EEOS 630 Biol. Ocean. Processes Chapter 6 Class 11-14 Revised: 12/4/08 E. D. Gallagher ©2008

# **BENTHIC POLLUTION BIOLOGY**

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## Assignment

#### Τορις

How does pollution affect soft-bottom benthic community structure?

#### REQUIRED

- Gallagher, E. D. & K. E. Keay. 1998. Organism-sediment-contaminant interactions in Boston Harbor. Pp. 89-132 in K. D. Stolzenbach and E. E. Adams, eds., Contaminated Sediments in Boston Harbor. MIT Sea Grant College Program, Cambridge MA. 170 p. [There is a slightly expanded version of this document available as a pdf at http://www.es.umb.edu/edg/ECOS630/GallagherKeay98.pdf]
- Grassle, J. F. and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. J. Marine Research 32: 253-284. [A classic paper. Describes the succession after the West Falmouth oilspill. Grassle & Grassle (1976) showed that the changes in allozyme frequencies in Capitella capitata are caused by the succession among Capitella sibling species].
- Grassle, J. F. and W. K. Smith. 1976. A similarity measure sensitive to rare species and its use in investigation of marine benthic communities. Oecologia 25: 13-22. [The NESS similarity index is introduced to analyze beta diversity at stations 9 and 35 in the West Falmouth oilspill survey. <u>Mediomastus</u> and <u>Capitella</u> abundant after the west Falmouth oilspill] {5, 20, 31, 65}
- Rosenberg, R. 2001. Marine benthic faunal successional stages and related sedimentary activity. Sci. Mar. 65 (Suppl. 2): 107-119. [A broad insightful review of theories from Petersen to Thorson to Pearson & Rosenberg & Fauchald & Jumars] {1}

#### SUPPLEMENTAL

- Gray J. M. Aschan, M. R. Carr, 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 Frierfjord/Langesundfjord, and in a mesocosm experiment. Mar. Ecol. Prog. Ser. 46: 235-243. [Description of a copper addition experiment and the fjord pollution gradient, analyzed as part of GEEP. The GEEP data, available as Appendix III are reanalyzed below.]
- Pearson, T. H. and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Ann. Rev. 16: 229-311. [One of the most widely cited benthic papers.]
- Rhoads, D. C., P. L. McCall, and J. L. Yingst. 1978. Disturbance and production on the estuarine seafloor. American Scientist 66: 577-586.
- Warwick, R. M. 1993. Environmental impact studies on marine communities: pragmatical considerations. Aust. J. Ecology 18: 63-80.



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## **Comments on the Readings**

**Grassle & Grassle's (1974)** description of the effects of the West Falmouth oilspill on the benthos of Buzzards Bay is a classic. This preliminary survey of the effects of the oilspill was followed up by **Grassle & Grassle (1976)**, **Grassle & Smith (1976)**, **Sanders (1978)** and the very important paper by **Sanders** *et al.* (1980). The Grassles' analyses of the West Falmouth oilspill set the stage for later studies of oil impacts and laid the foundation for theories of how opportunistic benthic populations respond to disturbance and organic enrichment. Data from two of the key stations from the West Falmouth oilspill study are reexamined in the Example section below.



**Figure 1**. A male *Capitella* sp. I. Note the glistening copulatory setae indicating that this individual is a male or a hermaphrodite and the lack of eggs indicating that it is a hermaphrodite. Also shown are two fecal pellets.

The genetic analysis in Grassle & Grassle (1974) was quickly revised in Grassle & Grassle (1976). Judy and Fred Grassle showed that Capitella capitata, used world-wide as the premier pollution indicator in marine systems, is a sibling species complex, consisting of six distinct species. Figure 1 shows Capitella sp. I, perhaps the most widespread of the Capitella sibling species. A sibling species is a true species, reproductively isolated from the other members of the sibling species complex. Sibling species are not distinguishable using standard morphological characters. Sibling species aren't just esoteric problems for the

taxonomists. Knowing your sibling species is important for environmental managers too. For example there are at least six sibling species of the *Anopheles* mosquito. Each sibling species lives in a different habitat. Only one of the sibling species carries the parasite that causes malaria. This list of *Capitella* species has now grown to more than twenty. **Grassle** *et al.* (1987) provides the most complete listing of the sibling species, their reproductive modes, and karyotypes, the number and structure of chromosomes. The *Capitella* sibling species are sufficiently distinct phylogenetically that they differ in the number of chromosomes.



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Figure 2. A schematic diagram showing the Pearson-Rosenberg (1976, 1978), Rhoads et al. (1978) successional conveyor-belt species. paradigm. The legend for the abscissa of the upper panel

from Rhoads et al. (1978) is Time since Disturbance, while Pearson & Rosenberg (1978) is a lengthy the legend for the lower panel from Pearson & Rosenberg analysis of the effects of pollution on (1976) is Distance from pollution source. The key features are a) deepening of the redox-potential discontinuity (r.p.d.) communities. The paper bears up quite well as organic carbon load decreases (or time since disturbance), b) replacement of small opportunistic surface and shallow subsurface deposit feeders (e.g., Capitella) by deeper feeding larger organisms, especially conveyor-belt feeders.

Rhoads et al. (1978) present a schematic model of how organic enrichment and disturbance affect benthic functional groups. This conceptual model, shown in Figure 2, extends ideas presented first by Grassle & Grassle (1974), McCall (1977), and Pearson & Rosenberg (1976). Pearson & Rosenberg (1978) extends the paradigm presented in their earlier 1976 Ambio article. Rhoads et al. (1978), Pearson & Rosenberg (1978) and Rosenberg (2001) argue that pollution causes successional changes in benthic communities. Shallow surface deposit feeders and shallow burrowers, especially small spionids and capitellids, are replaced by large head-down

temperate, shallow-water benthic under close scrutiny. Both Rhoads et al. (1978) and Pearson & Rosenberg (1978) are cited widely by regulatory agencies, e.g., the EPA and Mass. DEP. This paradigm of the effects of pollutant on benthic communities was extended by Rhoads & co-

workers in a paper of papers. Rhoads & Boyer (1982) focused on the effects of organic enrichment on benthic functional groups and includes one definition of succession: "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." Note that they reject the standard successional framework of succession being the replacement of one species by another. They favor the analysis of functional groups. Huston (1994) follows this view in ecology as focusing on the geographic patterns of functional groups. Rhoads & Germano (1986) extended the Rhoads et al. (1978) paradigm and described a method for quantifying a sample's position on the gradient using the Organism-Sediment-Index, or OSI. This index, which ranges from -10 to +11 provides scores in a sample based on the presence of features visible using the Remots camera system. Remots photographs the sedimentwater interface.



