. *" Although disturbance is infrequent, when it does occur, a few species slowly colonize. These species composition in the disturbed area remains different from the surrounding environment for years. This is in sharp contrast to high-latitude, shallow-water environments where recovery occurs in months or less. The very slow rates of colonization in the deep sea mean that an environmental mosaic is created. Each small patch differs, depending on the length of time following disturbance and the particular species that happen to settle there. The infrequent small disturbances...are the sources of environmental heterogeneity. These disturbances are so localized and occur so infrequently that the patchiness they produce is seldom demonstrated in quantitative samples."* **Grassle (1978, p. 49)**

Table 5. A list of key dates and ideas in the study of deep-sea diversity. Many of these ideas are reviewed in **Jumars & Gallagher (1982)**, **Rex (1983)**, and **Grassle (1989)**.

Year	Author	Description
1978-1979	**Osman & Whitlatch (1978)** **Abele & Walters (1979a)**	**The Island Biogeographic Hypothesis**. Two interesting hypotheses were invoked in this paper. They argued that deep-sea diversity is high because the deep sea is the largest habitat 'island' on earth. All else being equal, larger islands support larger numbers of species. **MacArthur & Wilson's (1967)** Theory of Island Biogeography provided an explanation for the island-area relation. This hypothesis is rejected by Rex's finding that the highest diversity is found on continental slopes and rises, which have much less area than the abyssal plains. The second hypothesis raised isn't so easily refuted. They argued that the species pool in the deep sea is the result of long-term, evolutionary time scale rates of speciation and extinction. The deep sea may have high species richness on the local scale because of a large species pool.
1979	Huston	**The dynamic equilibrium hypothesis**. A Lotka-Volterra model is used to show that it is the combination of low times to competitive exclusion (due presumably to low organic flux) and moderate predation that produce higher deep-sea diversity.
1981	Rex	The **dynamic equilibrium model** is used to explain the peak in diversity at continental slope and rise depths and the decline in diversity on the abyssal plains.
1982	**Jumars & Gallagher**	**Successional mode hypothesis**. As a follow-up to the dynamic equilibrium model, **Jumars & Gallagher (1982)** note that disturbance frequency has different effects on species evenness with different modes of succession. Using **Connell & Slatyer's (1977)** models of succession, low rates of disturbance (density-independent mortality) produce communities of decreasing evenness from the facilitation, to tolerance to inhibition models.

Table 5. A list of key dates and ideas in the study of deep-sea diversity. Many of these ideas are reviewed in **Jumars & Gallagher (1982)**, **Rex (1983)**, and **Grassle (1989)**.

Year	Author	Description
1989	**Carney (1989)**	Carney proposes a deep-sea variant of the tropical rainforest refuge hypothesis. Since the organic flux to the deep sea has varied cyclically that the slope-rise fauna range has expanded and contracted onto the abyssal plains. During periods of high organic flux, the rise fauna covers the plains allowing for genetic differentiation, if not allopatric speciation. During periods of lower organic carbon flux, this fauna contracts to the higher organic carbon fluxes of the slope and upper rise. The key question is: are we in a period of high or low organic carbon flux now?
1992	**Etter & Grassle**	**The silt-diversity hypothesis**. Species diversity at 2100 m depth, measured by **$E(S_{100})$** is positively correlated with the diversity in sizes of silt particles, measured with **Shannon's H'**.
2005	Rex et al. (2005)	The Source-Sink Hypothesis. Alpha diversity on the abyssal plains may be largely controlled by larval recruitment from the more species-rich bathyal region.

There is no clear winner in the sweepstakes to explain why there are so many species in the deep sea. There has been a great deal of work done documenting that the deep sea is very spatially heterogeneous at all scales. The leading explanation for the high deep-sea diversity is **Grassle's (1978)** spatial-temporal mosaic model. Low rates of disturbance or introduction of organic matter may create patches that persist for long periods of time in the deep sea. We now know that pulses of organic matter arrive at the deep-sea floor, especially the pulse of phytodetritus resulting from the spring phytoplankton bloom. These bloom diatoms form flocs of mucous-bound diatoms that can settle at relatively high rates (up to 100 m per day). Many deep-sea taxa may be adapted to utilize these periodic nutrient inputs. Other deep-sea taxa have evolved to utilize the occasional nekton fall (*e.g.*, dead fish, dead whales). Snelgrove *et al.* (**1992**, **1994**) placed trays on the deep-sea floor supplemented with different types of organic matter. The species that colonized these trays were different from those found in the surrounding sediment, and the community structure of these trays remained different from the surrounding area for some months. These findings are consistent with the spatio-temporal mosaic hypothesis for high deep-sea diversity.

Most recent work indicates that deep-sea taxa are habitat specialists. However, **Etter & Grassle (1992)** have shown that the diversity of silt particles in box cores is an excellent predictor of species richness. Are deep-sea deposit feeders food-type specialists, or is silt diversity merely related to habitat complexity. A complex surface topography would produce areas of different boundary shear stress allowing a greater diversity of silt particles to settle and accumulate.

The exciting features of the **Etter & Grassle (1992)** and **Grassle (1978)** spatial-temporal mosaic hypothesis is that they can be experimentally tested in the field. Howard Sanders, who still lives in Woods Hole, was adamant that his stability-time hypothesis was an evolutionary timescale hypothesis and could not be refuted by experiments done in ecological time. He argued firmly that the major cause of species richness in the deep sea was that evolutionary time had led to a large species pool due to long-term speciation and extinction rates. Simply finding that increased disturbance didn't alter species diversity, as in **Thistle (1983b)**, could not refute the hypothesis. He remained adamant that the species richness of the deep sea was the most important reason for high species diversity on the local scale. Sanders argument has now been cast in impressive form by **Ricklefs (1987)**, who showed that the local species diversity is usually a strong function of the local species pool:

> *"Local diversity bears a demonstrable dependency upon regional diversity. These observations suggest that regional and historical processes, as well as unique events and circumstances, profoundly influence local community structure. Ecologists must broaden their concepts of community precesses and incorporate data from systematics, biogeography and paleontology to analyses of ecological patterns and tests of community theory."*

Osman & Dean (1987) collected data on the species diversity on fouling panels placed all over the world. The best predictor of species diversity was the immigration rate (*i.e.*, the rate species were added to panels), panel size, and the number of species in the local area. There were few latitudinal or even inter-ocean patterns in the data. They argued that interregional comparisons must include the local species pool in any analysis before attributing diversity differences to other ecological or environmental factors:

> *"Regression analyses suggested that immigration rate, realized pool size (i.e., the total number of species observed locally) and the island size all had significant positive effects on S [species number]. Other factors such as latitude, temperature, salinity and regional pool size had no significant effect. Given the apparent importance of local factors in determining the number of species on hard substrate islands, we question the relevance of interregional comparisons in assessing factors which may influence the distribution and abundance of species."*

It will be a challenge for benthic ecologists to incorporate regional species richness in their tests of deep-sea diversity theories. They must avoid the tautology that "The deep sea has high species diversity because lots of species live there." Are the processes that result in high regional species diversity the same ones that control the number and distribution of species on the local scale (*e.g.*, a 0.25 m^2 box core)? Much needs to be done both theoretically and experimentally to test the relative importance of ecological and evolutionary timescale processes in the deep sea. Some would argue that the processes are the same; Sanders was adamant that the processes were different. Who is right?

Terms and Concepts

Community Definition from **Mills (1969)**: Communities are groups of potentially interacting populations that occur in a given area and are separable from other such groups by ecological survey

Continuum concept Due originally to Gleason: individuals are distributed according to their own environmental requirements and there are no such things as discrete communities.

Correlation A standardized form of covariance obtained by dividing the covariance of two variables by the product of the standard deviations of x and y.

Diversity

Alpha diversity [α diversity] A term coined by **Whittaker (1960)** for the diversity in a local area.. See also **Whittaker (1967)** **Cody (1986)** The number of species found in one uniform habitat type in one relatively local area.

Beta diversity [β diversity] Change in species composition along environmental gradients. Measured in half-change units. **Whittaker (1960)**: *"Beta or between-habitat diversity refers to the ...degree of contrast in species composition among samples of a set taken from a landscape."* Beta diversity is the amount of species turnover along an environmental gradient (Gauch 1973) and cannot be measured until the underlying structure of the data has been recovered successfully (**Noy-Meir & Whittaker 1977**, **ter Braak 1983, p. 455**)

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. Whittaker referred to Cody's gamma diversity as delta diversity. Sepkoski adopted Cody's definition of gamma diversity. [Using Peterson and Thorson's analogy, 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.]

Alpha diversity indices sensitive to both species richness and evenness:

Gini diversity (and related indices, from **Bhargava & Doyle 1974**)

Simpson (1949)

$$\begin{aligned} &Simpson's\ D = 1 - \sum_{j=1}^{S} \frac{N_j\,(N_j - 1)}{N\,(N-1)}. \\ &where,\ N_j = abundance\ of\ species\ j. \\ &N = total\ individuals. \\ &S = number\ of\ species. \end{aligned} \tag{10}$$

Gini (1912):

$$Gini = 1 - \sum \left(\frac{N_i}{N}\right)^2.$$

normalized **McIntosh (1967)**:

$$McIntosh = 1 - \sqrt{\sum \left(\frac{N_i}{N}\right)^2}$$

Gleason's D Number of species per sample divided by natural log of the number of individuals (**Gleason 1922**, **Washington 1984**).

$$Gleason's\ index\ D = \frac{S}{\ln N}.$$

H' see **Shannon-Wiener diversity**

Hurlbert's expected number of species E(S$_n$):

$$E(S_m) = \sum_{k=1}^{S} 1 - \frac{\binom{N-N_k}{m}}{\binom{N}{m}}. \tag{14}$$

$$\begin{aligned} where,\ \binom{N}{m} &= binomial\ coefficient. \\ &= No.\ of\ different\ ways\ of\ sampling\ N\ objects,\ m\ at\ a\ time. \end{aligned}$$

Shannon-Wiener diversity (**Shannon & Weaver 1949**):

$$\begin{gathered} \boldsymbol{H'} = -\sum_{i}^{S} p_i \log p_i \,, \\ \textit{where,} \\ p_i = \textit{frequency of species } i \textit{ in sample.} \\ p_i = \frac{N_i}{N}. \\ N_i = \textit{Number of individuals of species } i. \\ N = \textit{Total individuals in sample.} \\ S = \textit{Number of species.} \\ \log \textit{ could be base } 2,\ 10,\ \textit{or natural } \log. \end{gathered} \qquad \textbf{(15)}$$

Brillouin's (1951) diversity An information-based diversity statistic, appropriate whenever information-based diversity is being measured from a sample or full census. It is always highly correlated with but slightly smaller in magnitude than the Shannon-Wiener H'.

$$\begin{aligned} \textit{Brillouin's } H &= \frac{1}{N} * \ln\left(\frac{N!}{N_1!\ N_2!\ \ldots\ N_s!}\right). \\ &= \frac{1}{N} * \ln\left(\frac{N!}{\prod_{k=1}^{S} N_k!}\right). \\ \textit{where, } N &= \textit{Sample total.} \\ N_k &= \textit{Abundance of species } k. \\ \frac{N!}{N_1!N_2!\ \ldots\ N_s!} &= \textit{No. distinguishable permutations with the } N_i's. \end{aligned} \qquad \textbf{(16)}$$

Margalef's index (**Margalef 1958**):

$$\textit{Margalef's index } D = \frac{S - 1}{\ln N}. \qquad \textbf{(17)}$$

Menhinick's index (**Menhinick 1964**)

$$\textit{Menhinick's index } D = \frac{S}{\sqrt{N}}. \qquad \textbf{(18)}$$

McIntosh's diversity (**Pielou 1969, p. 234**)

U is the distance from the origin in s-dimensional coordinate frame. U is the species richness component and M is a richness measure, independent of N, the total number of individuals.

$$\begin{aligned} McIntosh's\ U &= \sqrt{\sum_{k=1}^{S} N_k^2}. \\ McIntosh's\ M &= \frac{N - U}{N - \sqrt{N}}. \\ McIntosh's\ Evenness &= \frac{N - U}{N - \frac{N}{\sqrt{S}}}. \\ where,\ N &= Total\ individuals\ in\ sample. \\ S &= Total\ species\ in\ sample. \end{aligned} \tag{19}$$

for given N, the larger S, the smaller U will be. **Pielou (1969)** proposed the evenness measure for McIntosh's diversity:
U measures uniformity, max when the collection contains only 1 species
max(U)=N, min(U)=sqrt(N);Δ=N-U;
measure independent of N:
Δ/max(Δ)=(N-U)/(N-SQRT(N))
Evenness:
Δ/max(Δ|N,s)=(N-U)/(N-(N/SQRT(s)))

Alpha diversity indices for equatability or evenness:

Berger-Parker index: (**Berger & Parker 1970**)

$$D = \frac{N_{\max}}{N} \tag{20}$$

Pielou's (1966) J':

$$J' = \frac{H'}{H'_{\max}}. \tag{21}$$

or Hurlbert's measure of evenness for **Shannon's H'**:

$$\begin{aligned} V &= \frac{H' - H_{\min}}{H_{\max} - H_{\min}}. \\ & where, \\ V &= Hurlbert's\ evenness\ index\ for\ H'. \\ H' &= Shannon's\ H'. \\ H_{\max} &= value\ parameter\ would\ assume \\ & if\ all\ \boldsymbol{S}\ species\ were\ equally\ abundant. \\ H_{\min} &= value\ parameter\ would\ assume \\ & if\ one\ species\ was\ represented\ by\ N-(S+1)\ individuals \\ & and\ the\ other\ species\ by\ one\ individual\ each. \end{aligned} \tag{22}$$

PIE= Probability of Interspecific encounter **Hurlbert (1971)**:

$$PIE = \delta_1 = \left(\frac{N}{N - 1} \right) \left(1 - \sum_{k=1}^{S} p_k^2 \right). \qquad \textbf{(23)}$$

$\delta_2 = 1 - \Sigma\, \underline{Pi}_i^2$= Simpson's measure of concentration
PIE is in A. R. Wallace's observations of Amazonian forests.

Faunal similarity and dissimilarity indices

Bray-Curtis. The Bray-Curtis similarity measure is used more than any other faunal similarity or dissimilarity measure. Most of this use is not because of the merits of the index. It is only a semimetric, which creates difficulties in using some multivariate statistical procedures, such as Gower's principal coordinates analysis.

$$\begin{aligned} \textit{Bray-Curtis Similarity} &= \textit{Sorensen's quantitative index.} \\ &= \textit{Pielou's \% Similarity.} \\ &= \textit{Legendre \& Legendre's Steinhaus index } S_{17}. \end{aligned}$$

$$SIM_{ij} = 2 * \frac{\sum_{k=1}^{S} \min(x_{ik}\,,\, x_{jk})}{\sum_{k=1}^{S} (x_{ik} + x_{jk})}. \qquad \textbf{(24)}$$

$$\begin{aligned} \textit{where, } S &= \textit{Number of species.} \\ x_{ik} &= \textit{Abundance of species } k \textit{ in sample } i. \end{aligned}$$

Canberra metric

$$CM_{ij} = \frac{1}{S} * \sum_{k=1}^{S} \frac{|x_{ik} - x_{jk}|}{x_{ik} + x_{jk}}\ .$$

$$\begin{aligned} \textit{where, } CM_{ij} &= \textit{Canberra metric for samples } i \textit{ and } j. \\ S &= \textit{Number of species.} \\ x_{ik} &= \textit{Abundance of species } k \textit{ in sample } i. \end{aligned}$$

chord distance Proposed by Orloci (1967), used by Cavalli-Sforza and Edwards. Chord distance is identical to Euclidean distance after the data have been standardized by sample normalization. **Cavalli-Sforza &**

> **Edwards (1967)** convert the range of chord distance to 1. They calculate the chord distance for each locus and then take the Pythagorean distance among loci as the genetic distance among populations.