## **Comments on applied benthic ecology**

### THE WHAT, WHY & WHERE OF BENTHIC MONITORING

#### What is monitoring?

**Chapman** *et al.* (1987a) provide this definition of monitoring: *"Monitoring consists of repetitive data collection for the purpose of determining trends in the parameters [sic] monitored."* According to Chapman *et al.* (1987a), monitoring must be based on three questions:

- 1. What beneficial uses should be protected?
- 2. What water-quality problems have been identified in the past or at present that need to be monitored?
- 3. What major natural and anthropogenic factors affect the ecosystem?

The first question is difficult to answer. **Chapman** *et al.* (1987a) urge ecologists to consider which changes are meaningful ecologically or for regulatory purposes. The intrinsic value in the preservation of individual populations, communities and ecosystems is discussed in three recent volumes: M. Soule, ed., "Conservation Biology" and the National Research Council's "Ecological Knowledge and Environmental Problem Solving" (National Research Council, 1986) and "Managing Troubled Waters" (National Research Council, 1990).

Green (1979, p. 68) divides the broad field of ecological survey sampling into three categories: baseline studies, monitoring studies, and impact studies.

- In a **baseline study**, a sampling program is designed to determine the present state of the system (*e.g.*, estimates of biological and chemical variables [not **parameters!**]).
- In an **impact study**, the effects of an impact (*e.g.*, a sediment plume from deep seabed mining) are assessed.
- In a **monitoring study**, the goal is merely to detect change from the present state. **Baseline data** must be available in an impact study to provide a standard against which to detect a change.

Green (1979) describes an optimal impact design study as one in which baseline data exist adjacent to the site of a potential environmental impact and at a spatially distant control area, removed from the potential influence of the impact. Green (1979) proposed that an impact could be assessed through the use of a two-factor analysis of variance (ANOVA), but his design was criticized by Hurlbert (1984) who argued that replicated affected areas must be sampled. A modified version of the optimal impact design study was proposed by Stewart-Oaten *et al.* (1986); their design had been used to assess the effects of nuclear power plant cooling water in near-shore California marine habitats.



**Green (1989)** analyzes the relative effectiveness of different impact designs and compares the power efficiency of univariate and multivariate statistics for determining an effect in environmental variables. The general conclusion is that multivariate statistics can be much more powerful than univariate statistics in detecting environmental change.

**Chapman** *et al.* (1987a) and **Green's** (1979) definitions of monitoring need to be 'fleshed out' to describe how indices of benthic community structure can be used as 'response' or 'criterion' variables in a monitoring plan, and to reconcile the differences between **Green** (1979) and **Hurlbert** (1984) on what constitutes a valid sample survey design for monitoring.

First a new definition of monitoring will be proposed:

Monitoring is a sampling program designed to detect significant changes in the distribution of 'response' variables and to account for observed changes in these variables in terms of 'explanatory' or 'predictor' variables.

A monitoring plan should be based on established principles of statistics, and where possible, all variables, hypotheses and statistical models should be specified in advance. The use of sample statistics in the broad sense should be an essential part of almost all monitoring plans. Unfortunately, despite token references to the contrary, hypothesis testing using a valid sampling design is rarely incorporated in most monitoring studies. A strong case could be made for the view that hypothesis testing need not be an essential feature of monitoring. Just as museum collections of bird shells provided essential baseline data for documenting the effects of DDT in the 1960's, some might feel that data collection per se has intrinsic value. However, when funds for monitoring are scarce and the potential array of variables that might be monitored is large, data collection without a rigorous sampling design can no longer be justified. One of the goals of baseline sampling is to determine the major sources of variation in the data, and if possible, to apportion this variation due to different factors (e.g., temporal and spatial factors). 'Statistics' are employed in the summary of these data, but may often be only descriptive (e.g., correlation matrices, principal components analysis, correspondence analysis, non-metric multidimensional scaling). Even though **hypothesis testing** is not essential to a valid monitoring program, the designer of a monitoring program should be careful that the appropriate variables are being measured and in the appropriate fashion.

#### Why monitor the benthos?

Benthic infaunal monitoring has been fundamental to, if not the foundation of, most recent interdisciplinary studies of anthropogenic influences on marine ecosystems. Some reasons for the efficacy of monitoring changes in benthic community structure are that benthic populations are relatively sedentary (*i.e.*, they can't migrate away from a pollution source or source of disturbance); their generation times are such that the populations are adapted to short-term fluctuations in environmental variables but are capable of a strong numerical response to significant long-term environmental changes (*i.e.*, the signal to noise ratio is presumed to be high). Moreover, the populations are sensitive enough to respond to relatively low levels of toxic



substances (*e.g.*, **Grassle** *et al.* **1981** observed pronounced community responses to 90 parts per billion of #2 diesel oil in the MERL ecosystem tanks). The recovery time of benthic populations is short enough that changes in community structure can be detected in a matter of months, but long enough that the community structure is to some extent a response to the integrated habitat quality over the previous months or even years. A final reason is that in many estuaries and coastal systems, there is a direct coupling between benthic and human populations. For example, flounder and lobster feed on *Capitella* (Becker & Chew 1987), and are then consumed by humans.

### **STATISTICS & SAMPLING DESIGNS**

### Type I & Type II error

Type II error is vitally important in assessing environmental effects. Whenever you hear, "There were no significant effects …", you should immediately think, "What was the power of the test?" **Jumars (1981)** provides an interesting example of calculating statistical power, (1- Probability of Type II error). Test mining of manganese nodules was conducted in the tropical Pacific abyssal plain, and **Jumars (1981)** could not detect a statistically significant effects on deep-sea benthic populations. However, **Jumars (1981)** also determined that the power of these statistical tests was extremely low (*i.e.*, the probability of Type II error was quite high). Most of the individuals of many populations could be killed without being able to detect the effect. Table 1 shows the logical relationship between Type I and Type II error:

Table 1. The relationship between Type I and Type II error				
		Null Hypothesis True	Null Hypothesis False	
DECISION BASED ON STATISTICAL TEST	Reject H <sub>o</sub>	Type I error	Correct Decision "Science Advances"	
	Accept H <sub>o</sub>	Correct Decision "No Advance"	Type II Error	

The goal of most statistical hypothesis testing is to reject false null hypotheses. Karl Popper based 'The Logic of Scientific Discovery' on deduction and refutation, not induction and confirmation. The creation of a null hypothesis and its refutation fits the logical paradigm known as the *modus tollens* (*i.e.*, '**If A then B** and '**not B**' implies '**not A**'). Popper stressed refutation in his method because confirmation of hypotheses could serve as the basis of a scientific method (*e.g.*, Given the null hypothesis **A** and the deduction, '**If A then B**', observation of the event '**B**', does not warrant the conclusion that '**A**' is true.)





In environmental monitoring, the traditional null hypothesis is that of 'no change' (e.g., H<sub>0</sub>:  $\mu_1 =$  $\mu_2$ ). The probability of **Type I error**, symbolized as  $\alpha$ , is the probability of rejecting a true null hypothesis; its magnitude is set through the choice of the critical value of the underlying statistical distribution against which the value of the test statistic is to be judged. Conventionally, the probability of Type I error is set at 0.05 or 0.01, so that the odds of rejected a true null hypothesis are only 1 in 20 or 1 in 100. The choice of a significance level is merely convention, and there is justification for choosing a relatively large  $\alpha$ -level (e.g., Prob.  $\approx 0.20$ ) for environmental monitoring studies. In environmental monitoring, Type II error, or the acceptance of a false null hypothesis, may have serious regulatory consequences. For example, the depletion of atmospheric ozone is of such immediate world-wide concern that sampling programs for Antarctic and Arctic ozone levels should be designed to minimize the probability of Type II error. If the null hypothesis is 'ozone levels are not changing', the environmental consequences of a large Type II error could be extremely serious. For a given sample size, increasing the probability of Type I error (e.g., testing at the  $\alpha$ =0.10 rather than  $\alpha$ =0.05 level) leads to a decrease in the probability of Type II error. Increasing sample size reduces the probabilities of both Type I and Type II error. However, if sample size can not be increased, then many scientists would argue for  $\alpha$ -levels larger than the conventional 0.05 level to reduce the probability of Type II error.

The probability of Type II error can not be calculated without specifying the alternate hypothesis (*e.g.*, mean of the variable at time<sub>0</sub> = 0.9 x mean of the variable at time<sub>1</sub>). The probability of Type II error for a given null hypothesis and a specified alternate hypothesis is symbolized as  $\beta$ . The **power of a test** is equal to 1- $\beta$  and is the probability of rejecting the null hypothesis when it is false (*i.e.*, an alternate hypothesis is correct). The power of a test, for a constant  $\alpha$ , can be increased through increased sample size.

The concept of **statistical power** is often invoked in discussions of monitoring of the marine environment, but the concept is too often misapplied. Ecologists and environmental biologists appear to have recently discovered the phrase 'statistical power'. At a recent environmental conference, a benthic ecologist argued that six benthic grab samples must be taken at each of dozens of locations in Massachusetts Bay at each of several sampling periods. The benthic ecologist was asked, "Why take 6 grab samples at each site; why not 2, or why not 20?" The ecologist responded that 6 samples had been found to be necessary to obtain adequate **statistical power** in the George's Bank infaunal monitoring program, and thus would probably be appropriate for the MA Bay benthos. Unfortunately, not a single null hypothesis nor alternate hypothesis had been specified in the ecologists monitoring plan. Statistical power can not be evaluated unless both the null hypothesis and the alternate hypotheses are specified.

There are only a few examples of power analyses in the benthic ecological literature. **Jumars** (1981), Caswell & Weinberg (1986), and Green (1989) present some of the only power analyses for infaunal benthic communities. **Jumars (1981)** provides a particularly sobering example of the importance of power calculations. To detect a 100% mortality of deep-sea benthic populations due to Mn-nodule mining with a probability of Type II error of less than 5% would require more than 50 0.25-m<sup>2</sup> box core samples for most deep-sea populations. Since a single 0.25 m<sup>2</sup> box core requires one full month to process, the costs of deep-sea monitoring would be



extraordinarily high. The number of samples required to reject the null hypothesis in favor of less drastic alternate hypotheses (at the same β level) would be considerably higher. **Caswell & Weinberg (1986)** analyze the power of several community-level statistics (*e.g.*, diversity estimates) and conclude that certain multivariate composite statistics (*e.g.*, diversity indices) are more likely to have higher statistical power than the univariate statistics on which they are based. **Green (1989)** concludes that multivariate statistical tests based on Hotelling's T statistic do not have inherently greater power than univariate tests. If environmental stress acts produces effects similar to natural patterns of variation in communities, multivariate tests can have considerably less power than their multivariate alternatives.

#### Beyond Type II error & 'the Oscar Wilde test'

Most scientists agree that monitoring programs should be designed to detect change. The monitoring plan should clearly address the following items:

- The null hypotheses to be tested (usually specified as `no change in the distribution of a specific variable or variables)
- The statistical model and test statistics to be employed.
- Alternate hypotheses necessary for the calculation of statistical power. Another way of specifying the alternate hypothesis is to answer the question, "What level of change should the monitoring program be designed to detect?"

It is possible in theory to increase sample size sufficiently to reject most null hypotheses, and to reduce the probability of Type II error to very low levels for most alternate hypothesis. Scientists must think beyond minimizing the probabilities of Type I and Type II error. In this section, I will introduce the concept of **moving beyond Type II error**. Minimizing Type I and Type II error will allow the statistician to state, "The environment has changed." Scientists must do more than detect change; they must assess the extent, causes of, and ecological implications of that change.

At first glance, the definition of monitoring that I have proposed above seems to be unwieldy. Chapman *et al.*'s (1987a) and Green's (1979) definitions of monitoring fail a test, which I call the Oscar Wilde Test. One of Oscar Wilde's famous aphorisms is:

Question:	`What is the <b>second</b> worst thing that could happen to a man?'
Answer:	"Not obtaining his heart's desire".
Question:	`And what is the worst?'
Answer:	"Obtaining it."

The heart's desire of every field ecologist since Fisher's book on experimentation has probably been for more replicated field samples and statistical tests with greater statistical power. The reason is obvious: significant results get published but nonsignificant results often do not. In the **Oscar Wilde Test**, one evaluates the quality of a sampling design, assuming that the null hypotheses **will** always be rejected. Assume that a change is detected in the environment with an  $\alpha$  level <0.05. What accessory data need to be collected in order to assess this change? Is it really



due to a change in pollution intensity, or is it merely natural change? If assessing large-scale changes in population abundances or changes far in excess of natural variation is the goal, then statistical designs to detect any change whatsoever set only a minimal standard for a monitoring plan.

Another example may clarify the uses of the Oscar Wilde test. In a hypothetical doctoral candidacy examination, the candidate presented a sampling design to evaluate phytoplankton standing stocks in MA Bay. The doctoral candidate had dutifully specified his null hypothesis as "Chl <u>a</u> concentration does not change seasonally" and described an ANOVA design to test his null hypothesis. I applied the Oscar Wilde test by saying, "OK let's assume that you can reject that null hypothesis at the  $\alpha$ = 0.0001 level, what have you learned? Everyone knows that Chl <u>a</u> concentrations change seasonally, and probably even change on a diel time scale. Are you going to be content with rejecting that trivial null hypothesis using tests with high power. He eventually designed his field program to collect data appropriate for applying Model II multiple regression analyses to assess the relative importance of a wide variety of environmental factors (e.g., primary production, temperature, rainfall, salinity, total organic matter) in explaining the variance in Chl *a* concentrations, his dependent variable. Dayton (1979) had reached a similar conclusion a decade earlier: scientists often devote too much effort rejecting trivial null hypotheses.