Orloci (1967): Compute the Euclidean distance based on normalized quadrat vectors: the distance so computed is called a **chord distance** indicating the length of the chord connecting two points on the surface of a sphere of unit radius has been measured. The chord distance can be obtained directly based on the formula:

$$\begin{aligned} CD_{ij} &= \sqrt{2\left(1 - \frac{q_{ik}}{\sqrt{q_{ii}\ q_{jj}}}\right)}. \\ where,\ q_{ij} &= \sum_{k=1}^{S} X_{ik}\ X_{jk}. \\ q_{jj} &= \sum_{k=1}^{S} X_{ik}^{2}. \\ q_{kk} &= \sum_{k=1}^{S} X_{jk}^{2}. \\ X_{ik} &= Abund.\ of\ species\ k\ in\ sample\ i. \end{aligned} \qquad \textbf{(26)}$$

CNESS Chord-normalized expected species shared. A metric version of NNESS, developed by Gallagher and described in **Trueblood et al. (1994)**:

$$CNESS_{ij|m} = \sqrt{2 * \left(1 - \frac{ESS_{ij|m}}{\sqrt{ESS_{ii|m} * ESS_{jj|m}}}\right)}\ . \qquad \textbf{(27)}$$

$ESS_{ij|m}$ The Expected Species Shared between samples i and j with a random draw of m individuals from each sample, without replacement.

NESS$_{ij|m}$ Normalized Expected Species Shared in a random draw of m individuals from two samples i and j. NESS is a family of faunal similarity measures, described by **Grassle & Smith (1976)**, depending on the sample size m. NNESS is described by **Trueblood *et al.* (1994)**, short for NewNESS. NNESS corrects a mathematical problem in the original NESS similarity index. The NNESS index can be made sensitive to only the most abundant species in the community by lowering the random sample size m. At m=1, NNESS is the Morisita-Horn similarity index. At a large random sample size m, NNESS converges on the presence/absence Sorensen index.

$$NNESS_{ij|m} = \frac{ESS_{ij|m}}{\frac{1}{2} * (ESS_{ii|m} + ESS_{jj|m})} . \qquad \textbf{(28)}$$

Percentage similarity This faunal similarity index was introduced to ecology by **Sanders (1960)** under the name dominance affinity. This index is closely related to the Bray-Curtis index. Like Bray-Curtis it is a semimetric in that the 1-% similarity produces a distance coefficient which does not meet the triangular inequality required of a metric.

Multiple stable equilibria a stable model system that, if perturbed sufficiently can return to one or more different equilibria has multiple stable points.

Parallel level-bottom communities Convergent development of community structure in soft-bottom benthic communities, originally proposed for Danish neritic benthos by **Petersen (1918)** and extended to the world's benthos by Thorson (**1956**, **1957**). Benthic communities occurring at the similar depths and grain sizes are dominated by members of the same genera, but different species, worldwide. **Thorson (1971)**, in his last work, finally recanted his belief in the concept because numerically dominant or characteristic species could not be identified from the tropics.

Outlines of papers

Required and Recommended

Mills, E. L. 1969. The community concept in marine zoology, with comments on continua and instability in some marine communities: a review. J. Fish. Res. Bd. Can. *26*: 1415-1428. {5, 6, 12}

I. Abstract:

II. **Definitions:**

  A. **Community: an ecological unit of any degree**

  B. Formation: a major grouping of organisms with a definite physiognomy and structure (*e.g.*, boreal forest, tundra, prairie)

  C. Association: Units of which the formations are composed, i.e., groupings of plants in a habitat, marked by unique dominant species or overall community composition

III. History of the community concept

A. Zurich-Montpelier school, influenced by Braun-Blanquet

1. vegetation as a mosaic

2. lists of species, degree of clumping and area cored by it.

3. “character species where diagnostic, found with great fidelity

4. the lowest category, the association, came to be regarded as analogous to the species.

B. Uppsala school and other Scandinavian plant ecologists

1. Associations were regarded as real or concrete, and were based on actual counts of plants (not just estimates of cover or clumping) from small quadrats

2. Analysis by mathematical methods

3. Also entering were the “life forms” of the plants (*e.g.*, height, especially position of wintering buds)

4. goal to classify communities, although the units were regarded as concrete

IV. Holistic views of communities.

A. **Clements (1916)**

B. **Allee’s definition of community:** A natural assemblage of organisms, which together with its habitat, has reached a survival level such that it is relatively independent of adjacent assemblages of equal rank; to this extent given radiant energy, it is self-sustaining.” The major community has anatomy, physiology, and heredity, and also a form of evolution through succession to a stable climax, which is in equilibrium with the environment. This definition does not assume that the community must have discrete boundaries.

C. Clements Alee *et al.*, and Tansley regarded communities as organisms or as analogous to organisms because of the seeming unity and interdependence of biotic units in nature. these views did not go unchallenged.

V. Communities as aspects of continua.

A. **Gleason (1926)**: Are we not justified in coming to the general conclusion, far removed from the prevailing opinion, than an association is not an organism, scarcely even a vegetational unit, but merely a coincidence?

B. Gleason’s ideas involve ordination studies, as opposed to the older, hierarchical classification of vegetation. Ordination can be direct or indirect.

VI. The community concept in marine zoology and other disciplines.

A. Many of the ideas and terms used by marine ecologists seem to have been borrowed from plant ecology without specification of what is implied and with even less attempt to rigorously verify or disprove the principles suggested.

B. Möbius put forward **biocoenosis** for oyster beds.

C. **Petersen (1918)** found a regular occurrence of eight communities.

1. stressed depth and sediment type

2. no mention of biological interactions

D. **Clements & Shelford (1939)**

“The system is strongly synthetic and is based on large, conspicuous plants and animals across large geographic areas. It assumes the concreteness and organismic unity of communities,

listing 10 biomes for Puget Sound and North Atlantic areas, requires intermediate groupings ("faciations" governed by "subclimates") to maintain coherence. After the passage of 20 years, this attempt at classification now appears an almost meaningless oversimplification. Incomplete faunal and floral lists were forced into a theoretical framework of succession, climax and organismic unity, ideas which are not supported by any kind of evidence."

E. **Jones (1950)**

F. Thorson's parallel communities

1. the implications of Thorson's ideas are that because of similar selective forces and responses to them we can expect to find closely similar animals under similar environmental conditions no matter where we look...Benthic communities, in this view, are not just abstractions from species lists, but concrete, biologically organized, ecological entities, and are a complex function of adaptations to particular environments.

G. Johnson's (1964) definition of community: an assemblage of organisms which often occur together.

H. Species constancy and dynamic stability.

1. Thorson's *Syndosmya* community
2. Mill's *Ampelisca* community

I. Mills' definition of a community

"A community means a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups."

Web Resources

Table 6. Web resources on community structure

URL	Site	Description
http://books.nap.edu/books/0309052254/html/index.html	National Academy Press	Full html text of 'Understanding Marine Biodiversity' Committee on Biological Diversity in Marine Systems, National Research Council
http://life.bio.sunysb.edu/marinebio/rockyshore.html	SUNY StonyBrook (Jeff Levinton & Raymond Seed)	Rocky Shores

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Calow, P. 1981. Invertebrate biology: a functional approach. Croom Helm Ltd., London. *[An excellent, concise description of invertebrate functional biology]*

Chia, F. and M. E. Rice (eds). 1978. Settlement and metamorphosis of marine invertebrate larvae. Elsevier, New York.

Coull, B. C. (ed.). 1977. Ecology of marine benthos. University of South Carolina Press, Columbia. *[Contains some excellent articles: Boesch, Grassle & Grassle, Jumars & Fauchald, Levinton]*

Eltringham, S. K. 1981. Life in mud and sand. English Universities Press, London. *[This is a very general undergraduate-level text]*

Ernst, W. G. and J. G. Morin. 1982. The environment of the deep sea. Rubey Volume II. Prentice-Hall, Inc. Englewood Cliffs, New Jersey. *[Contains* ***Jumars & Gallagher (1982)****]*

Friedrich, H. 1969. Marine Biology. Sidgwick and Jackson, London. *[The benthic section is excellent.]*{?}

Gray, J. S. 1981. The ecology of marine sediments. Cambridge University Press. *[An extremely interesting (but somewhat subjective) view of benthic ecology. I used this as a text when I first taught benthic ecology in 1982. Contains a lengthy exposition of the break in the lognormal distribution method for assessing pollution]*

Hedgpeth, J. W. (ed.) 1957. Treatise on marine ecology and paleoecology. Vol. I. Ecology. Geol. Soc. Amer. Mem. 67. *[Includes Thorson's major paper on the parallel level-bottom community concept]*

Holme, N. A. and A. D. McIntyre. (eds.) 1985. Methods for the study of marine benthos. Blackwell Scientific, Oxford. *[QH91.57/D7M47 in UMASS library. An excellent guide to sampling]*

Jumars, P. A. 1993. Concepts in Biological Oceanography: An interdisciplinary primer. Oxford University Press, New York. *[An interesting approach to presenting biological oceanographic processes to non-biological oceanographers. His discussion of optimal foraging and digestion theory to biological oceanographic problems is the highlight of the book]*{?}

Jumars, P. A., and E. D. Gallagher. 1982. Deep-sea community structure: three plays on the benthic proscenium. Pp. 217-255 *in* W. G. Ernst and J. G. Morin, eds., The environment of the deep sea. Prentice-Hall, Englewood Cliffs, New Jersey. *[A summary of deep-sea patterns and processes, intended for the advanced undergraduate or graduate student]*{**27**, **28**, **29**, **30**, **31**, **34**}

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benthic studies by Thorson, Sanders, Frank, and Connell]

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Reise, K. 1985b. Tidal flat ecology. Springer-Verlag, Berlin. *[A personal view of benthic ecology from Europe's best benthic experimenter]* {**26**}

Schäfer, W. 1972. Ecology and paleoecology of marine environments. University of Chicago Press, Chicago. *[Excellent natural history observations of animal-sediment interactions.]*

Sieburth, J. M. 1975. Microbial seascapes. Univ. Park Press, Baltimore. *[Scanning electron micrographs of benthic organisms]*

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Valiella, I. 1984. Marine Ecological Processes. Springer-Verlag, New York. *[A very good summary of the field. Particularly strong on salt marshes, sea grasses, carbon and nitrogen cycles.]*

Vermeij, G. J. 1978. Biogeography and adaptation. Harvard Press, Cambridge. *[Excellent discussion of the role of predation controlling phenotypes]*

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Andrewartha, H. G. and L. C. Birch. 1984. The ecological web: more on the distribution and abundance of animals. U. of Chicago Press, Chicago. *[An interesting follow up to* ***their 1954 classic****, with the major message that species are distributed according to a web of abiotic and biotic factors, factors which have a negative effect on organisms, such as pollutants, are called* ***malenities****]* [?]

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Hubbell (2001)

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Benthic clustering

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Boesch, D. F. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. Marine Biology *21*: 226-244.

Boesch (1977)

Boesch, D. F. 1977b. A new look at the zonation of benthos along the estuarine gradient. Pp. 245-266 *in* B. C. Coull, *ed.*, Ecology of Marine Benthos. University of S. Carolina Press. *[Includes an ordination of the estuarine benthos of Australia and Virginia]* {?}

Dyer, M.F., W. G. Fry, P. D. Fry and G. J. Cranmer. 1983. Benthic regions within the North Sea. J. mar. biol. Ass. U.K. *63*: 683-693.

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Gage, J. 1974. Shallow-water zonation of sea-loch benthos and its relation to hydrographic and other physical factors. J. Mar. Biol. Assoc. U.K. *54*: 223-249.

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 Publication 98-1. *[Describes the alpha, beta and gamma diversity of benthic communities. Both R- and Q-mode clustering of Boston Harbor communities with CNESS]*{**22**}

Grassle, J. F. and W. Smith. 1976. A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. Oecologia (Berlin) *25*: 13-22. *[NESS is introduced and applied to the West Falmouth oilspill data using flexible average sorting.]*

Gray, J. S., M. Aschan, M. R. Car, K. R. Clarke, R. H. Green, T. H. Pearson, R. Rosenberg, and R. M. Warwick. 1988. Analysis of community attributes of the benthic macrofauna of Friefjord/Langesundfjord and in a mesocosm experiment. Mar. Ecol. Prog. Ser. *46*: 151-165. *[These authors use 4-th root transformed data and Bray-Curtis similarity]*

Heip, C., R. M. Warwick, M. R. Carr., P. M. J. Herman, R Huys, N. Smol, and K. Van Holsbeke. 1988. Analysis of community attributes of the benthic meiofauna of Frierfjord/Langesundfjord. Mar. Ecol. Prog. Ser. *46*: 171-180.

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Hyland, J., E. Baptiste, J. Cambell, J. Kennedy, R. Kropp and S. Williams. 1991. Macroinfaunal communities of the Santa Maria Basin on the California outer continental shelf and slope. Mar. Ecol. Prog. Ser. *78*: 147-161.*[Part of the Minerals Management Service survey for outer continental shelf oil exploration]*

Johnson, R. K. and T. Wiederholm. 1989. Classification and ordination of profundal macro invertebrate communities in nutrient poor, oligo-mesohumic lakes in relation to environmental data. Freshwater Biol. *21*: 375-386. *[Two-way indicator species analysis TWINSPAN]*

Mauer, D., W. Leathem and C. Menzie. 1981. The impact of drilling fluid and well cuttings on polychaete feeding guilds for the Northeastern continental shelf. Marine Pollution Bulletin *12*: 342-347.

Sepkoski, J. J. and M. A. Rex. 1974. Distribution of freshwater mussels: coastal rivers as biogeographic islands. Syst. Zool. *23*: 165-188.{**53**}

Smith, R. W. 1976. Numerical analysis of ecological survey data. Ph.D. Dissertation, Biology. U. Southern California.

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Stephenson, W., W. T. Williams, and S. D. Cook. 1972. Computer analysis of Petersen's original data on bottom communities. Ecological Monographs *42*: 387-415. *[Petersen was biased towards ubiquitous species, especially Macoma balthica. In samples with Macoma, Petersen's classifications matched those produced through objective clustering.]*

Stull, J. K, C. I. Haydock, R. W. Smith and D. E. Montagne. 1986. Long-term changes in the benthic community on the coastal shelf of Palos Verdes, Southern California. Marine Biology *91*: 539-551. *[They use a new step-across distance measure, developed by Smith, to classify and order benthic community structure data at the 60-m outfall off LA.]* {?}

Taasen, J. P. and T. Hiosaeter. 1989. The shallow-water soft-bottom benthos in Lindaspollene, Western Norway. 5. Benthic marine diatoms, seasonal and spatial assemblages. Sarsia *74*: 43-57.

Trueblood, D. D., E. D. Gallagher, and D. M. Gould. 1994. Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. Limnol. Oceanogr. *39*: 1440-1454. *[The introduction of CNESS and PCA-H]* {**42**}

Warwick, R. M., H. M. Platt, K. R. Clarke, J. Aghard. and J. Gobin. 1990. Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. J. exp. Mar. Biol. Ecol. *138*: 119-142. *[They use ABC, NMDS, neutral model, H', and higher OTU's]*

Clustering physico-chemical variables

Grimm, E. C. 1987. CONISS: a Fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Computers and Geosciences *13*: 13-35.