A monitoring program which is designed solely to detect change in a variable, without explaining the reasons for the change, fails the Oscar Wilde test. Such monitoring programs are inadequate. A sample survey design for monitoring should do more than achieve high statistical power; it should attempt to detect change and **explain** the changes observed. The field ecologist must analyze the appropriate 'explanatory' or 'predictor' variables at the same time as the 'response' or 'criterion' variables in order to achieve a successful monitoring program.

Too often, environmental scientists focus too intently on **hypothesis testing** and the **detection of environmental impact** rather than **explanation** and **assessment of environmental impact**. The statistician's solution to moving beyond Type II error is through proper identification of the hypothesis to be tested and through replication of the appropriate sampling units. If there is only one impacted area, a monitoring program should be designed to assess any changes observed in this area (*i.e.*, changes in response variables) and to generate structural models to explain the changes in response variables with meaningful predictor variables. The structural model may be merely a multiple regression model, an analysis of covariance, a Sewall Wright path analysis, or a log-linear contingency table model.

**Chapman** *et al.* (1987a) go one step further in solving the Type II dilemma, when they state that the goal of monitoring is not merely to detect **a change** in environmental variables, but **a trend**. **'Trend'** usually implies a non-random temporal pattern in the data. Using the Oscar Wilde test, it would be possible to take enough samples so that a change in an environmental variable could be detected between each and every sampling period; roughly half of these changes would be positive and half negative. However, the demonstration of a significant **trend** in an environmental variable is much more difficult to achieve by increasing the number of samples



and solves the Oscar Wilde test. Increasing the number of replicates will not produce a trend if none exists. However, the recent debate over increasing global temperatures, highlighted by **Solow & Broadus (1989)**, illustrates that describing a trend statistically by itself can not be used as the basis for a causal explanation. Hanson, a global climate expert from NOAA, had stated that the decade of the eighties had three of the warmest years in the century, which statistically was unlikely to be due to chance alone. He argued that this was strong evidence in favor of the greenhouse effect. **Solow & Broadus (1989)** demonstrated an increasing trend in the data, perhaps dating to the 1880's when fossil-fuel input was not increasing much. The lesson from **Solow & Broadus (1989)** is important. Just because pollutant input is increasing simultaneously with changes in community structure, don't assume that there is a causal relationship.

It should be noted the detection of a significant temporal trend in a variable (at an  $\alpha$ -level of 0.05) requires **at least** four and preferably far more sampling periods. In trend analyses there is one null hypothesis, 'No trend', but there are many alternate hypotheses:

- A short-period cycle plus a unidirectional trend.
- Unidirectional trend.
- Unidirectional trend confounded with a long-term cyclic trend.
- Cyclic trend.

Fred Nichols' (1985, 1988) documentated a long-term change in benthic community structure in the deepest portion of Puget Sound, the 100-fathom ( $\approx 200$  m) hole in the main basin of Puget Sound should give pause to any benthic ecologist who assumes that a 2- or 3- year trend is due to a degradation of the marine environment. Nichols (1985) initially attributed the decline in the biomass dominant, Pectinaria californiensis, to increases in organic enrichment, citing the Pearson-Rosenberg (1978) organic enrichment paradigm. When the benthic community, especially the abundance of P. californiensis, in the 1980's returned to resemble that observed in the mid-1960's, Nichols was forced to reject his hypothesis of a long-term unidirectional trend (alternate 2 above) in favor of multidecadal trend driven by long-term hydrographic changes in the Sound, coupled to the Pacific decadal oscillation. Gray & Christie (1983) document other long-term trends in benthic populations, driven presumably by allogenic trends especially hydrography.

The goal of a monitoring program should be to detect **either** the temporal or spatial change or trend in response variables and to link those variables in a causal model with `explanatory' variables. The dictionary definition of trend emphasizes the spatial, not the temporal connotation:

*trend*, *n*. 1. *the general direction of a coast, river, road, etc.* 2. *the general tendency or course, as of events, a discussion, etc.; drift....* 

Spatial information has been used very effectively in many benthic monitoring programs. **Pearson & Rosenberg (1978)** discuss migrating benthic communities. That is, an increasing pollutant flux to the marine environment (*e.g.*, at the head of a fjord) results in an expanding zone of pollution-tolerant species. A declining flux of pollutants from a point source results in a shrinking zone of pollution tolerant species. **Stull** *et al.* (1986) provide a good example of the



effects of reduced pollution load on the spatial distribution of benthic communities. In the early 1970s, pollution tolerant species, notably *Capitella* spp., dominated large areas downstream from the Los Angeles sewer outfalls on the Palos Verdes shelf. After the implementation of a rigorous pretreatment program that resulted in dramatic reductions in heavy metal, and organic pollutant input, the zone of pollution tolerant species shrank to a small zone immediately adjacent to the outfall. Superimposed on this pollution-related pattern on the Palos Verdes shelf was one of the strange long-term patterns that **Gray & Christie (1983)** noted pose such problems for benthic monitoring programs. **Stull et al. (1986)**, using LA County's long-term monitoring data, document that in the mid-1970s large numbers of gutter worms (the Echiuran worm *Listriolobus pelodes*) appeared on the Palos Verdes shelf. This worm appeared in large numbers in the mid-1970s, changed the sediment porewater properties and community structure, and then disappeared. Since the late 1970s this species has been found only in low numbers on the Palos Verdes shelf.

#### **DUBIOUS INDICES, STATISTICS & THE KURT VONNEGUT TEST**

In his novel Player Piano, Kurt Vonnegut wrote that any scientist that could not explain his work to a 12-year old is probably a charlatan. Using this criterion, much of modern community analysis would qualify as charlatanism. Many of the statistical methods employed by benthic ecologists are not widely understood even by other well-read ecologists.

Little space has been devoted here to the discussion of which dependent variables might be used to characterize soft-bottom benthic community structure. These variables would certainly include abundances of individual species, estimates of species diversity (*e.g.*, as calculated using Hurlbert's expected number of species index), species composition, biomass, and perhaps even size composition (*e.g.*, as described by Schwinghamer 1988).

Not all statistics are valid and certainly not all approaches to monitoring are valid. In soft-bottom benthic ecology, there has been a plethora of dubious indices proposed to assess community structure. Most of these indices and approaches share a few common features:

- They are less expensive than standard benthic sampling which relies on the identification of all individuals to species.
- They rarely require taxonomic identifications or competent taxonomists.
- Some require no benthic sampling or a reduced number of replicate samples.

While some of these indices may have merit, all should be viewed with caution, and none should be made the sole basis of a monitoring program. Some indices, such as Jack Word's (1978, 1980a, 1980b, 1980c) infaunal trophic index (published only in the SCCWRP biennial reports), can be ruled out almost immediately as being too seriously flawed to merit discussion as a monitoring tool. Word's index forces improper trophic guild classifications into an improperly constructed mathematical formula to produce an index of pollution effects. Ironically, Word's ITI was the monitoring method proposed by the MDC in their application for the Section 301 (h) waiver from the clean water act. The dubious indices include:



- The nematode/copepod ratio [*Raffaelli & Mason 1981, Warwick 1981, Raffaelli 1982 & 1987, criticized by Amjad & Gray 1983, Coull et al. 1981, Lambshead 1984, Shaw et al. 1983*].
- Rhoads' organism-sediment index (OSI) *[Rhoads & Germano 1986]* This index is a valid supplement to more traditional sampling, as the authors indicate. Unfortunately, many groups think that the OSI provides a sufficient description of benthic community structure.
- BRAT, the benthic resource assessment technique [Lunz & Kendall 1982]
- Jack Word's infaunal trophic index (ITI) [Word 1978, 1980a, 1980b, 1980c]
- Departures from the log-normal distribution of individuals among species [Gray & Mirza 1979, Gray 1979a & b, Stenseth 1979, Gray 1980, Mirza & Gray 1981, Gray 1982, 1983, 1989, Gray & Pearson 1982, Pearson et al. 1983, Nelson 1987; poor fit found by Rygg 1986]
- Warwick's species abundance-biomass comparison (the ABC method). As reviewed by McManus & Pauly (1990), Warwick's ABC method has 9 components: 1) with low pollution stress, communities are in equilibrium; 2) approaching equilibrium, communities are dominated by a few large benthic species; 3) spp. dominating biomass approach equilibrium with resources 4) Numerical dominance by small species; 5) small species not in equilibrium with resources; 6) Stochastic variation in the abundance of small species; 7) large species eliminated by pollution; 8) Under severe pollution, community dominated by small species; 9) Under severe pollution the few remaining large species will contribute more to community biomass. As a consequence of 8 & 9, biomass is more evenly distributed among species than the number of individuals. Using kdominance curves (cumulative frequency distribution (cfd) vs. sp. rank), the biomass cfd will be greater than the numbers cfd.. This cfd curves are reversed in pristine communities. The ABC method is used by Warwick 1986, and Warwick et al. 1987. Beukema (1988) found it useless and it is evaluated favorably by McManus and Pauly (1990). Dauer et al. (1993) didn't feel that it could identify polluted Chesapeake Bay benthic communities.
- **Caswell's (1976)** neutral model as a pollution index. Caswell proposed the model to test for the effects of biological interactions. Lambshead adapted the model to test for recent disturbance. **Warwick (1993)** applied it to a Pearson pollution gradient, finding it didn't work. **Karakassis** *et al.* **(1996)** applied it to 240 samples of Greek shelf communities, finding uninterpretable results.
- Ordination of higher taxonomic units. Warwick (1988a) and Warwick & Clark (1991) argue that the major patterns in community structure are evident using ordination even if the individuals are identified at only the family and even phylum level. Vanderklift *et al.* (1996) analyze this hypothesis, finding it needs further work.



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### ECOTOXICOLOGY

#### Introduction

Benthic community structure changes in response to pollution gradients. Species diversity and species composition change in response to changes in pollutant loads. But how do pollutants affect the benthic infauna and can we predict the effects of pollutants at the community-level? In particular, can we establish sediment quality criteria (SQC) for pollutants that will predict whether a given concentration of pollutant in the sediments will cause a change in community structure? It is now well established that the total concentration of a potentially toxic substance is a poor predictor of effects at the community level. Much of the pollutants in sediments are not bioavailable. For example, PAHs may be bound in relatively inaccessible charcoal-like soot particles. Heavy metals may be bound to sulfides or organic compounds, rendering them relatively non-toxic.

#### Predicting pollutant effects at the community level

There are three major approaches being used to define Sediment Quality Criteria for heavy metals and hydrophobic organic pollutants:

- ERM & ERLs
- Equilibrium partitioning for nonionic hydrophobic pollutants
- SEM/AVS ratios for divalent heavy metals

The Long & Morgan (1990), Long et al. (1995) ERM & ERL approaches are an atheoretical approach to assessing toxicity. ERM stands for Effects Range Median and ERL stands for Effects Range Low. These authors have compiled a large database including studies of chronic toxicity using amphipod tests, bioaccumulation, and alterations in community structure. Studies that include both a pollutant concentration and an effect are eligible for inclusion in the database. All effects are assumed equal. Thus, a study documenting a dramatic change in community structure associated with increased concentrations of a variety of heavy metals and hydrophobic organic pollutants would count as 1 effect. A study with a single compound showing bioaccumulation relative to a control sediment would count as another effect. Hundreds of studies are compiled in the database. For each pollutant (e.g., copper), the records in the database are sorted from highest to lowest concentrations of the pollutant. The pollutant concentration at the point at which 50% of the studies have shown one effect or another is marked as the ERM concentration. The pollutant concentration below which only 10% of the studies showed some kind of effect is marked as the ERL concentration. The ERM and ERL values are expressed as the weight of pollutant over the dry weight of sediment. Since organic carbon concentration is often not measured in studies used in the database, there is no normalization by organic carbon.





#### **Bioavailability**

#### Metals & the SEM/AVS ratio

It is well established that the free-ion activity determines the toxicity of a metal. In both sediments and the water column, metals that are complexed with ligands are not toxic. Heavy metals, like copper, can be complexed with organic ligands and as metal-sulfide complexes. DiToro *et al.* (1989, 1992) have argued persuasively that acid-volatile sulfides (AVS) can effectively bind to and detoxify heavy metals in sediments. Acid volatile sulfides are usually found as FeS or iron sulfides. DiToro *et al.* (1989) showed that in the presence of unbound divalent cationic heavy metals, like Cd, Cr, Cu, Hg, Ni, Pb, Zn, the Fe is displaced from the FeS complex by the heavy metal, which forms an insoluble Me-S complex. Metals bound as insoluble sulfide complexes are not bioavailable and are not toxic.