Malins, D. *et al.*, *[Classification analysis is used to infer causation between high PAH concentrations and liver cancer in Puget sound sole]*

Poulton, D. J. 1989. Statistical zonation of sediment samples using ratio matching and cluster analysis. Envtl. Monit. Assess. *12*: 379-404. *[Contaminant concentrations from samples of Gt. Lakes sediments are converted to ratios; the ratios of all pair-wise combinations of pollutants are evaluated and summed with a combinatorially nightmarish formula producing a similarity matrix that is then clustered. What a mess!]*

Phylogenetic clustering

Cavalli-Sforza, L. L, and A.W.F. Edwards. 1965. Analysis of human evolution. Pp. 923-933 *in* Genetics today: Proc. XI Int Congress of Genetics *3*. *[First proposed use of trees based on similarity indices.]*

Cavalli-Sforza, L. L, and A. W. F. Edwards. 1967. Phylogenetic analysis: models and estimation procedures. Evolution *22*: 550-570. *[also published in Am. J. Hum Gen. 19: 233-257; cited by Felsenstein 1988]* {**42**}

Cavalli-Sforza, L.,, A. Piazza, P. Menozzi and J. Montain. 1989. Genetic and linguistic evaluation. Science *244*: 1128-1129.

Faith, D. P. 1985. A model of immunological distances in systematics. J. theor. Bio. *114*: 511-526.

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Feller, R. J., G. L. Taghon, E. D. Gallagher, G. E. Kenny, and P. A. Jumars. 1979. Immunological methods for food web analysis in a soft-bottom benthic community. Marine Biology *54*: 61-74. *[Antisera produced to 20 Skagit flat taxa, cross-reactions documented, and 1 food web produced]* {?}

Feller, R. J. and E. D. Gallagher. 1982. Antigenic similarities among estuarine soft-bottom benthic taxa. Oecologia *52*: 305-310. *[A classification analysis is performed comparing the antigenic similarities of east and west coast littoral invertebrates]* {?}

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Foulds, L. R. 1986. Testing the theory of evolution: a novel application of combinatorial optimization. Discrete Applied Math *15*: 271-282. *[The same phylogenetic tree is produced from analysis of different proteins using Steiner trees.]*

Jardine, N. and R. Sibson. 1971. Mathematical taxonomy. Wiley, London *[QH83.J36 at UMASS/Boston]*

Lynch, M. 1989. Phylogenetic hypotheses under the assumption of neutral quantitative genetic variation. Evolution *43*: 1-17. *[Phylogenetic trees assume the characters under consideration have neutral selective value.]*

Mickevich, M. F, N. I. Platnick. 1989. On the information content of classifications. Cladistics *5*: 33-47.

Raup, D. M. 1985. Mathematical models of cladogenesis. Paleobiology *11*: 42-52.

Sneath, P. H. A. and R. R. Sokal. 1973. Numerical taxonomy. Freeman, San Francisco.*[A classic guide to the use of numerical taxonomy & cluster analysis]*

Sokal, R. R., J. Kim and F. J. Rohlf. 1992. Character and OTU stability in five taxonomic groups. J. Classification *9*: 117-140. *[Simple matching with UPGMA clustering compared to maximal parsimony: "The overall conclusions of this study are that form the standpoint of stability UPGMA performs well and in many cases, especially with respect to OTU stability, is superior to maximal parsimony."]*

Vigilant, L, M. Stoneking, H. Harpending, K. Hooks and A. C. Wilson. 1991. African populations and the evolution of human mitochondrial DNA. Science *253*: 1503-1507. *[A beautiful cluster diagram showing the African origin of the ancestral EVE. This work has been roundly criticized for misapplying the PAUP algorithm. The tree is not the most parsimonious]*

Miscellaneous classification analysis

Fager (1957)

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Lie, U. 1974. Distribution and structure of benthic assemblages in Puget Sound, Washington, U.S.A. Marine Biology *26*: 203-223. *[Includes ternary plots of community structure, which appears to fit the continuum model.]* {?}

Lie, U. and J. C. Kelley. 1970. Benthic infauna communities off the coast of Washington and in Puget Sound: identification and distribution of the communities. J. Fish. Res. Bd. Can. *27*: 621-651. *[PCA with a ternary diagram are used to show the distribution of benthic communities in Puget Sound fit the continua model.]* [?]

Classics

Petersen, C. G. J. 1918. The sea-bottom and its production of fish food. A survey of work done in connection with the valuation of Danish waters from 1883-1917. Rep. Danish. Biol. Stat. *25*: 1-62. *[A classic paper. See* ***Stephenson et al.'s*** *reanalysis of Petersen's original data]* {**12**, **56**}

Sanders, H. L. 1956. The biology of marine bottom communities. Bulletin of the Bingham Oceanographic Collection *15*: 345-414. *[Howard Sander's Yale Ph.D. dissertation, which applies the Peterson-Thorson scheme to New England benthic communities.]* {**13**, **57**}

Sanders, H. L. 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. Limnol. Oceanogr. *3*: 245-258. *[The Station R Nephtys incisa-Nucula assemblage is identified. He introduced quantitative methods of analysis to US Benthic ecology]* {?}

Sanders, H. L. 1960. Benthic studies in Buzzard's Bay III. The structure of the soft-bottom community. Limnol. Oceanogr. *5*: 138-153. *[A classic paper describing the benthic community structure of Station R in Buzzard's bay. This site is heterogeneous and exhibits no evident seasonality or longer term change in community structure.]* {**13**, **57**}

Sanders, H. L., E. M. Goudsmit, E. L. Mills, and G. E. Hampson. 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. Limnol. Oceanogr. *7*: 63-79. *[The first US study to analyze the diets of the major infauna. See Whitlatch for a detailed study of the same communities]*

Stephenson, W., W. T. Williams and S. D. Cook. 1972. Computer analyses of Petersen's original data on bottom communities. Ecol. Monogr. *42*: 387-415. *[A reanalysis of* ***Petersen's 1918*** *data using classification analysis. Most of Petersen's communities are still recognizable using objective methods]* {***12***, ***56***}

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. *25*: 1-45. *[Most benthic invertebrates have planktotrophic development]*

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Thorson, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. of Sea Res. *3*: 267-293. *[Discusses habitat selection and the mortality sources for a settling larva]*

Thorson (1971)

The effects of salinity and grain size on benthic community structure

Boesch, D. F. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. Marine Biology *21*: 226-244. *[A variety of cluster analyses]*

Boesch, D. F. (1977b). *[Terborgh's zonal analysis applied to estuarine gradients in Chesapeake Bay and Australia. Ordination would have been better. Salinity controls community structure.] {?}*

Boesch et al. (1976a)

Boesch, D. F, M. L Wass, and R. W. Virnstein. 1976b. The dynamics of estuarine benthic communities. Pp. 177-196 *in* M. Wiley, ed. Estuarine processes. Academic Press, New York.

Carriker, M. R. 1967. Ecology of estuarine benthic invertebrates: A perspective. Pp. 442-487 *in* G. H. Lauff, ed., Estuaries, Publ. No. 83. AAAS, Washington D.C.

Dauer, D. M., T. L. Stokes, H. R. Barker, R. M. Ewing, and J. W. Sourbeer. 1984. Macrobenthic communities of the lower Chesapeake Bay. IV. Bay-wide transects and the inner continental shelf. Benthic studies of the lower Chesapeake Bay 7. Int. Revue ges. Hydrobiol. *69*: 1-22.

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Day, J. W., C. A. S. Hall, W. M. Kemp and A. Yanez-Arancibia. 1989. Estuarine Ecology. John Wiley and Sons, New York. *[Estuaries have lower species diversity than oceanic and oligotrophic lake ecosystems]*

Diaz, R. J. and L. J. Schaffner. 1990. The functional role of estuarine benthos. Pp. 25-56 in M Haire and E. C. Krome, eds., Perspectives on the Chesapeake Bay, 1990. Advances in estuarine sciences. Chesapeake Research Consortium, Gloucester Pt. Virginia. *[An excellent summary of the major communities, and their zonation by grain size and salinity]*

Etter, R. J. and J. F. Grassle. 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. Nature *360*: 576-578. *[Species diversity at 2100 m positively correlated with silt diversity]*

Ewing, R. M., D. M. Dauer. 1982. Macrobenthic communities of the lower Chesapeake Bay. I. Old Plantation Creek, Kings Creek, Cherrystone Inlet and the adjacent offshore area. Benthic studies of the lower Chesapeake Bay 4. Int. Revue ges. Hydrobiol. *67*: 777-791.

Gage, J. 1974. Shallow-water zonation of sea-loch benthos and its relation to hydrographic and other physical factors. J. Mar. Biol. Assoc. U. K. *54*: 223-249. *[Variation in salinity seems to limit the upper (vertical) range of quite a number of species. Cluster analysis of 1-mm sieved samples shows a break at 10 m in the 0 to 25-m transect. Salinity and temperature both important.* ***It is the variance in salinity, not the mean, that sets the limit****. The salinity-tolerant species include Nereis diversicolor, Pygospio elegans, Phallodrilus, Corophium volutator, H. ulvae, M. balthica,and Mya arenaria.]* {?}

Hampson, G. R. 1971. A species pair of the genus *Nucula* (Bivalvia) from the eastern coast of the United States. Proc. malcal. Soc. Lond. *39*: 333-342. *[Sanders' Nucula proxima, described for Long Island Sound* ***Sanders 1956*** *and Buzzards Bay* ***Sanders 1960****, consists of 2 species: N. annulata, found only in mud, and N. proxima, found predominately in sand.]*

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Sanders, H. L., P. C. Mangelsdorf, and G. R. Hampson. 1965. Salinity and faunal distribution in the Pocasset River, Massachusetts. Limnol. Oceanogr. *10*(Suppl.): R216-R228. *[Salinity has a profound effect on species composition]*

Schaffner, L. C., R. J. Diaz, C. R. Olsen and I. L. Larsen. 1987. Faunal characteristics and sediment accumulation processes in the James River estuary Virginia. Estuar. Coast. Shelf Sci. *25*: 211-226.

Snelgrove, P. V. R. and C. A. Butman. 1994. Animal-sediment relationships revisited: cause versus effect. Oceanography and Marine Biology: an Annual Review *32*: 111-177. *[Little evidence that grain size per se is a factor controlling macroinfaunal distributions. Evidence for trophic-group amensalism is weak. Causal factors affecting community structure that covary with grain size include hydrodynamic regime, larval supply, and food supply]*.

Tortellotte, G. H. and D. M. Dauer. 1983. Macrobenthic communities of the lower Chesapeake Bay. II. Lynnhaven Roads, Lynnhaven Bay, Broad Bay and Linkhorn Bay. Int. Rev. ges Hydrobiol. *68*: 59-72.

Warinner, J. E., and M. L. Brehmer. 1966. The effects of thermal effluents on marine organisms. Inter. J. Air Water Poll. *10*: 277-289.

Whitlatch, R. B. 1980. Patterns of resource utilization and coexistence in marine intertidal deposit-feeding communities. J. Mar. Res. *38*: 743-765. *[Shannon's diversity of sediment particles correlated with species diversity - see* ***Etter and Grassle 1992*** *for a deep-sea example]* {?}

Wulff, W. J. 1983. Estuarine benthos. Pp. 151-182 *in* B. H. Ketchum, ed., Estuaries and enclosed seas, ecosystems of the world 26. Elsevier Scientific Publishing Company, New York.

Other references on benthic community structure

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Buchanan, J. B., P. F. Kingston and M. Sheader. 1974. Long-term population trends of the benthic macrofauna in the offshore mud of the Northumberland coast. J. Mar. Biol. Ass. U.K. *54*: 785-795. *[One of the few long-term subtidal benthic data sets]*

Commito, J. A. and E. M. Boncavage. 1989. Suspension-feeders and coexisting infauna: an enhancement counterexample. J. exp. Mar. Biol. Ecol. *125*: 33-42. *[As Mytilus edulis abundances increased Tubificoides, an oligochaete increased as well]*

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Gray, J. S. 1977. The stability of benthic ecosystems. Helg. wiss. Meeresunters. *30*: 427-444.

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Lie, U. 1974. Distribution and structure of benthic assemblages in Puget Sound, Washington, U.S.A. Marine Biology *26*: 203-223. *[Includes ternary plots of community structure, which appears to fit the continuum model.]* {?}

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Lie, U. and J. C. Kelley. 1970. Benthic infauna communities off the coast of Washington and in Puget Sound: identification and distribution of the communities. J. Fish. Res. Bd. Can. *27*: 621-651. *[A study that clearly documents the effects of depth and grain size on shelf community structure. Communities distributed as discrete entities on the shelf, as continua in Puget Sound. Nichols M.Sc. work analyzed the species turnover on a Puget Sound transect]*{?}

Lie, U. and D. S. Kisker. 1970. Species composition and structure of benthic infauna communities off the coast of Washington. J. Fish. Res. Bd. Can. *27*: 2273-2285. *[Grain size and depth produce discrete communities]*{?}

Mills, E. L. 1980. The structure and dynamics of shelf and slope ecosystems off the north east coast of North America. p. 25-47 *In*: K. R. Tenore and B. C. Coull, Eds., Marine Benthic Dynamics. University of South Carolina Press.

Nichols, F. H. 1979. Benthic polychaete assemblages and their relationship to the sediment in Port Madison, Washington. Mar. Biol. *6*: 48-57. *[A paper from Fred Nichols' M.Sc. dissertation.]*

Reise, K. 1983. Biotic enrichment of intertidal sediments by experimental aggregates of the deposit-feeding bivalve *Macoma balthica*. Mar. Ecol. Prog. Ser. *12*: 229-236.

Rhoads, D. C. and D. K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. *28*: 150-178. *[Trophic group amensalism is proposed. Deposit feeders destabilize sediment which causes reduced abundances of suspension feeders]*{**10**}

Rhoads, D. C. and D. K. Young. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by *Molpadia oolitica* (Holothuroidea). Marine Biology *11:* 255-261. *[Molpadia, a holothuroid echinoderm, is a classic conveyor-belt species, whose fecal mounds are often colonized by other organisms, especially the suspension-feeding sabellid feather duster worm Euchone incolor]*{**10**}

Rhoads, D. C., P. L. McCall, and J. L. Yingst. 1978. Disturbance and production on the estuarine seafloor. American Scientist 66: 577-586. *[They extend Pearson & Rosenberg's (1976) paradigm of the effects of organic enrichment on community structure to the effects of disturbance. They apply the model to the New Haven dump site and* ***McCall's 1977*** *anoxic mud recolonization experiment]{**10**, **25**, **64**}*

Rhoads, D. C. and L. F. Boyer. 1982. The effect of marine benthos on physical properties of sediments: a successional perspective. Pp. 3-52 *in* P. L. McCall and J. Tevesz, *eds*, Animal-Sediment Interactions.*["We define primary succession as the predictable appearance of macrobenthic invertebrates belonging to specific functional types following a benthic disturbance. These invertebrates interact with sediment in specific ways. Because functional types are the biological units of interest for this study our definition does not demand a sequential appearance of particular invertebrate species or genera."]{**10**}*

Rice, D. L. and D. C. Rhoads. 1989. Early diagenesis of organic matter and the nutritional value of sediments. Pp. 59-97 *in* G. Lopez, G. Taghon and J. Levintion, *eds*. Ecology of marine deposit feeders. Springer-Verlag, New York. *[A superb paper and conceptual model showing how subsurface deposit feeders interact with labile organic matter in sediments]*{**12**}

Sutherland, J. P. 1974. Multiple stable points in natural communities. Amer. Natur. *108*: 859-873. *[The communities found at one time are more accidents of history and larval availability than deterministic ecological processes]*{?}

Thistle, D. 1981. Natural physical disturbances and communities of marine soft bottoms. Mar. Ecol. Prog. Ser. *6*: 223-228. [*Is it physical disturbance or organic enrichment that controls the pioneer stage of succession. Thistle thinks the latter]*

Trueblood, D. D., E. D. Gallagher, and D. M. Gould. 1994. Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. Limnol. Oceanogr. *39*: 1440-1454. *[Introduction of* ***CNESS****]* {**42**}

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology *58*: 1199-1217. *[One of the best caging studies in the literature, with a flaw in the ANOVA results noted by* ***Hurlbert***

(1984)] {**26**, **92**}

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Coull (1986)
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Holland, A. F., A. T. Schaughnessy, and M. H. Hiegel. 1987. Long-term variation in mesohaline Chesapeake Bay macrobenthos: spatial and temporal patterns. Estuaries *10*: 227-245.