DiToro *et al.* (1989, 1992) have argued that there are a variety of sulfide phases in natural sediments. The 'reactive' sulfide phase can be extracted using cold 0.5 M hydrochloric acid. DiToro *et al.* (1989, 1992) argue that the cationic heavy metals should be measured using the same cold HCl extraction. Metals extracted in this way are called the SEM, for simultaneously extractable metals. If the molar ratio of SEM to AVS, or SEM/AVS, is less than 1.0, then none of the divalent cationic heavy metals are toxic. If the SEM/AVS ratio is greater than 1.0, then the sediments may or may not be toxic. Even if SEM>AVS, the metals may be bound by organic ligands and not bioavailable.

#### Nonionic hydrophobic organic compounds

Like heavy metals, it is only the bioavailable fraction of potentially toxic organic compounds that controls toxicity. In general, only the dissolved unbound form of potentially toxic organic compounds that controls toxicity and bioaccumulation. **DiToro** *et al.* (1992) proposed an equilibrium partitioning approach to predict the SQC for nonionic hydrophobic organic pollutants. Their proposal has the following components:

- Only the unbound, dissolved form of organic pollutants is toxic.
- The concentration of the dissolved form in the porewater is inversely proportional to the sediment organic carbon concentration.
- The fraction of unbound and bound organic pollutants can be predicted if the octanol water partition coefficient is known and if the concentration of organic carbon in the sediment is known.
- It is assumed that the major route of exposure is via the porewater.
- An analysis of benthic and pelagic organisms indicate similar chronic toxicity to the unbound dissolved forms.
- If this is true, then water quality criteria (WQC) can be extended to the sediments if the octanol-water partition coefficients are known.





#### What is the route of exposure?



**Figure 3** Some routes of exposure of toxic pollutants to benthic organisms. The dissolved, unbound form of the pollutant, shown in red, is the major toxic form, and the most likely route of exposure is via porewater and overlying water used for respiration. Animals can also be exposed to toxic substances via their food: for deposit feeders this is indicated by ingestion of deposits and predation. The kinetics and partitioning of bound and unbound pollutants in the gut is largely unknown. Pollutants bound in pellets and soot particles are not readily bioavailable.

Figure 3 shows a schematic diagram showing the two major modes of exposure to benthic organisms: respiration and food. Campfens & Mackay (1997) modeled the process of biaccumulation and bioconcentration in benthic and pelagic organisms. Respiration is a major route of exposure for all organisms. Organisms will acquire pollutants in direct proportion to the partition coefficient between the organism and the concentration of the dissolved form in the water used for respiration. In essence, animals are modeled as if they are bags of lipids. In nature, organisms can also acquire pollutants from their food. This can include both the sediments, associated organic matter and pollutants and other organisms. Without these trophic pathways, organisms would come to a chemical equilibrium with the water used for respiration. Benthic organisms, which can use the overlying water for respiration, will have a lower pollutant concentration than one that uses sediment interstitial water for respiration,

since interstitial water has a higher pollutant concentration.

A benthic organism that eats other benthic organisms can receive higher pollutant loads, if the prey contains a higher body burden. The organism can come to a steady-state pollutant concentration, even though its body burden is not in chemical equilibrium with the surrounding porewater. Biomagnification refers to the accumulation of a pollutant in excess of that expected from equilibrium partitioning. **Campfens & Mackay (1997)** model a food web in which two fish species, with identical lipid contents (an important parameter in modeling the partitioning of hydrophobic pollutants) could have drastically different pollutant loads. The fish could differ even though they respire with the same water if one feeds on benthic organisms with a high pollutant concentration and the other feeds on pelagic organisms with a lower pollutant load. The trophic pathways of fish are an important component in modeling bioaccumulation and biomagnification.

Deposit feeders pose a challenge for equilibrium partitioning theory. These organisms ingest sediments with a high concentrations of pollutants, and they respire using interstitial water (and the immediately overlying water). **DiToro** *et al.* (1991, p. 1568) argue that the route of exposure





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could be either the deposits or the porewater, but pragmatically it makes little difference. If the sediments are in chemical equilibrium with the porewater (at equifugacity), then the partitioning from the particles to the organism via the gut should be similar to the partitioning between the porewater and the organisms respiratory surfaces (*e.g.*, gills, branchiae, or body walls). The unknown feature involves the digestive process. Presumably, the proteolytic enzymes in a deposit-feeder's gut would make pollutants more bioavailable, increasing the importance of this mode of exposure.

#### Colloids, fecal pellets, and soot

Brownawell & Farrington (1985, 1986) and Farrington (1985) have argued that it is insufficient to consider sediments as a two-phase system: porewater and sediment particles. They provide persuasive evidence that colloids, which are organic-rich particles which pass through conventional 0.4-µm sieves must be considered as well. This organic colloid phase is often indistinguishable from the dissolved organic phase in sediments. Hydrophobic organic pollutants will partition onto this organic colloid phase. **DiToro** *et al.* (1991) argue that this organic colloid phase is not bioavailable.

This colloid phase can affect the distribution of hydrophobic organic pollutants in sediments. Pollutants in the colloidal phase will diffuse in the porewater and can be moved by bioirrigation from the benthic infauna. Particle-bound heavy metals and particulate-bound organic compounds would not be moved by bioirrigation.

Fecal pellets can be an important phase in polluted marine environments. For example, up to 75% of the weight of sediments in some areas of Boston Harbor are bound into fecal pellets. Karichoff was the first to model the effects of pellets on pollutant profiles. Pellets tend to be organic-rich and anoxic particles. Both nonionic hydrophobic pollutants and heavy metals can be sequestered in pellets, and are not readily available for chemical partitioning into the porewater. Pollutants in pellets are not bioavailable for two reasons: they are generally bound to organic matter, and organisms rarely ingest fecal pellets.

**Chin & Gschwend (1992)** and **McGroddy et al. (1996)** have modeled the role of soot in controlling the distribution and bioavailability of PAHs in Boston Harbor sediments. After running three phase models — dissolved PAH, colloidal PAH, and particulate PAH — it was found that far too much PAH remained bound to the particulate phase. These authors have argued that the PAHs are bound in soot particles and the PAHs are not available for partitioning into the dissolved and colloidal phases. **Wang et al. (2001)** also argued that soot plays a role in controlling the partitioning between dissolved, colloidal and particulate phases, but they also noted that Boston Harbor sediment PAHs are sorbed within *Capitella* fecal pellets.



#### **EXAMPLES**

#### The West Falmouth oilspill

In September 1969, the barge Florida went aground off West Falmouth. Scientists from the Woods Hole Oceanographic Institution began taking samples within a few days of the grounding. **Grassle & Smith (1976)** from the assigned reading describes a cluster analysis of stations 9 and 35, a heavily and lightly oiled pair of stations. I'll analyze these data more fully to tease out the major patterns associated with the oilspill.