Nichols (1985)

Nichols, F. H. 1988. Long-term changes in a deep Puget Sound benthic community: local or basin-wide? Pp. 65-71 *in* Proceedings of the 1st Annual Meeting on Puget Sound Research. Puget Sound Water Quality Authority, Olympia WA. *[Pectinaria, among the dominants in the 1960s had disappeared by the early 80s, leading* ***Nichols 1985*** *to conclude that organic enrichment had led to a Pearson-Rosenberg successional replacement. After* ***Nichols (1985)*** *published this conclusion, Pectinaria returned, leading Nichols to argue for long-term cycles]* {**64**, **66**}

Nichols, F. H. 2001. Is climate change a factor in observed interdecadal change in the deep Puget Sound benthos? Puget Sound Research Conference 2001 [pdf available online]{**64**, **66**}

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Pearson, T. H., G. Duncan, and J. Nuttall. 1986. Long term changes in the benthic communities of Loch Linnhe and Loch Eil (Scotland). Hydrobiologia *142*: 113-119.

Read, P. 1987. The intertidal benthos and sediments of particulate shores in the Firth of Forth, Scotland, with particular reference to waste water discharge. Proc. R. Soc. Edin. 93B: 401-413. *[Capitella the most abundant species near outfall. SAB curves used. Over 10 y of data described.]*

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Service, S. K. and R. J. Feller. 1992. Long-term trends of subtidal macrobenthos in North Inlet, South Carolina. Hydrobiologia *231*: 13-40.

Tunberg, B. G. and W. G. Nelson. 1998. Do climatic oscillations influence cyclical patterns of soft bottom macrobenthic communities on the Swedish west coast? Mar. Ecol. Prog. Ser. *170*: 170: 85-94. *[They fit OLS polynomial regressions to benthic macrofaunal abundance and tried to couple these patterns with the North Atlantic Oscillation]* [?]

Ziegelmeir, E. 1978. Macrobenthic investigations in the eastern part of the German Bight from 1950 to 1974. Rapp. P.-V. Reun. cons. In. Explor. Mer. 172: 432-444 *[Used by* ***Connell & Sousa (1983)*** *to assess long-term stability of benthic communities]*

Hard-substrate succession

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Chalmer, P. N. 1982. Settlement patterns of species in a marine fouling community and some mechanisms of succession. Oecologia *58*: 73-86.

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist *111*: 1119-1144. *[A classic review of three models of succession: facilitation, tolerance & inhibition]* [**27**, **28**, **34**, **61**, **68**]

Connell, J. H. and M. J. Keough. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. Pp. 125-151 *in* White and Pickett, eds. The Ecology of Natural Disturbance and Patch Dynamics.

Davis, A. N. and R. T. Wilce. 1987. Algal diversity in relation to physical disturbance: a mosaic of successional stages in subtidal cobble habitat. Mar. Ecol. Prog. Ser. *37*: 229-237.

Day, R. W. and R. W. Osman. 1981. Predation by *Patiria miniata* (Asteroidea) on bryozoans: prey diversity may depend on the mechanism of succession. Oecologia (Berlin) *51*: 300-309. *[A good discussion of the effects of predation on species diversity: "If an early colonizer facilitates the establishment of many later species, predation on the early colonizer should decrease diversity during succession. The effect of predators on diversity during succession would thus seem to depend on the mechanisms of succession as well as the selectivity of the predator and the relative abundance of the preferred prey.]*

Dean, T. A. 1977. Succession in a marine fouling community: changes in community structure and mechanisms of development. Oecologia *51*: 300-309.

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Dethier, M. N. 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. Ecological Monographs *54*: 99-118.

Duggins, D. O. 1981. Interspecific facilitation in a guild of benthic marine herbivores. Oecologia *48*: 157-163.

Farrell, T. M. 1989. Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. J. exp. Mar. Biol. Ecol. *128*: 57-73.

Farrell, T. M. 1991. Models and mechanisms of succession: an example from a rocky intertidal community. Ecol. Monogr. *61*: 95-113. *[An application of* ***Connell & Slatyer's (1977)*** *successional models. Direct and indirect effects are important]*

Greene, C. H. and A. Schoener. 1982. Succession on marine hard substrata: a fixed lottery. Oecologia (Berlin) *55*: 289-297. *[A Markov model is proposed but never applied to field data.]*

Greene, C. H., A. Schoener, and E. Corets. 1983. Succession on marine hard substrata: the adaptive significance of solitary and colonial strategies in temperate fouling communities. Mar. Ecol. Prog. Ser. *13*: 121-129.

Harris, L. G., A. W. Ebeling, D. R. Lauer, and R. J. Rowley. 1984. Community recovery after storm damage: a case of facilitation in primary succession. Science *224*: 1336-1338.

Levin, S. A. and R. T. Paine. 1974. Disturbance, patch formation, and community structure. Proc. Nat. Acad. Sci. *71*: 2744-2747. *[Introduction of a model described more fully by* ***Paine & Levin (1981)****. This is a mathematical realization of Watt's (****1947****,* ***1964****) spatial-temporal mosaic model of community structure]* {?}

Lewin, R. 1986. Supply-side ecology. Science *234*: 25-27. *[The popular science article that established the phrase — introduced by Roughgarden's research that larval supply strongly affects community structure]*

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Lubchenco, J. and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. *59*: 67-94. *[Predators can speed the rate of succession.]* {?}

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Menge, B. A. and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Amer. Natur. *130*: 730-757.

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Osman, R. W. 1977. The establishment and development of a marine epifuanal community. Ecological Monographs *47*: 37-63.

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Paine, R. T. and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs *51*: 145-178. *["A classic"]*{}

Paine, R. T., J. C. Castilla, and J. Cancino. 1985. Perturbation and recovery patterns of starfish dominated intertidal assemblages in Chile, New Zealand, and Washington State. Amer. Natur *125*: 679-691.

Quinn, J. F. 1979. Disturbance, predation, and diversity in the rocky intertidal zone. Ph.D. dissertation. University of Washington. *[Quinn's Ph.D. is one of the nicest expositions of Markov modelling of succession. He also describes manipulations of the Torch Bay, Alaska intertidal zone. None of this work has been published.]*

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Schoener, A. 1974. Experimental zoogeography: colonization of marine miniislands. American Naturalist *108*: 715-738.

Sebens, K. P. 198 . Community ecology of vertical rock walls in the Gulf of Maine, U.S.A.: small-scale processes and alternative community states. Pp. 346-372 *in* P. D. Moore and R. Seed, eds. The Ecology of Rocky Coasts.

Sebens, K. 1985. The ecology of the rocky subtidal zone. American Scientist *73*: 548-557. *[Examples from the New England subtidal (off Nahant)]*{?}

Simenstead, C. A., J. A. Estes, K. W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. Science *200*: 403-411.

Sousa, W. P. 1979a. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology *60*: 1225-1239. *[Disturbance is proportional to rollover frequency in boulders and smaller boulders roll more frequently. Diversity is lower on small and large boulders than on middle-sized boulders; on large boulders Gigartina, the competitive dominant takes over]*

Sousa, W. P. 1979b. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs *49*: 227-254.

Sousa, W. P. 1980. The responses of a community to disturbance: the importance of successional age and species' life histories. Oecologia (Berlin) *45*: 72-81.

Sousa, W. P. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology *65*: 1918-1935. *[Algae on rocks - rock overturning creates open patches]*

Sousa, W. P. 1984. The role of disturbance in natural communities. Ann. Rev. Ecol. Syst. *15*: 353-391.

Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pp. 101-124 *in* T. A. Pickett and P. S. White, eds., The ecology of natural disturbance and patch dynamics. Academic Press, Orlando Fl.{?}

Sousa, W. P. 2001. Natural disturbance and the dynamics of marine benthic communities. Pp. 85-130 in M. D. Bertness, S. D. Gaines and M. E. Hay, eds., Marine Community Ecology. Sinauer Assoc., Sunderland MA. 550 pp.

Sutherland, J. P. 1974. Multiple stable points in natural communities. Amer. Natur. *108*: 859-873. *[Communities on fouling panels placed in the field at different times reach different final states - no convergence and history important]* {?}

Sutherland, J. P. 1978. Functional roles of *Schizoporella* and *Styela* in the fouling community at Beaufort, N. Carolina. Ecology *59*: 257-269.

Sutherland, J. P. 1981. The fouling community at Beaufort, North Carolina: a study in stability. Amer. Natur. *118*: 499-519. *[The study that led to the concept of multiple stable equilibria]*

Sutherland, J. P. and R. H. Karlson. 1977. Development and stability of the fouling community of Beaufort, North Carolina. Ecol. Monogr. *47*: 425-446.

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Underwood, A. J. 2001. Supply-side ecology: the nature and consequences of variations in recruitment of intertidal organisms. Pp. 183-200 in M. D. Bertness, S. D. Gaines and M. E. Hay, eds., Marine Community Ecology. Sinauer Assoc., Sunderland MA. 550 pp.

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Vance, R. R. 1988. Ecological succession and the climax community on a marine subtidal rock wall. Mar. Ecol. Prog. Ser. *48*: 125-136.

Whittaker, R. H. and S. A. Levin. 1977. The role of mosaic phenomena in natural communities. Theor. Pop. Biol. *12*: 117-139.

Species diversity

Biodiversity, broadly defined

National Research Council 1995. Understanding marine biodiversity: a research agenda for the nation. National Academy Press, Washington D.C. 114 pp. [?]

Norse, E. A., K.L. Rosenbaum, D. S. Wilcowe, B. A. Wilcox, W. H. Romme, D. W. Johnston, and M. L. Stout. 1986. Conserving biological diversity in our national forests. The Wilderness Society, Washington, DC. {?}

Orians, G. 1997. Global biodiversity I. Pp. 87-121 in Principles of Conservation Biology, 2nd Edition. Sinauer Associates, Sunderland MA.[Provides a comprehensive definition of biodiversity, much broader than **Hubbell (2001)**]{?}

Components of diversity: α, β, γ *[and* ω*]*

ter Braak, C. J. J. 1983. Principal components biplots and α and beta diversity. Ecology *64*: 454-462. *[A superb paper. Simpson's diversity* ($\Sigma i=1:S\ x_i^2$)*, an α-diversity measure, is inversely related to PCA axis 1 in an uncentered PCA, β diversity is displayed in the 2nd and higher dimensions. Cited by Eric Smith]*

Cody, M. L. 1975. Towards a theory of continental species diversity: bird distributions over Mediterranean habitat gradients. Pp. 214-257 *in* M. L. Cody and J. M. Diamond, eds., Belknap Press, Cambridge. *[Analyzes the species addition and loss in Chile, California and Africa as a function of a habitat gradient, based on foliage height and ½-height. A and Beta diversity are discussed]* {?}

Cody, M. L. 1986. Diversity, rarity, and conservation in Mediterranean-climate regions. Pp. 122-152 *in* M. E. Soule, *ed.*, Conservation Biology: the science of scarcity and diversity. Sinauer Associates, Sunderland MA. *[See his Fig. 1 for a somewhat confusing graphical display of the components of diversity]* [**37**]

Cody, M. L. 1989. Structure and assembly of communities. Pp. 227-241 *in* J. Roughgarden, R. M. May, and S. A. Levin, eds., Perspectives in Ecological Theory. Princeton University Press, Princeton.

Cody, M. L. 1993. Bird diversity components within and between habitats in Australia. Pp. 147-158 *in* R. E. Ricklefs and D. Schluter, eds., Species diversity in ecological communities. University of Chicago Press, Chicago.{?}

Dodson, S. 1992. Predicting zooplankton species richness. Limnol. Oceanogr. 37: 848-856. *[Data from 66 North American lakes is used in a regression model to predict species richness as a function of lake size, primary production and number of nearby lakes. N. American species richness is much less than in European lakes.]*

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 Publication 98-1. *[Describes the alpha, beta and gamma diversity of benthic communities. Both R- and Q-mode clustering of Boston Harbor communities with CNESS]*{**22**}

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge. *[Page 100 contains a description of Whittaker and Gauch's original formulation of α and β diversity. This is quite different from Cody's reformulation of the concept]* [?]

McIntosh, R. P. 1967. An index of diversity and the relation of certain concepts to diversity. Ecology *48*: 392-404. *[The geometry of diversity is discussed; this index is discussed by **Pielou (1969)** and **Washington (1984)**]*

Noy-Meir, I. and R. H. Whittaker. 1977. Continuous multivariate methods in community analysis: some problems and developments. Vegetatio *33*: 79-98. *[β diversity cannot be measured until the underlying structure of the data has been recovered successfully: "The conclusion is that some linear ordination techniques can be used for defining coenoclines in samples with beta-diversity of 4-5 HC or less. In real vegetation samples sets beta-diversity is difficult to measure until the data have been successfully ordinated. However, a prior estimate could be obtained by considering the distribution of between-site similarity values, and in particular the proportion of zero values]*{**37**}

Sepkoski, J. J. 1988. Alpha, beta or gamma: where does all the diversity go? Paleobiology *14*: 221-234. *[Sepkoski analyzes species richness from the Cambrian (600+MYA through the Paleozoic 250 MYA. He divides marine benthic communities into 6 zones, corresponding to distances from nearshore to off the shelf break. In the Ordovician period, ≈440-510 MYA, global benthic diversity increased 300%. Alpha diversity increased only about 70%, Beta diversity, calculated using the inverse of Jaccard's index could account for about a doubling of diversity. Gamma diversity, the degree of endemism or provinciality couldn't account for the difference which might be due to species-rich reef communities developing during this period.]*

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 279-338. *[Beta or between-habitat diversity refers to the ...degree of contrast in species composition among samples of a set taken from a landscape.]{?}*

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biological Reviews *42*: 207-264. *[Definitions of beta diversity]* [**37**]

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251. *[Cited by **Cody 1975**, **Sepkoski 1988**]*

Whittaker (1975)

Whittaker, R. H. 1977. Evolution of species diversity in land communities. Evolutionary Biology *10*: 1-67.

Deep-sea diversity and succession

Theories of deep-sea diversity maintenance

Abele, L. G. and K. Walters. 1979a. Marine benthic diversity: a critique and alternative explanation. J. Biogeography *6*: 115-126. *[Applied **MacArthur & Wilson's (1967)** Theory of Island biogeography: large area=more species]*

Abele, L. G. and K. Walters. 1979b. The stability-time hypothesis: reevaluation of the data. Amer. Natur. *114*: 559-568.

Carney, R. S. 1989. Examining relationships between organic carbon flux and deep-sea deposit feeding. Pp. 24-58 *in* G. Lopez, G. Taghon and J. Levinton, *eds.*, Ecology of Marine Deposit Feeders. Springer-Verlag, New York. 322 pp. *[He proposes a variety of the tropical rainforest refuge hypothesis (Haeffer 1969) - diversity is highest on the slope because of long-term variations in detrital flux to the deep-sea leading to the geographic expansion and contraction of the lower slope-rise fauna onto the abyssal plains]*

Carney, R. S. 1997. Basing conservation policies for the deep-sea floor on current-diversity concepts: a consideration of rarity. Biodiversity and Conservation 6: 1463-1485. *[Analyzes the frequency of singletons in deep-sea samples off the Texas shelf and reviews the history of deep-sea diversity hypotheses]*

Coull, B. C. 1972. Species diversity and faunal affinities of meiobenthic Copepoda in the deep sea. Marine Biology *14*: 48-51.

Dayton, P. K and R. R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep sea. Deep-Sea Res *19*: 199-208. *[Disturbance and predation in the form of the 'cropper hypothesis' is proposed as an alternative to* ***Sanders' (1968)*** *Stability-time hypothesis. See the rebuttal by* ***Grassle & Sanders (1973)****]*

Desbruyeres, D., J. Y. Bervas, A. Khripounoff. 1980. Un cas de colonisation rapide d'un se'diment profund. Oceanological Acta *3*: 285-291. *[One of the early papers showing that deep-sea colonization can be rapid—* ***Grassle (1977)*** *had found slow recolonization into trays to support the temporal-mosaic theory]*

Gage, J. D. 1977. Structure of the abyssal macrobenthic community in the Rockall Trough. Pp. 247-260 *in* B. E. Keegan, P. O. Ceidigh and P. J. S. Boaden, Eds., Biology of Benthic Organisms. Pergamon Press, Oxford.

Gage, J. D. 1985. The analysis of population dynamics in deep-sea benthos. Pp. 201-212 *in* P. E. Gibbs, *ed.*, 19th Eur. Mar. Biol. Symp. Proc. Cambridge Univ. Press, Cambridge.

Gage, J. D. and P. A. Tyler. 1991. Deep-sea biology. Cambridge Univ. Press, New York.

Grassle, J. F. 1977. Slow recolonisation of deep-sea sediment. Nature *265*: 618-619. *[The infauna in recolonization trays is different from the surrounding community for long periods of time]* [**33**, **63**, **72**]

Grassle, J. F. 1978. Diversity and population dynamics of benthic organisms. Oceanus *21*: 42-49. *[Introduction of the temporal spatial mosaic theory of deep-sea community structure]* {**33**, **35**, **36**}

Grassle, J. F. 1986. The ecology of deep-sea hydrothermal vent communities. Adv. Mar. Biol. 23: 301-362.

Grassle, J. F. 1989. Species diversity in deep-sea communities. Trends in Ecology and Evolution *4*: 12-15. *[A brief review of the major ideas, stressing spatial and temporal variability. "Small-scale disturbance resulting from the activities of organisms and material settling from the water column produces a mosaic of disequilibrium populations" Some areas of the deep sea have low diversity: trenches, upwelling & low DO areas, High latitude areas (Norwegian sea), high energy areas (HEBBLE), hydrothermal vents]* {**31**}

Grassle, J. F. 1991. Deep-sea benthic biodiversity. BioScience 41: 464-469. *[Estimates of the number of deep-sea species]*

Grassle, J. F. and H. L. Sanders. 1973. Life history and the role of disturbance. Deep Sea Res. *20*: 643-659. *[A rebuttal to* ***Dayton & Hessler (1972)****]*

Grassle, J. F., H. L. Sanders, R. R. Hessler, G. T. Rowe and T. McLellan. 1975. Pattern and zonation: a study of bathyal megafauna using the research submersible Alvin. Deep-Sea Res. *22*: 457-481.

Grassle, J. F. and L. S. Morse-Porteus. 1987. Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities. Deep-Sea Res. *34*: 1911-1950.

Hessler, R. R. and H. L. Sanders. 1967. Faunal diversity in the deep sea. Deep-Sea Res. *14*: 65-78. *[The first major description of high deep-sea diversity, covered in more depth in* ***Sanders (1968)*** *who provided the stability-time hypothesis to explain the patterns.]* {**5**, **31**}

Hessler, R. R. and P. A. Jumars. 1974. Abyssal community analysis from replicate box cores in the central North Pacific. Deep-Sea res. *21*: 185-209. *[The first use of the 0.25 m^2 box corer]* {?}

Huston, M. 1979. A general hypothesis of species diversity. Amer. Natur. *113*: 81-101.

Josefson, A. B. 1986. Temporal heterogeneity in deep-water soft-sediment benthos-an attempt to reveal structure. Est. Coastal Shelf Sci. *23*: 147-169. *[Looked at correlation of species in time at a 100-m and 300-m site]*

Jumars, P. A. 1975a. Methods for measurement of community structure in deep-sea macrobenthos. Marine Biology *30*: 245-252. *[Introduction of the heterogeneity χ-square statistic & vegematic box core to benthic ecology]* {**14**, **32**}

Jumars, P. A. 1975b. Environmental grain and polychaete species diversity in a bathyal benthic community. Marine Biology *30*: 253-266.*[Describes non-random spatial patterns at the 10cm x 10 cm scale using the 0.25-m^{-2} box corer with Vegematic-like partions] {**32**}*

Jumars, P. A. 1976. Deep-sea species diversity: Does it have a characteristic scale? J. Mar. Res. *34*: 217-246. *[Heterogeneity at all spatial scales]* {**32**}

Jumars, P. A. 1978. Spatial autocorrelation with RUM (remote underwater manipulator): vertical and horizontal structure of a bathyal benthic community. Deep-Sea Res. *25*: 589-604.

Jumars, P. A. 1981. Limits in predicting and detecting benthic community responses to manganese nodule mining. Marine Mining *3*: 213-229. *[Includes a power analysis indicating large numbers of box cores required to detect catastrophic changes in individual populations]*

Jumars, P. A. and R. R. Hessler. 1976. Hadal community structure: implications from the Aleutian Trench. J. Mar. Res. *34*: 547-560.

Jumars, P. A. and J. E. Eckman. 1980. Spatial structure of deep-sea benthic communities. *In*: G. T. Rowe, Ed., The Sea. Vol. 8. Deep-Sea Biology. Wiley Interscience, N.Y. *[A thorough review of spatial statistics and patterns found in Jumars' Ph.D. work and his RUM sampling]* {?}

Jumars & Gallagher (1982)

Killingsley, J. S. and M. A. Rex. 1985. Mode of larval development in some deep-sea gastropods indicated by oxygen-18 ratios of their carbonate shells. Deep-Sea Res. *32*: 805-818. *[Planktotrophic larval development in warm surface waters. The $\delta^{18}O$ ratio difference between the larval and adult shells is much higher in deep-sea gastropods with planktotrophic development. **Rex & Warén (1982)** had previously noted the high wide dispersal of planktotrophic deep-sea gastropods.]{}*

Lampitt, R. S., D. S. M. Billett and A. L. Rice. 1986. Biomass of invertebrates megabenthos from 500 to 4100 m in the northeast Atlantic Ocean. Marine Biology *93*: 69-81.

Levin, L. A. and C. R. Smith. 1984. Response of background fauna to disturbance and enrichment in the deep-sea: a sediment tray experiment. Deep-Sea Res. *31*: 1277-1285.

Levin, L. A., R. J. Etter, M. A. Rex, A. J. Gooday, C. R. Smith, J. Pineda, C. T. Stuart, R. R. Hessler and D. Pawson. 2001. Environmental influences on regional deep-sea diversity. Ann. Rev. Ecol. Syst.. *32*: 51-93.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Amer. Natur. *110*: 351-369.

Osman, R. W. and R. B. Whitlatch. 1978. Patterns of species diversity -fact or artifact. Paleobiology *4*: 41-54. *[They propose several explanations for deep sea diversity, including that the deep-sea has a long term greater value of spceciation-extinction rates compared to shallow water and the **MacArthur & Wilson's (1967)** Island biogeographic explanation: larger habitat islands allow for more species. The island biogeographic argument that the more area, the higher the species diversity was refuted by Rex (1979) because diversity peaks at rise depths]{**34**}*

Rex, M. A. 1973. Deep-sea species diversity: decreased gastropod diversity at abyssal depths. Science *181*: 1051-1053. *[First documentation of the parabolic diversity with depth curve]*

Rex, M. A. 1976. Biological accommodation in the deep-sea benthos: comparative evidence on the importance of predation and productivity. Deep-Sea Res. *23*: 975-987. *[Proposes that high deep-sea diversity at intermediate depths due to both competition and predation, mediated by low productivity. **Huston (1979)** provides one model for this type of process based on the Lotka-Volterra competition equations]*

Rex, M. A. 1977. Zonation in deep-sea gastropods: the importance of biological interactions to rates of zonation. pp. - *In*: B. F. Keegan, P. O. Ceidigh and P. J. S. Boaden (eds.), Biology of Benthic Organisms. Pergamon Press, New York.{?}

Rex, M. A. 1981. Community structure in the deep-sea benthos. Ann. Rev. Ecol. Syst. *12*: 331-353.{**25**}

Rex, M. A. 1983. Geographic patterns of species diversity in deep-sea benthos. Pp. 453-472 *in* G. T. Rowe, Ed., Deep-Sea Biology, The Sea, Vol. 8. *[Reviews theories of diversity, the parabolic patterns of diversity with depth and discusses factors that might account for depth-related patterns: organic carbon input]*

Rex, M. A., R. J. Etter, and P. W. Nimeskern. 1990. Density estimates for deep-sea gastropod assemblages. Deep-Sea Res. *37*: 555-569.

Rex, M. A., C. T. Stuart, R. R. Hessler, J. A. Allen, H. L. Sanders and G. D. F. Wilson. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. Nature *365*: 636-639.{?}

Rex, M. A., C. T. Stuart, and G. Coyne. 2000. Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. Proc. Nat. Acad. Sci. 97: 4082-4085. *[Bivalves, gastropods and isopods show decreases in species richness and evenness from the equator to the poles in the N. Atlantic using species number, Shannon's H' and Pielou's evenness (J)]* {?}

Rex, M. A., C. R. McClain, N. A. Johson, R. J. Etter, J. A. Allen, P. Bouchet and A. Warén. 2005. A source-sink hypothesis for abyssal biodiversity. Amer. Natur. *165*: 163-178. {?}

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. Amer. Natur. *102*: 243-282. *[The classic paper, the most important ever in benthic ecology, that proposed and explanation for high deep-sea diversity, the stability-time hypothesis, and introduced the rarefaction method]*{**5**, **18**, **31**, **72**, **80**, **81**, **82**, **83**, **91**}

Sanders, H. L. 1969. Benthic marine diversity and the stability-time hypothesis. Brookhaven Symp. Biol. *22*: 71-80. [Data reanalyzed by **May (1975)** who fit them to **Fisher et al.'s (1943)** logseries] {**82**}

Shirayama, Y. and M. Horkoshi. 1989. Comparison of the benthic size structure between sublittoral upper-slope and deep-sea areas of the Western Pacific. Int. Revue ges. Hydrobiol. *74*: 1-13. *[Size is inversely proportional to depth]*

Smith, C. R. 1985. Food for the deep sea: utilization, dispersal and flux of nekton falls of the Santa Catalina Basin floor. Deep-Sea Res. *32*: 417-422.

Smith, C. R. 1986. Nekton falls, low-intensity disturbance and community structure of infaunal benthos in the deep sea. J. Mar. Res. *44*: 567-600.

Smith, C. R., P. A. Jumars and D. J. DeMaster. 1986. *In situ* studies of megafuanal mounds indicate rapid sediment turnover and community response at the deep-sea floor. Nature *323*: 251-253.

Smith, C. R. and R. R. Hessler. 1987. Colonization and succession in deep-sea ecosystems. Trends in Evolution and Ecology *2*: 359-363.

Smith, C. R., H. Kukert, R. A. Wheatcroft, P. A. Jumars and J. W. Deming. 1989. Vent fauna on whale remains. Nature 341: 27-28.

Snelgrove, P. V. R, J. F. Grassle and R. F. Petrecca. 1994. Macrofaunal response to artificial enrichments and depressions in a deep-sea habitat. J. Mar. Res. *52*: 345-369.

Snelgrove, P. V. R. and C. R. Smith. 2002. A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. Oceanography and Marine Biology: an annual review 40: 311-342. *[A nice review of theories of deep-sea diversity, especially the temporal mosaic model]*

Sverdrup, H. U., M. W. Johnson, and R. H. Fleming. 1942. The Oceans: their physics, chemistry, and general biology. Prentice-Hall. 1087 p. *[Contains a description of the fauna dredeged during the Challenger expedition] {**31**}*

Thiel, H. 1975. The size structure of the deep-sea benthos. Int. Revue ges. Hydrobiol. *60*: 575-606.

Thistle, D. 1979. Harpacticoid copepods and biogenic structures: implications for deep-sea diversity maintenance. Pp. 217-231 *in* R. J. Livingston, *ed.*, Ecological Processes in coastal and marine systems. Plenum Press, New York. *[Harps hang around polychaete tubes (mud balls)]*

Thistle, D. 1979. Deep-sea harpacticoid copepod diversity maintenance: the role of polychaetes. Marine Biology *52*: 371-376.

Thistle, D. 1983a. The role of biologically produced habitat heterogeneity in deep-sea diversity maintenance. Deep-Sea Res. *30*: 1235- .

Thistle, D. 1983b. The stability-time hypothesis as a predictor of diversity in deep-sea soft-bottom communities: a test. Deep-Sea Res. *30*: 267-277. *[Thistle compares the harpacticoid copepod species diversity from the unstable Scotian rise region, sampled as part of the HEBBLE project and known to be disturbed by storms, with the stable San Diego Trough community. Both sites are similar in rarefied diversity. Sanders never liked this test, arguing that one needed to compare the macrofauna. In fact, Yingst found that the macrofaunal diversity was quite low at the HEBBLE site]*{**36**}

Thistle, D. and J. E. Eckman. 1990. The effect of a biologically produced structure on the benthic copepods of a deep-sea site. Deep-Sea Res. 37: 541-554.

Tietjen, J. H. 1976. Distribution and species diversity of deep-sea nematodes off North Carolina. Deep-Sea Res. *23*: 755-768.

Turner, R. D. 1973. Wood-boring bivalves, opportunistic species in the deep sea. Science *180*: 1377-1379.

Wilson, G. D. F. and R. R. Hessler. 1987. Speciation in the deep sea. Ann. Rev. Ecol. Syst. *18*: 185-207.