#### 6/70 7/70 0.5 5/70 8/70 PCA-H Axis 2 (16%) 4/70 6/71 4/71 9/70 11/70 3/72 8/71 12/71 9/69 12/69 11/69 10/69 -0.5 -0.5 0.5 0 PCA-H Axis 1 (37%)

#### Station 9: a heavily oiled inshore station

**Figure 4**. Metric scaling of the 18 Station 9 samples. Convex hulls, based on a UPGMA cluster analysis of CNESS m=18 are also shown.

The metric scaling of the 18 Station 9 samples with CNESS m=18 is shown in Fig. 4. The striking feature in this metric scaling, which also shows the results of a cluster analysis, is the rapid change in community structure, especially during summer 1970. Grassle & Grassle (1974) and Sanders et al. (1980) document that the most severe effects from the oilspill did not occur in fall 1969, but during the summer and fall of 1970. Immediately after the oilspill, there was evidence of high mortality of the amphipods in the community. During the summer of 1970, there was a rapid change in community structure resulting from the summer larval recruitment.





**Figure 5**. The Gabriel Euclidean distance biplot showing the species that account for the CNESS distance among stations. The importance of a species indicated by the vector length.

The Gabriel Euclidean distance biplot, shown in Fig. 4 reveals the species that changed rapidly during the West Falmouth succession. The figure contains somewhat of a surprise. It is not surprising that *Capitella* spp. increased in frequency in early 1970. However, the species that made up a high frequency of the individuals during the crucial summer 1970 period was the omnivorous polychaete Nephtys incisa, which was one of Howard Sanders' key indicator species for the Buzzards Bay community. The species that came to dominate Station 9 by late 1970 was the capitellid polychaete *Mediomastus ambiseta*. *M. ambiseta* is a normal component of the Buzzards Bay community. However, its very high frequency in the samples taken after July 1970 is out of the ordinary.



The Sanders-Hurlbert rarefaction curves, shown in Fig. 5, show a strange pattern. During this oilspill, the species richness of the Buzzards Bay community remained relatively high. The samples with the highest number of species were collected during late summer and early fall 1970, a period when the oil was causing rapid changes in species composition and drastic reductions in species evenness. Rarefaction curves like Fig. 5 led **Smith** *et al.* (1979) and



**Figure 5**. Sanders-Hurlbert rarefaction curves for West Falmouth Station 9.

**Sanders** *et al.* (1980) to conclude that species diversity was not a good indicator of pollutant effects or organic enrichment in soft-bottom benthic communities. Pollutants can cause major changes in species composition, without drastically affecting species diversity.

**May (1975)** showed that rarefaction curves like those shown in Fig. 5 often are identical to those produced under the assumption that the individuals among species follow the log-series distribution. I developed a plotting procedure called a non-dimensional diversity plot to show the relationship between rarefaction curves and their log-series expectations. The log-series provides a benchmark against which to judge the expected evenness for a Sanders-Hurlbert rarefaction curve Figure 5 shows the 18 curves produced by dividing the Sanders-Hurlbert rarefaction curve by their log-series expectations. John Lambshead at the British museum has found that the departures from the log-series is indicative of recent disturbance.





**Figure 6**. A non-dimensional diversity graph, produced by dividing the log-series expectation by the rarefaction curves (shown in Fig. 5. The horizontal dashed lines at 0.75 and 1.25 are rough benchmarks for severe departures from log-series expectation.



**Figure 7**. Shannon's H' and Pielou's J', the evenness measure for Shannon's diversity plotted *vs.* days since the oilspill.

periods of larval recruitment. Wintertime species evenness is relatively high.

Using a cutoff of 75% of expected logseries diversity, samples from the late summer 1970 show the most uneven distribution of individuals among species relative to log-series expectation. Samples taken immediately after the oilspill through June 1970 didn't depart noticeably from log-series expectation. By July 1970, departures from the log series were severe. The cause of this departure was the massive recruitment of two normal components of the Buzzards Bay community: the omnivorous polychaete Nephtys incisa and the capitellid polychaete Mediomastus ambiseta. The high frequency of Nephtys incisa is interesting, because some benthic

ecologists have proposed this taxon as a pollution- or disturbance sensitive climax species (*e.g.*, McCall 1977, Rhoads *et al.* 1978)

The decrease in diversity at Station 9 was largely due to a decline in the evenness component of diversity. Figure 7 shows the change in Shannon's H' and the evenness measure for Shannon's diversity, Pielou's J'. This figure shows that the most severe effects of the oilspill occurred nearly one year after the spill and persisted throughout much of 1971. Sanders et al. (1980) concluded that the community at station 9 still had not recovered completely after 2.5 years. By December 1971, the community was returning to a log-series distribution. However, the March 1972 sample exhibited a relatively severe departure from the logseries expectation. Departures from the logseries are most evident during and just after



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#### Station 35: a lightly oiled offshore station



**Figure 8**. Metric scaling of the Station 35 samples. Convex hulls based on a UPGMA cluster analysis of CNESS m=10...

The metric scaling of the 14 Station 35 samples with CNESS m=10 is shown in Fig. 8. The immediate image from this figure is that the July 1971 sample is a distinct outlier. So different that it looks like a completely different community. The solid line connects samples taken on consecutive dates and shows rapid changes in community structure throughout the twoyear sampling period. There is a clear Winter-Spring assemblage and a late summer-early fall assemblage. The point of highest diversity is associated with the winter of 1970-1971.





**Figure 9**. The Gabriel Euclidean distance biplot for West Falmouth Station 35 showing the species that account for the CNESS distance among stations.

The Gabriel Euclidean distance biplot, shown in Fig. 9 reveals the species that controlled differences in Station 35 community structure. Mediomastus ambiseta, a capitellid polychaete that is a normal member of the Buzzards Bay community, was responsible for the pronounced difference between the three late summerearly fall samples and the other 11 samples. *Mediomastus ambiseta* was an important contributor to both Station 9 and 35 community structure. At Station. 9, M. *ambiseta* was the most important contributor to CNESS distances among stations, accounting for 19% of total CNESS variation. At Station. 35, *M. ambiseta* was the fourth most important contributor, accounting for 9% of community structure

0.5 variation. Nephtys incisa, an important contributor to CNESS distances in the oiled t inshore Station 9 (4th ranked, 6% of CNESS variation) was a relatively small component at Station. 35 (18th ranked, 1% of variation). Capitella spp., the 2nd most important

contributor to CNESS variation at Station. 9, was a very minor component of the offshore community (20th ranked, <1% of the variation in community structure).