Latitudinal diversity gradients

Buzas, M. A., L. S. Collins, and S. J. Culver. 2002. Latitudinal difference in biodiversity caused by higher tropical rate of increase. Proc.Natl. Acad. Sci. USA *99*: 7841–7843. *[Fossil foram diversity, measured with Fisher's α, was higher in the tropics 10 million years ago, but increased more in the tropics, making the latitudinal gradient steeper.alpha at temperate latitudes increased 1.4 times whereas in the tropics it increased 2.1 times] {?}*

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405: 220-227. *["To a first approximation, the distribution of biodiversity across the Earth can be described in terms of a relatively small number of broad-scale spatial patterns. Although these patterns are increasingly well documented, understanding why they exist constitutes one of the most significant intellectual challenges to ecologists and biogeographers. Theory is, however, developing rapidly, improving in its internal consistency, and more readily subjected to empirical challenge...More than 25 different mechanisms have been suggested for generating systematic latitudinal variation in these processes (Brown et al. 1998), commonly emphasizing reasons as to why the tropics are highly speciose (although there is no a priori expectation that either tropical or temperate zones in any sense represent an 'unusual' condition12). These include explanations based on chance, historical perturbation, environmental stability, habitat heterogeneity, productivity and interspecific interactions."]{?}*

Grassle (1989)

Lambshead P.J.D., J. Tietjen, T. Ferrero, and P. Jensen. 2000. Latitudinal diversity gradients in the deep-sea with special reference to North Atlantic nematodes. Mar. Ecol. Prog. Ser. *194*: 159–167.

Lambshead, P. J. D., C. J. Brown, T. J. Ferrero, J. Nicola Mitchell, C. R. Smith, L. E. Hawkins, and J. Tietjen. 2002. Latitudinal diversity patterns for deep-sea marine nematodes and organic fluxes – a test from the central equatorial Pacific. Mar. Ecol. Prog. Ser. *236*: 129–135.

Lambshead, P. J. D., C. J. Brown, T. J. Ferrero, L. E. Hawkins, C. R. Smith, and J. Nicola Mitchell. 2003. Biodiversity of nematode assemblages from the region of the Clarion-Clipperton Fracture Zone, an area of commercial mining interest. BMC Ecology 3: 1-12. *[Nematode diversity is analyzed at a 5-station meridional transect from equator to 23ºN, an area with 4-fold decrease om in organic matter flux from the equator to 9ºN. Colwell's EstimateS used to estimate species richness, which declines about 2 times from the productive equatorial zone (0º, 2º, 5º to lower productivity latitudes (9º & 23º)]{?}*

Osman, R. W. and T. A. Dean. 1987. Intra- and interregional comparison of number of species on marine hart substrate islands. Journal of Biogeography *14*: 53-67. *[Local species richness is perhaps the most important variable controlling number of species on a panel, along with panel size. Regional history can't be ignored — a conclusion also reached by **Ricklefs 1987**. See also **Witman et al. 2004**]* {?}

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of the concepts. Am. Natur. *100*: 33-46.

Rex et al. (1993)
Rex et al. (2000)

Roy, K., Jablonski, D and Valentine, J.W. (1994). Eastern Pacific molluscan provinces and latitudinal diversity gradient: No evidence for "Rapoport's Rule". Proc. National Academy of Sciences, USA *91*: 8871-8874.

Roy, K., D. Jablonski, J. W. Valentine and G. Rosenberg 1998. Marine latitudinal diversity gradients: Tests of causal hypotheses. Proc.Natl. Acad. Sci. USA *95*: 3699-3702. *[Striking unimodal gradients in gastropod snail diversity on continental shelves, similar on Atlantic & Pacific coasts. Strong linear increase with temperature but not with shelf area or apparent geologic history] {**76**}*

Smith C. R., W. Berelson, D. J. Demaster, F. C. Dobbs, D. Hammond, D. J. Hoover, R. H. Pope, and M. Stephens. 1997. Latitudinal variations in benthic processes in the abyssal equatorial Pacific: Control by biogenic particle flux. Deep Sea Res *44*: 2295–2317.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. Amer. Natur. *133*: 240-256. *[Low diversity in high latitudes since species have broad geographic ranges. Tested for prosobranch bivalves on shelves by **Roy et al. 1998** & rejected]*

Witman, J. D., Ron J. Etter, and F. Smith. 2004. The relationship between regional and local species diversity in marine benthic communities: A global perspective. Proc. Natl. Acad. Sci. USA *101*: 15664-15660. *["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.']{**48**, **76**}*

Explanations for patterns of diversity (e.g., intermediate disturbance hypothesis)

Abele, L. G. and K. Walters. 1979. The stability-time hypothesis: reevaluation of the data. Amer. Natur. *114*: 559-568.

Birch, D. W. 1981. Dominance in marine ecosystems. Am. Nat. *118*: 262-272.

Brooks, J. L. and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science *150:* 28-35. *[In explaining changes in the size structure of New England lakes after the introduction of fish, proposed that intermediate levels of fish predation permits the coexistence of competing zooplankton with reduced diversity at lower & higher levels of predation, This paper described the role of top predator in enhancing the diversity of competitors before **Paine (1966)**. It even proposed an intermediate peak in diversity] {**78**}*

Brown, J. H. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. Am. Zool. *21*: 877-888.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. Amer. Natur. *124*: 255-279.

Cody (1975)

Collins, S. L. S. M. Glenn, and D. J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology *76*: 486-492. *[The former model predicts an intermediate peak in diversity after disturbance, the latter a monotonic decline. Neither strictly fits these experimental data]* {**77**}

Condit, R., S. P. Hubbell, and R. B. Foster. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a Neotropical forest. Amer. Natur. *140*: 261-286.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pp. 460-490 *in* M. L. Cody and J. M. Diamond, *eds*., Ecology and Evolution of Communities. Belknap Press. *[Discussion of the intermediate-disturbance hypothesis and emphasis on predation and disturbance controlling community structure]{**26**}*

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science *199*: 1302-1310. *[The intermediate disturbance hypothesis applied to these ecosystems]* {**78**}

Connell, J. H. 1979. Tropical rain forests and coral reefs as open non-equilibrium systems. Pp. 141-163 *in* R. M. Anderson, B. D. Turner, L. R. Taylor, eds. Population Dynamics. Blackwell, Oxford. {?}

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos *35*: 131-138.{?}

Connell, J. H., J. G. Tracey and L. J. Webb. 1984. Compensatory recruitment, growth and mortality as factors maintaining forest tree diversity. Ecol. Monogr. *54*: 141-164. *[Compensatory recruitment hypothesis: conspecifics compete more, therefore higher diversity. Not much evidence for this hypothesis found]*

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. *41*: 351-389. *[A major paper showing that disturbance produces higher diversity, analogous to Paine's predation, and documented the decrease in diversity at high disturbance levels]* {**25**, **27**}

Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. *45*: 137-159 {**25**}

Dayton, P. K. 1981. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. *41*: 351-389. *[Diversity often declines at high levels of disturbance, e.g., log battering in the Pacific Northwest intertidal]*

Death, R. G. and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. Ecology *76*: 1446-1460. *[An explicit analysis of **Huston's (1979)** dynamic equilibrium model. Huston's model is contrasted with Hildrew & Townsend's (1987) model relating disturbance to diversity. Neither model fits these data. Number of species declines linearly with instability/disturbance {see **Collins et al. 1995** for a similar analysis}]* {**80**}

Dodson, S. 1992. Predicting crustacean zooplankton species richness. Limnol. Oceanogr. *37*: 848-856. *[Reviews **MacArthur & Wilson's (1967)**, Island biogeography. Regresses log species no. vs area, R^2=0.57, other variables: depth log mean depth, log distance to nearest lake, log # lakes within 20 km.]*

Fox, J. F. 1979. Intermediate-disturbance hypothesis. Science *204*: 1344-1345.

Gilinsky, N. L. and R. K. Bambach. 1986. The evolutionary bootstrap: a new approach to the study of taxonomic diversity. Paleobiology *12*: 251-268.

Hughes, R. G. 1984. A model of the structure and dynamics of benthic marine invertebrate communities. Mar. Ecol. Prog. Ser. *15*: 1-11. *[A dynamic model to explain patterns of benthic diversity. Species recruit from an external pool and the first can increase rapidly. Gregarious settlement can lead to exponential growth. The carrying capacity fills, and disturbances create new gaps. The model yields dominance-diversity curves different from either the log-normal or log-series but similar to real soft-bottom benthic data.]*

Hughes, R. G. 1986. Theories and models of species abundance. Amer. Natur. *128*: 879-899. *[Hughes' dynamic model, which produces a modified log series (the abundant species are more abundant than log-series), fits species abundance data better than either* ***Fisher et al.'s (1943)*** *log-series or* ***Preston's (1948)*** *canonical log-normal.]* [**81**, **85**, **86**]

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. *113*: 81-101. *[A Lotka-Volterra competition model is used to show that species diversity peaks at intermediate levels of disturbance and production. At high production levels, the dominant competitor excludes the others. With lower production, the growth rate of the dominant competitor, and all other species is slowed. Huston's model has emerged as the leading explanation of patterns of high deep-sea diversity]* {**77**}

Lake, P. S. 1990. Disturbing hard and soft-bottom communities: a comparison of marine and freshwater environments. Aust. J. Ecology *15*: 477-488.

Loucks, O. 1979. Evolution of diversity, efficiency and community stability. American Zoologist *10*: 17-25.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton. *[A good book describing the major diversity indices, faunal similarity indices and species-abundance distributions (geometric, log-series, log-normal). The book is strongly influenced by* ***May (1975)****]* {?}

May (1975)

May, R. M. 1986. The search for patterns in the balance of nature: advances and retreats. Ecology *67*: 1115-1126. *[Summarizes* ***Sugihara's (1980)*** *findings on the canonical log-normal: the canonical log-normal is more than a consequence of chance acting on a multiplicative process]*

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Amer. Natur. *110*: 351-369. *[Model supplanted by Menge & Sutherland 1987]*

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Amer. Natur. *130*: 730-757.

Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. Amer. Natur. *120*: 533-536.

Molles, M. C. 1978. Fish species diversity on model and natural reef patches: experimental insular biography. Ecol. Monogr. *48*: 289-305.

Osman & Whitlatach (1978)
Osman & Dean (1987)

Pacala, S. W. and M. J. Crawley. 1992. Herbivores and plant diversity. Amer. Natur. *140*: 243-260.

Pagel, M. D., R. M. May and A. R. Collie. 1991. Ecological aspects of the geographical distribution and diversity of mammalian species. Amer. Natur. *137*: 791-815.

Paine, R. T. 1966. Food web complexity and species diversity. Amer. Natur. *100*: 493-532. *[Increased predation leads to increased diversity. Later modified by* ***Connell (1978)*** *to the intermediate disturbance hypothesis. Note that* ***Brooks & Dodson (1965)*** *proposed a similar peak in (zooplankton) diversity at intermediate levels of (fish) predation.]*

Paine, R. T., 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory., The Changing Scenes in the Natural Sciences, Philadelphia, Academy of Natural Sciences, p. 245-270. {**26**}

Paine, R. T. 1994. Marine rocky shores and community ecology: an experimentalist's perspective. Ecology Institute. Oldendorf/Luhe, Germany.

Peterson, C. H. 1979a. The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. Oecologia *39*: 1-24.

Peterson, C. H. 1979b. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. Pp. 233-264 *in* R. J. Livingston, ed., Ecological processes in coastal and marine systems. Plenum Press, New York. *[A review of caging studies. He argues that they produce experimental artefacts, but nevertheless diversity tends to increase as predation declines in shallow benthic systems. This was particularly true of Young & Young's (1975) study, but Young, Buzas, and Young argued that the cage produced higher abundances of small epifaunal predators]*

Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. Quart. Rev. Bio. *64*: 393-418.

Pielou, E. C. 1966. Species diversity and pattern diversity in the study of ecological succession. J. theor. Biol. *10*: 370-383. *[Introduction of Pielou's J']*

Pielou, E. C. 1975. Ecological diversity. Wiley, New York. *[The best book written on the subject]*

Pimm, S. L. 1986. Community structure and stability. Pp. 309-329 *in* M. E. Soule, *ed*., Conservation Biology: the science of scarcity and diversity. Sinauer Associates, Sunderland MA.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. Amer. Natur. *132*: 652-661. *[mass effect, cited by* ***Rosenzweig 1995****]*

Reynolds, C. S., J. Padsiak, and U. Sommer. 1993. Intermediate disturbance in the ecology of phytoplankton and the maintenance of species diversity: a synthesis. Hydrobiologia *249*: 183-188.

Ricklefs, R. E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. Amer. Natur. *111*: 376-381.

Ricklefs, R. E. 1987. Community diversity: relative role of local and regional processes. Science *235*: 167-171. *[A very important paper pointing out that history and biogeography and the local species pool are often major determinants of local species diversity]*

Ricklefs, R. E. 1989. Speciation and diversity: the integration of local and regional processes. P. 599-622 *in* D. Otte and J. A. Endler, eds. Speciation and its consequences. Sinauer Assoc. Sunderland, MA.

Ricklefs, R. E. and D. Schluter, eds. 1993. Species diversity in ecological communities: historical factors and geographical perspectives. U. Chicago Press, Chicago Ill. *[Reviewed by Wilbur Ecology 76: 319.]*

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge. [Quite a good and interesting book, providing a nice overview of diversity, especially **MacArthur & Wilson (1967)**] {**79**, **81**}

Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. Amer. Natur. *111*: 337-359. *[The lottery model.]*{**29**}

Sanders (1968)

Schoener, T. W. and D. A. Spiller. 1987. Effect of lizards on spider populations: manipulative reconstruction of a natural experiments. Science *236*: 949-952. *[Predator removal leads to increased? spider diversity]*

Schupp, E. W. 1992. The Janzen-Connell model for tropical tree diversity: population implications and the importance of spatial scale Amer. Natur. *140*: 526-530.

Sebens, K. P. 1987. Competition for space: effects of disturbance and indeterminate competitive success. Theor. Pop. Biol *32*: 430-441

Sebens, K. P. and B. L. Thone. 1985. Coexistence of clones, clonal diversity and the effects of disturbance. Pp. 357-398 in JBC Jackson, LW Buss and RE Cook, eds., Population biology and evolution of clonal organisms. Yale University Press

Shmida, A. and S. Ellner. 1984. Coexistence of plant species with similar niches. Vegetatio 58: 29-55. *[mass effect]*

Shmida, A. and M. V. Whittaker. 1981. Pattern and biological microsite effects in two shrub communities, southern California. Ecology *62*: 234-251. *[mass effect]*

Shmida, A. and M. V. Wilson. 1985. Biological determinants of species diversity. J. Biogeography *12*: 1-20. *[mass effect]*

Slobodkin, L. B. and H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. Pp. 82-95 *in* Diversity and Stability in Ecological Systems. Brookhaven symposium in Biology No. 22. NTIS, Sprinfield VA.[Test of **Sanders (1968)** stability-time hypothesis]{**80**}

Snelgrove, P. V. R., J. F. Grassle and R. F. Petrecca. 1992. The role of food patches in maintaining high deep-sea diversity: field experiments with hydrodynamically unbiased colonization trays. Limnol. Oceanogr. *37*: 1543-1550.

Snelgrove, P. V. R, J. F. Grassle and R. F. Petrecca. 1994. Macrofaunal response to artificial enrichments and depressions in a deep-sea habitat. J. Mar. Res. *52*: 345-369. *[Experiments at 900 m; recolonization of Capitella and other species to organically enriched trays high. "fauna may respond quickly and selectively to artificial food patches and disturbance, and this fauna is different from ... ambient sediment. Thus, a patch mosaic may be part of the reason for high deep-sea diversity]*

Sommer, U. 1995. An experimental test of the intermediate disturbance hypothesis using cultures of marine phytoplankton. Limnol. Oceanogr. *40*: 1271-1277.*[Theory supported if diversity based on species numbers or Shannon's index based on biomass - not supported if numbers using H' used]*

Terborgh, J. 1973. On the notion of favorableness in plant ecology. Am. Natur *107*: 481-501. *[Tropics more diverse because there is more tropical area]*

Terborgh, J. W. and J. Faaborg. 1980. Saturation of bird communities in the West Indies. Amer. Natur. *116*: 178-195. *[As discussed by **Ricklefs 1987**, they found that α diversity topped out at roughly 10 species when the total (regional species pool?) was above 40. Biological interactions believed to set the number of local species]*

Whitlatch (1980)

Diversity Indices

Adams, J. E. and E. D. McCune. 1979. Application of the generalized jack-knife to Shannon's measure of information used as an index of diversity. Pp. 117-131. *in* J. F. Grassle, G. P. Patil, W. Smith and C. Taille, *eds*., Ecological diversity in theory and practice. International Co-operative Publishing House, Fairland MD. *[See Heltshe and Forester (**1983**, **1985**) for a similar application of the jackknife]*

Berger, W. H. and F. L. Parker. 1970. Diversity of planktonic Foraminifera in deep-sea sediments. Science *168*: 1345-1347. *[Introduction of a dominance index, now referred to as the Berger-Parker Index. It is the number of individuals of the most abundant species divided by the total number of individuals {see **Death & Winterbourn (1995)** for an application}]*{**40**}

Bhargava, T. N. and P. H. Doyle. 1974. A geometric study of diversity. J. Theor. Biol. *43*: 241-251. *[Using Gini's (1912) diversity as a model, B & D show how diversity is directly related to the squared distance from the origin in a plot of stations in n-dimensional species space. 2 different sets of proportions can have the same diversity. Not much here for the ecologist.]*{**38**}

ter Braak, C. J. J. 1983. Principal components biplots and α and β diversity. Ecology *64*: 454-462. *[A superb paper. Simpson's diversity* $(\Sigma i=1{:}S\ x_i^2)$*, an α-diversity measure, is inversely related to PCA axis 1 in an uncentered PCA, β diversity is displayed in the 2nd and higher dimensions.]*

Brewer, A. and M. Williamson. 1994. A new relationship for rarefaction. Biodiversity and Conservation *3*: 373-379.

Brillouin, L. 1951. Maxwell's demon cannot operate: information and entropy. I and II. J. appl. Phys. *22*: 334-343.

Clayton, M. K. and E. W. Frees. 1987. Nonparametric estimation of the probability of discovering a new species. J. Am. Stat. Assoc. *82*: 305-311.

Coleman, B. D. 1981. On random placement and species-area relations. Math. Biosc. *54*: 191-215.

Coleman, B. D, M. A. Mares, M. R. Willig, and Y.-H. Hsie. 1982. Randomness, area, and species richness. Ecology *63*: 1121-1133.

Colwell, R. K, and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Phil Trans. Roy. Soc. B *345*: 101-118. *[Cited on* *the use of capture-recapture statistics by* ***Rosenzweig 1995****, p. 200,* ***Hughes et al. (2001)****]{?}*

Cousins, S. H. 1991. Species diversity measurement: choosing the right index. Trends in Ecology and Evolution *6*: 190-192.*[Species are different, using ranked indices (ordinal) may be preferable to cardinal indices. You shouldn't add apples and pears, don't treat sparrows and hawks as the same in an index. Species can be separated based on size and trophic type]*

DeBenedictis, P. 1973. On the correlations between certain diversity indices. Am. Nat. *107*: 295-302.

Dennis, B., G. P. Patil, O. Rossi, and C. Taille. 1979. A bibliography of literature on ecological diversity and related methodology. *In*: Ecological diversity in theory and practice I. CPH 319-354. *[A comprehensive listing of methods papers]*

Fager, E. W. 1972. Diversity: a sampling study. Amer. Natur. *106*: 293-310.

Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecology *12*: *42-58. [The log series is introduced as an explanation of animal abundance.* ***Hubbell (2001)*** *provides an excellent and brief history of the introduction of the concept.* ***May (1975)*** *and* ***Rosenzweig (1995, p. 193)*** *provide nice summaries. The log series model was replaced by Preston's canonical log-normal model, but as* ***Hughes (1986)*** *and Lambshead et al. showed, the log series might provide a better fit]* [**74**, **78**, **85**, **88**]

Gleason, H. A. 1922. On the relation between species and area. Ecology 3: 158 *[Cited in* ***Washington 1984****. The Gleason's D diversity index (S/ln N) was used by the EPA EMAP-E program]*

Grieg-Smith, P. 1983. Quantitative Plant Ecology. U. California Press, Berkeley.

Heck, K. L., G. van Belle and D. Simberloff. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology *56*: 1459-1461. *[cited by* ***Smith et al. 1985****, variance formula for* $E(S_n)$ *given in* ***Simberloff (1979)*** *Equation 2.]*

Heltshe, J. F. and D. W. Bitz. 1979. Comparing diversity measures in sampled communities. Pp. 133-144 *in* J. F. Grassle, G. P. Patil, W. Smith and C. Taille, eds., Ecological Diversity in Theory and Practice. International Co-operative Publishing House, Fairland MD.

Heltshe, J. F. and N. E. Forrester. 1983. Estimating species richness using the jackknife procedure. Biometrics *39*: 1-11.

Heltshe, J. R. and N. E. Forrester. 1985. Statistical evaluation of the jackknife estimate of diversity when using quadrat samples. Ecology *66*: 107-111. *[Provides a jackknife estimator for the mean and variance. Tested for Brillouin's and Simpson's index]*{**80**}

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology *54*: 427-432. *[As reviewed by Soetart and Heip (1990), 1/Simpson's, H', and number of species per sample can be calculated from* $N_a=\{\Sigma_{i=1:S}\, p_i^{a}\}^{(1/1-a)}$*, Number of species (a=1),* $N_1=\exp(H'),N_2=1/\theta$*, where* θ *is Simpson's index.]*

Hughes, J. B., J. A. Hellman, T. H. Ricketts, and B. J. M. Bohannan. 2001. Counting the uncountable: statistical approaches to estimating microbial diversity. Applied Env. Microbiology 67: 4399-4406. *[Cites* ***Colwell & Coddington (1994)*** *on the use of chao1 and ACE]* {**81**}

Hurlbert, S. M. 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology *52*: 577-586. *[Corrects* ***Sanders' (1968)*** *rarefaction algorithm, introduces PIE. Probability of interspecific encounter, and attacks information theory indices like H']{****18, 41, 51, 82, 83, 87, 91****}*

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. J. Theoret. Biol. *29*: 151-154.

Jackson, M. W. 1990. The estimation of species richness by extrapolation. Ecology *71*: 1145-1148. *[Uses Heltshe and Forester's JACK1]*

Jumars, P. A. 1975. Methods for measurement of community structure in deep-sea macrobenthos. Marine Biology *30*: 245-252. *[Discusses the Fisher's heterogeneity* χ^2 *method for assessing patchiness in species frequencies and applies* ***Hurlbert's (1971)*** $E(S_n)$ *to deep-sea benthos]*

Kalff, J. and R. Knoechel. 1978. Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. Ann. Rev. Ecol. Syst. *9*: 475-495. *[K & K are opposed to the use of diversity indices for phytoplankton regulatory purposes. "We urge algal ecologists to stop wasting their time on such mathematically simple but ecologically obscure indexes [H']. If ease of computation makes them irresistible, we suggest that they be computed on the basis of biomass rather than on the usual cell numbers (on which basis the smallest flagellate is given the same weight as the largest diatom)."]*{?}

Kalowtar, A. H. 1987. Using the hyperbolic model to estimate species richness. Mathematical Geology *19*: 151-154.

Keefe, T. J. and E. P. Bergersen. 1977. A simple diversity index based on the theory of runs. Water Res. *11*: *689-691. [This index is discussed favorably by* ***Washington (1984)****]*

Lambshead, P. J. D., H. M. Platt. and K. M. Shaw. 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. J. Natural History *17*: 859-874.

Lambshead, P. J. D. and H. M. Platt. 1988. Analyzing disturbance with the Ewens/Caswell neutral model: theoretical review and practical assessment. Mar. Ecol. Prog. Ser. *43*: 31-41. *[Application of the Platt-Lambshead CASVAR program]* {**84**, **86**}

Laxton, R. R. 1978. The measure of diversity. J. Theor. Biol. *70*: 51-67.

Legendre, L., and P. Legendre. 1983. Numerical Ecology. Elsevier, Amsterdam.

Legendre, P. and L. Legendre. 1998. Numerical Ecology Second English Edition. Elsevier, Amsterdam

Margalef, R. 1958. Information theory in ecology. General Systems 3: 36-71.

McIntosh (1967)

May, R. M. 1975. Patterns of species abundance and diversity. Pp. 81-120 *in* M. L. Cody and J. M. Diamond, *eds*., Belknap Press, Cambridge. *[May argues here that the* ***Preston's (1948)*** *canonical log-normal is simply due to the product of random normal deviates.* ***Sugihara (1980)*** *showed, and* ***May (1986)*** *later agreed, that the fit of real data to the canonical log normal is far closer than implied here. He shows that for* ***Sanders' (1969)*** *Buzzards Bay and deep-sea data, Fisher's log series produces a rarefaction curve nearly identical to the* ***Sanders (1968)*** *-* ***Hurlbert (1971)*** *rarefaction curve]* {**74**, **78**, **86**, **87**, **89**}

Menhinick, E. P. 1964. A comparison of some species —individuals diversity indices applied to samples of field insects. Ecology *45*: *859-861. [Proposes a widely used index of species evenness]*

Palmer, M. W. 1991. Estimating specie richness: the second-order jackknife reconsidered. Ecology *72*: 1512-1513.

Peet, R. K. 1974. The measurement of species diversity. Ann. Rev. Ecol. Syst. *5*: 285-307. *[A very nice review, but the criticism of* $E(S_n)$*, 2 different assemblages could have the same* $E(S_n)$*, could apply to any diversity index]{**17**}*

Peterson, C. H. 1976. Measurement of community patterns by indices of local segregation and species diversity. J. Ecology *46*: 157-169. *[Provides a measure of local diversity, later refined by* ***Smith & Grassle (1977)****]*

Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley-Interscience, New York.*[Chapter 18 on Ecological diversity and its measurement]*{**15**, **17**, **18**, **37**, **39**, **40**, **71**}

Pielou, E. C. 1977. Mathematical ecology. John Wiley and Sons, New York. *[Ecological diversity and its measurement pp. 291-311]*

Pielou, E. C. 1981. The broken-stick model: a common misunderstanding. Amer. Natur. *117*: 609-610.

Preston, F. W. 1948. The commonness, and rarity of species. Ecology *29*: 254-283. *[Introduced the log-normal distribution as a better explanation of species distribution patterns than* ***Fisher et al.'s (1943)*** *log series] [**78**, **82**, **88**]*

Preston, F. W. 1960. Time and space and the variation of species. Ecology *41*: 785-790. *[?]*

Preston, F. W. 1962a. The canonical distribution of commoness and rarity. Ecology *43*: 185-215. *[**85**]*

Preston, F. W. 1962b. The canonical distribution of commoness and rarity. Ecology *43*: 410-432. *[?]*

Raup, D. M. 1975. Taxonomic diversity estimation using rarefaction. Paleobiology *1*: 333-342. *[Provides a computational formula for the variance of* ***Hurlbert's (1971)*** $E(S_n)$*, later used by* ***Smith & Grassle (1977)****]*

Sanders, H. L. 1968. Marine benthic diversity: A comparative study. Amer. Natur. *102*: 243-282. *[One of the most important papers in the history of ecology, which documented high deep-sea benthic diversity using the new rarefaction method and explained it with the stability-time hypothesis.* ***Hurlbert (1971)*** *corrected the algorithm used to create rarefaction curves] {**5**, **18**, **31**, **72**, **80**, **81**, **82**, **83**, **91**}*

Shannon, C. E. and W. Weaver. 1949. The mathematical theory of communication. Univ. Illinois. Press, Urbana IL *[Shannon's H']*

Siegel, A. F. and R. Z. German. 1982. Rarefaction and taxonomic diversity. Biometrics *38*: 235-241.

Simberloff, D. 1972. Properties of the rarefaction diversity measurement . Amer. Natur. *106*: 414-418. *[Found flaws in Sanders original formulation, proposed using the* ***Hurlbert (1971)*** *formula]*

Simberloff, D. S. 1978. Use of rarefaction and related methods in ecology. pp. 150-165 *in* K. L. Dickson, J. Cairns, and R. J. Livingston, eds., Biological data in water pollution assessment: quantitative and statistical analyses. A.S.T.M., Philadelphia. *[see also Simberloff 1979]*

Simberloff, D. 1979. Rarefaction as a distribution-free method of expressing and estimating diversity. Pp. 159-176 *in* J. F. Grassle, G. P. Patil, W. Smith, and C. Tallie (*eds.*), Ecological diversity in theory and practice. International Cooperative Publishing House, Fairland, MD.

Smith, E. P. and G. vanBelle. 1984. Nonparametric estimation of species richness. Biometrics *40*: 119-129.

Smith, E. P., P. M. Stewart and J. Cairns. 1985. Similarities between rarefaction methods. Hydrobiologia *120*: 167-170.*[Reviews* ***Sanders (1968)****,* ***Hurlbert (1971)*** *and recent formulae by Kobayashi. They advocate using Shinozaki's (1963) equation to predict the expected number of species per quadrat.]* {**81**}

Smith, W. and J. F. Grassle. 1977. Sampling properties of a family of diversity measures. Biometrics *33*: 283-292. *[The definitive guide to the family history and sampling properties of* ***Hurlbert's (1971)*** $E(S_n)$*]* {**19**, **82**, **83**}

Smith, W., V. R. Gibson, L. S. Brown-Leger and J. F. Grassle. 1979. Diversity as an indicator of pollution: cautionary results from microcosm experiments. Pp. 269-277 *in* J. F. Grassle, G. P. Patil, W. Smith, and C. Tallie (eds.), Ecological diversity in theory and practice. International Cooperative Publishing House, Fairland, MD. *[No change in diversity despite increased pollutant flux; species composition did change]* [?]

Smith, W., J. F. Grassle, and D. Kravitz. 1979b. Measures of diversity with unbiased estimates. Pp. 177-191 *in* J. F. Grassle, G. P. Patil, W. Smith, and C. Tallie (eds.), Ecological diversity in theory and practice. International Cooperative Publishing House, Fairland, MD.

Soetaert, K. and C. Heip. 1990. Sample-size dependence of diversity indices and the determination of sufficient sample size in a high diversity deep-sea environment. Mar. Ecol. Prog. Ser. *59*: 305-307. *[Considers* $E(S_n)$*]*

Warwick, R. M. and K. R. Clarke. 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. Mar. Ecol. Prog. Ser. *129*: 301-305. *[Species diversity remains constant along a gradient of increasing pollution, but taxonomic distinctness is reduced. A new index based on H', called* Δ *is proposed]* {?}

Washington, H. G. 1984. Diversity, biotic and similarity indices: a review with special relevance to aquatic systems. Water res. *18*: 653-694. *[A nice review, but gives short shrift to rarefaction. Includes a description of* ***Gleason's (1922)*** *D diversity]*

Zahl, S. 1977. Jackknifing an index of diversity. Ecology *58*: 907-913.

How many species?

Grassle, J. F. and N. J. Maciolek. 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. Amer. Natur. *139*: 313-341. [**29**]

May, R. M. 1988. How many species are there on Earth? Science 241: 1441-1449. [?]

May, R. M. 1992. Bottoms up for the oceans. Nature 357: 278-279 .

Poore, G. C. B. and G. D. F. Wilson. 1993. Marine species richness. Nature *361*: 597-599. {**29**}

Wilson, E. O. (Editor) 1988. Biodiversity. National Academy Press, Washington D. C. 521 pp.

Hubbell's & other neutral models of diversity

Bell, G. 2001. Neutral macroecology. Science 293: 2413-2418. *[A review of neutral models, including a superb graphical summary of **Hubbell's (2001)** neutral theory with extenstions to coenoclines]{[?]}*

Caswell, H. 1976. Community structure: a neutral model analysis. Ecol. Monogr. *46*: 327-354. *[Caswell uses Ewens' infinite alleles model to generate expected H' and variances for H'. The infinite alleles model was originally proposed by Kimura and Crow (1964). The Ewens algorithm needs only the number of alleles and the number of individuals to predict the expected frequencies.. Caswell uses the analogy that species can be regarded as analogous to alleles. I doubt whether the analogy is valid. I have **Platt & Lambshead's (1985)** FORTRAN code for the infinite alleles model, called CASVAR.FOR Caswell's neutral model can generate a logarithmic series. It is based on the Ewens infinite allele model in genetics. **Goldman & Lambshead (1989)** have applied the neutral model to assess degradation of benthic communities.]* {**85**, **86**, **87**, **88**, **89**}

Caswell, H. 1983. Reply to a comment by Ugland and Gray. Ecology *64*: 605-606.*[Rebuttal to **Ugland & Gray 1983**]{86}*

Chisholm & Burgman (2004) Ecology 85: 3172

Crowder, L. B. 1980. Ecological convergence of community structure: a neutral model analysis. Ecology *61*: 194-204. *[A reanalysis of Fuentes' study of convergence in lizard communities (Ecology 57: 3-17) using a neutral model. Fuentes had argued that microhabitat utilization was similar in CA and Chile because of similar environments. Crowder argued that the microhabitat utilization patterns were exactly what would be expected by chance alone. Fuentes responded to Crowder's article and disputed the null model used.]*

Ewens, W. J. 1972. The sampling theory of selectively neutral alleles. Theor. Pop. Biol. *3*: 87-112. *[Ewens analyzes the sampling distribution of Crow & Kimura's (1964) infinite alleles model. His expected diversities, under the infinite alleles neutral model, provides the basis for Caswell's null model for community diversity.]*

Goldman, N. and P. J. D. Lambshead. 1988. Optimization of the Ewens/Caswell neutral model program for community analysis. Mar. Ecol. Prog. Ser. *50*: 255-261. *[Introduction of the CASVAR program]*

Gotelli, N. J. and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington D.C. *[see **Hubbell 2001**]*

Gray, J. S. 1978. The structure of meiofauna communities. Sarsia *64*: 265-272. *[Summarized by **Lambshead & Platt (1988)**. Used **Caswell's (1976)** expected H' values]* {?}

Hartl, D. L. and A. G. Clark. 1989. Principles of population genetics, 2nd Edition. Sinauer Associates, Sunderland MA. *[Provides an excellent discussion of the Ewens-Watterston infinite alleles model on pp. 122-140.]*

Harvey, P. H., R. K. Colwell, J. W. Silvertown, and R. M. May. 1983. Null models in ecology. Ann. Rev. Ecol. Syst. *14*: 189-211.

Hubbell, S. P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. Coral reefs 16 (Suppl): S9-S21 . *[Cited in **Hubbell 2001, p. 58** as the introduction of the zero-sum multinomial model]* [?]

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton & Oxford. 375 pp.*[Criticizes most previous species-abundance models, including **Fisher et al.'s 1943** logseries and **Preston's (1962)** canonical lognormal and introduces a neutral model that produces his zero-sum multinomial distribution, similar to Hughes (**1984**, **1986**)]* [**5**, **70**, **81**, **84**, **85**, **86**, **88**, **89**]

Hubbell, S. P. 2003. Modes of speciation and the lifespans of species under neutrality: a response to the comment of Robert E. Ricklefs. Oikos *100*: 193.

Hubbell, S. P. and R. B. Foster. 1986. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. Pp. 205-231 *in* M. E. Soule, *ed*., Conservation Biology: the science of scarcity and diver sity. Sinauer Associates, Sunderland MA. *[Times to competitive exclusion long for species with similar resource requirements]* {?}

Hubbell & Borda-de-Agua (2004) Ecology 85: 3175

Hughes, R. G. 1984. A model of the structure and dynamics of benthic marine invertebrate communities. Mar. Ecol. Prog. Ser. *15*: 1-11. *[Few benthic samples fit either the log-series or the log-normal distribution. A dynamic model is proposed. **Hubbell (2001, p. 55-56)** regards this model as being similar but more complex than his neutral model.]* [**86**]

Hughes, R. G. 1986. Theories and models of species abundance. Amer. Natur. *128*: 879-899. *[Most distributions fit Hughes dynamic model, which isn't really described well here, rather than the log normal or canonical log-normal. Hughes distribution looks like the log series of **Fisher et al. (1943)**, but the highest ranked few species have more individuals than the log series predicts. A log abundance vs. rank graph is convex up at low rank rather than linear]* [**81**, **85**, **86**]

Joyce, P. and S. Tavare. 1990. Random permutations and neutral evolution models. Stoch. Proc. and App. *36*: 245-261. *[An alternative to **Ewens 1972**]*

Lambshead, P. J. D. 1986. Sub-catastrophic sewage and industrial waste contamination as revealed by marine nematode faunal analysis. Mar. Ecol. Prog. Ser. *29*: 247-260. *[**Caswell's (1976)** neutral model a sensitive indicator of pollution]*

Lambshead, P. J. and H. M Platt. 1985. Structural patterns of marine benthic assemblages and relationship with empirical statistical models. Pp. 371-380 *in* P. E. Gibbs, *ed*., Proc. 19th Eur. Marine Biol. Symposium, Cambridge University Press, Cambridge. *[Benthic data can't be fitted to the log-normal distribution and such distributions are not helpful. Even the data used by **Preston (1962a)** and **Williams (1964)** to describe the log-normal aren't log normal. According to **Hubbell (2001, p. 36)**, the Rothamstead moth data used by **Fisher et al. 1943** were lognormal, but they pooled data inappropriately -- pooled logseries can look lognormal. **Hubbell (2001, p. 40)** notes that **Routledge (1980)** had argued that lognormals arise by pooling unrelated samples.]* [**85**, **88**, **89**]

Lambshead, P. J. D. and H. M. Platt. 1988. Analyzing disturbance with the Ewens/Caswell neutral model: theoretical review and practical assessment. Mar. Ecol. Prog. Ser. *43*: 31-41. *[Application of the Platt-Lambshead CASVAR program]* {**84**, **86**}

May, R. M. 1984. An overview: real and apparent patterns in community structure. Pp. 3-16 *in* D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle, eds. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton. *[May introduces the famous, contentious Strong et al. symposium volume. He also has a cogent discussion of the use of null hypotheses and neutral models in community analyses]*

McGill, B. J. 2003. A test of the unified neutral theory of biodiversity. Nature 422: 881-885.

Platt, H. M. N. and P. J. D. Lambshead. 1985. Neutral model analysis of patterns of marine benthic species diversity. Mar. Ecol. Prog. Ser. *24*: 75-81. *[They wrote the CASVAR program (EDG has a copy) to analyze Caswell's neutral model. They and Lambshead use it to routinely assess disturbance on benthic communities.]* {**84**}

Rainer, S. 1981. Temporal patterns in the structure of macrobenthic communities of an Australian estuary. Estuar. coast. mar. Sci. *13*: 597-620. *[As reviewed by **Lambshead &Platt (1985)** he fit succession data with the neutral model and found that diversity matched neutral model predictions at an ecotone point, but in areas with expected important biological interactions, diversity was lower than expected.]*

Ugland, K. I. and J. S. Gray. 1983. Reanalysis of Caswell’s neutral model. Ecology 64: 603-605. *[**Caswell’s (1976)** model is not neutral, they say, but **Caswell (1983)** rebuts. The meaning of neutrality is more clearly presented in **Hubbell 2001**]* {**84**}

Volkov, I, J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. Nature *424*: 1035-1037.

Warwick, R. M. 1981. Survival strategies of meiofauna. Pp. 39-52 *in* N. V. Jones, and W. J. Wolff, *eds*. Feeding and survival strategies of estuarine organisms. Plenum press, New York. *[As reviewed by Lambshead and Platt, Warwick found meiofauna communities fit neutral model predictions]*

Warwick, R. M. and J. M. Gee. 1984. Community structure of estuarine meiobenthos. Mar. Ecol. Prog. Ser. *18*: 97-111. *[Summarized in **Lambshead & Platt (1988)**. Three sites analyzed. Diversity is lower than Caswell model expectation in sights where competitive exclusion was more likely]*

Warwick, R. M., H. M. Platt, K. R. Clarke, J. Aghard. and J. Gobin. 1990. Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. J. exp. Mar. Biol. Ecol. *138*: 119-142. *[They use ABC, NMDC, neutral model, H’, and higher OTU’s]*

Williamson, M. And K. J. Gaston. 2005. The lognormal distribution is not an appropriate null hypothesis for the species–abundance distribution. J. Animal Ecology *74*: 409-422.

Sampling Distributions *per se*

Aschan, M. M. and A. M. Skallerad. 1990. Effects of changes in sewage pollution on soft-bottom macrofauna communities in the inner Oslofjord, Norway. Sarsia *75*: 169-190.

Austen, M. C., R. M. Warwick, and M. C. Rosado. 1989. Meiobenthic and macrobenthic community structure along a putative pollution gradient in southern Portugal. Mar. Poll. Bull. *20*: 398-405. *[The ABC method is used, along with NMDS of 4th root transformed data with Bray-Curtis similarity.]*

Bayne, B. L, K. R. Clarke and J. S. Gray. 1988. Biological effects of pollutants: results of a practical workshop. Mar. Ecol. Prog. Ser. *47*: *[ABC method one of many tried in the GEEP workshop]*

Beukema, J. J. 1988. An evaluation of the ABC method (abundance/biomass comparison) as applied to macrobenthic communities living on tidal flats in the Dutch Wadden Sea. Marine Biology *99*: 425-433. *[The ABC method doesn’t work on intertidal flats without reference to control areas, spatial patterns, and long-term patterns. Single species dominate the analysis.]*

Bonsdoff, E. and V. Kovisto. 1982. The use of the log-normal distribution of individuals among species in monitoring zoobenthos in the northern Baltic Archipelago. Mar. Poll. Bull. *13*: 324 *[From Reish et al. 1983 literature review]*

Boswell, M. T. and G. P. Patil. 1971. Chance mechanisms generating the logarithmic series distribution used in the analysis of number of species and individuals, pp. 121-134. *In*: G. P. Patil, E. C. Pielou, and W. E. Waters, editors. Pennsylvania State Univ. Press, Philadelphia. *[Describes explanations for the logarithmic series, cited by **May (1975)**, Hughes (**1984**, **1986**)]* {?}

Bullock, J. A. 1971. The investigation of samples containing many species. I. Sample description. Biol. J. Linn. Soc. *3*: 1-21 *[Cited by Grieg-Smith as providing methods for fitting the lognormal to data]*

Bulmer, M. G. 1974. On fitting the Poisson lognormal to relative abundance data. Biometrics 30: 101-110. *[Cited by **Hubbell 2001**, p. 35 as providing the max likelihood method for fitting the lognormal to data, see also **Slocumb et al. 1977**] {**88**}*

Caswell (1976)

Clarke, K. R. 1990. Comparisons of dominance curves. J. exp. Mar. Biol. Ecol. *138*: 143-157. *[Updated dominance-diversity curves. Statistical analysis of k-dominance and ABC curves and description of partial dominance curves.]*

Coleman, B. D., M. A. Mares, M. R. Willig, and Y-H Hsieh. 1982. Randomness, area and species richness. Ecology *63*: 1121-1133. *[They review the history of equations predicting species vs. area curves, including Preston's derivation of* $s=c*a^z$*, z=0.26 {later revised by* ***May (1975)*** *and Sugihara} and propose a test rarefaction method. Their rarefaction method, later shown by* ***Brewer & Williamson (1994)*** *to be similar to and convertible to* ***Hurlbert's (1971)*** *rarefaction, indicates that the number of bird species on different islands is close to random expectations.]*

Dennis, B. and G. P. Patil. 1979. Species abundance, diversity and environmental predictability. Pp. 93-114 in J. F. Grassle, *et al.*, ed. Ecological diversity in theory and practice. Int. Co-operative publishing house, Fairland MD.*[As reviewed by Lambshead and Shaw 1985, Dennis and Patil argue that the log-series should be found in biologically controlled communities, where density-dependent factors check exponential growth. The log-series in more disturbed communities.]*

Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. *12*: 42-58. *[See discussion by* ***May (1975)****, Fisher's sampling formula for the log series usually produces identical results to the* ***Hurlbert (1971)*** *rarefaction formula]*

Goldman, N. and P. J. D. Lambshead. 1989. Optimization of the Ewens/Caswell neutral model program for community diversity analysis. Mar. Ecol. Prog. Ser. *50*: 255-261. *[They developed a program, called CASVAR.FOR for applying* ***Caswell's (1976)*** *neutral model. I have a copy]* [**84**]

Gray, J. S. 1979a. Pollution-induced changes in populations. Phil. Trans. R. Soc. B. 286: 545-561. {?}

Gray, J. S. 1980. The measurement of effects of pollutants on benthic communities. Rapp. P.-v. Re'un Cons. perm int. Explor. Mer. *179*: 188-193. {?}

Gray, J. S. 1982. Effects of pollutants on marine ecosystems. Neth. J. Sea Res. *16*: 424-443.

Gray, J. S. 1983. Use and misuse of the log-normal plotting method for detection of effects of pollution - a reply to Shaw *et al.* (1983). Mar. Ecol. Prog. Ser. *11*: 203-204. *[The log-normal and log series fit about equally. Use the lognormal since it is found to fit heterogeneous data (lizards to birds)]*

Gray, J. S. 1989. Effects of environmental stress on species-rich assemblages. Biol. J. Linnaen Soc. 37: 19-32.

Gray, J. S. and F. B. Mirza. 1979. A possible method for the detection of pollution-induced disturbance on marine benthic communities. Marine Pollution Bulletin *10*: 142-146. *[Breaks in the log-normal distribution indicate a community making the transition from or two pollution-stressed]* {**88**, **89**}

Gray, J. S. and T. H. Pearson. 1982. Objective selection of sensitive species indicative of pollution-induced change in benthic communities. I. Comparative methodology. Mar. Ecol. Prog. Ser. 9: 111-119. *[The break in the log-normal distribution method]*

Gray et al. 1988 *[Compares the ABC method with other methods]*

Hayek, Lee-Ann C. and Martin A. Buzas. 1997. Surveying Natural Populations. Columbia University Press, New York. 563 pp. *[Includes an interesting discussion of the relationship of species richness and evenness, which the incorporate in their SHE analysis]* [?]

Hubbell (1997)
Hubbell (2001)
Hughes (1984)
Hughes (1986)

Kalowtar, A. H. 1987. Using the hyperbolic model to estimate species richness. Mathematical Geology *19*: 151-154.

Karakassis, I., C. J. Smith and A. Eleftheriou. 1996. Performance of neutral model analysis in a spatio-temporal series of macrobenthic replicates. Mar. Ecol. Prog. Ser. *137*: 173-179. *[**Caswell's (1976) neutral model** applied to 240 samples at 4 depths and 6 seasons from the Greek shelf. The neutral model produced negative departures from neutrality, Caswell's V, in 88% of samples {34% significantly so}. No apparent indication of disturbance. **Warwick 1993** found similar uninterpretable results with the neutral model]*

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