The Sanders-Hurlbert rarefaction curves, shown in Fig. 10, show nothing remarkable. The August 1970 sample, which contained high numbers of *M. ambiseta* has a low species richness compared to the other 13 stations. The August 1971 sample, which had an anomalous community structure has the highest diversity of the 14 samples.

**Figure 10**. Sanders Hurlbert-rarefaction curves for the Station 35 data.





Figure 11 shows the non-dimensional diversity plots for Station 35. The three samples taken after the September 1969 oilspill are far less even than log-series expectation. The two samples from August and September 1970, dominated by *M. ambiseta* show the most severe departures from log series expectation. often are identical to those produced under the assumption that the individuals among species follow the log-series distribution. I developed a plotting procedure called a nondimensional diversity plot to show the relationship between rarefaction curves and their log-series expectations. The log-series

**Figure 11**. A non-dimensional diversity graph, produced by provides a benchmark against which to dividing the log-series expectation by the rarefaction curves judge the expected evenness for a Sanders-(shown in Fig. 10). The three Oct.  $70 \rightarrow$  Jan. 71samples and the late summer 1970 samples show drastic departures

from log-series expectation. The August and September 1970 samples had a very high frequency of *M. ambiseta* individuals.



**Figure 12**. Shannon's H' and Pielou's J' for Station 35, plotted against days from the oilspill.

Figure 12 shows Station. 35 Shannon's H' diversity and the evenness measure for Shannon's diversity, Pielou's J'. The only striking feature of this figure is the low Shannon's H' and Pielou J' for the August 1970 sample. Figures 11 and 12 show that this low diversity is due to a very high frequency of *Mediomastus ambiseta*, a normal component of the Buzzards Bay community. The striking departures from log-series expectation for the Oct.→Dec. 1970 samples observed in Fig. 14 is not evident in Pielou's J'.



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#### **Conclusions from West Falmouth**

The West Falmouth study is probably hated by the oil industry. Most studies of oil spills reveal rather short-term effects on benthic communities. Often the most harmful effects from oilspills results from the detergents used to remove the oil from littoral rocks. Howard Sanders, Fred Grassle, George Hampson, John Farrington and the other WHOI scientists who sampled after the West Falmouth oilspill were able to document the long-term pernicious effects of even a modest oilspill.

In recent reports summarizing the Exxon Valdez oilspill, the West Falmouth study was again cited as the exception to the general rule of the short-term effects of oil pollution. Some of the conclusions from the West Falmouth oilspill study are:

- The immediate effect of the oil was to drastically reduce the amphipod component from inshore moderately oiled sites. There was nearly complete mortality of the natural fauna in the most heavily oiled sites.
- Species richness was not a good indicator of the long-term effects of pollution. Species richness remained high throughout the West Falmouth study at both heavily oiled inshore and lightly oiled offshore stations.
- The oilspill caused severe changes in community composition and species evenness
- The long-term effects of oil alter the normal recruitment patterns to the community. This could be from the removal of key predators of settling larvae or alterations of the habitat that increase the larval recruitment of opportunistic species.
- While there was initially a bloom of opportunistic *Capitella* spp., the major alterations in community structure were due to anomalous frequencies of species that were normal components of the Buzzards Bay community
  - *Nephtys incisa* and *Mediomastus ambiseta* increased tremendously in abundance relative to other species.
  - Species evenness declined rapidly
- The effects of the oilspill was long-lasting: at least 2.5 years.

Many of the features observed first in the West Falmouth oilspill were observed on a much larger scale in the Amoco Cadiz oilspill off the Normandy Coast of France (Cabioch *et al.* 1982).

Species richness was a poor predictor of the long-term effects of oil. However, there were drastic changes in species composition attributed to the effects of oil.



#### The Exxon Valdez oilspill



## O Reference △ Light □ Moderate ◇Heavy

**Figure 16**. Ordination diagram for middle intertidal pebble/gravel samples from the 1990 Prince William Sound survey. The 95% probability ellipse is estimated from the subset of samples from unoiled reference sites, assuming a bivariate normal distribution of sample scores. Only a single heavily oiled site had community structure sufficiently different from the reference are to fall outside the 95% confidence ellipse. Fig. 8 from Gilfillan et al. (1995).

Gilfillan et al. (1995) used canonical correspondence analysis (ter Braak 1986) to assess changes in benthic community structure due the March 24, 1989 oilspill due to the grounding of the Exxon Valdez on Bligh reef in Prince William Sound in Alaska. The spill of  $4.1 \times 10^7$  liters of Alaska North Slope Crude oil was assessed by a probability-based survey design during the summer of 1990. Gilfillan et al. (1995) analyzed the effect of oil on changes in community structure as documented by canonical correspondence analysis. The ordination was constrained so that to assess only those changes in species composition not related to changes due to wave action, grain size and total organic carbon loading. Figure 16 shows the results of their ordination. These authors don't present what portion of total community variation were explained by their ordination. Using this method, there is a possibility that the effects of the oil spill could have been

underestimated if oil effects were correlated with their covariates of wave exposure, grain size, and total organic carbon.





Figure 17. The salinity and Total Organic Carbon normalization used by Schimmel et al. (1994) in developing species or trophic groups were affected by the 1991 EMAP-E biotic index is plotted. The expected number of species continues to decline, reaching about -150 expected species at 8 x  $10^4 \mu g/g$  (8%) Total Organic Carbon. Figure based on equations in Schimmel et al. (1994)

Figure 17 shows the effects of total organic carbon and salinity on the expected number of benthic species per grab in the Virginian province EMAP benthic survey conducted from 1990-1993. Total organic carbon is a master variable in coastal sediment systems. It not only causes changes benthic community structure, especially due to its association with increased benthic oxygen utilization leading to anoxia and hypoxia, but it is also affected by changes in benthic community structure. The presence of an active benthic community is associated with higher bioirrigation rates which tends to 4keep organic matter concentrations low. Gilfillan et al (1995) had the appropriate data for determining whether individual the oil. Gilfillan et al. (1995) only assessed the effects of oil on univariate response variables after removing the statistical

variation due to percentage sand, percentage silt/clay, TOC and wave exposure.

Since grain size, wave exposure and organic carbon concentration in the sediments are often the major correlates of changes in community structure, the decision by Gilfillan et al. (1995) to restrict their analysis to only those changes statistically independent of these variables, may have resulted in their ordination explaining a tiny percentage of community structure variation. Note, that it was perfectly appropriate for Gilfillan et al. (1995) to include these covariates in their canonical analysis, a procedure described as one of the strengths of canonical correspondence analysis (CCA) by Palmer (1993, p. 2224):

"CCA offers a new opportunity for gradient analysis: the ability to "factor out" environmental variation in what is termed a partial ordination (ter Braak 1988). This could be very important, for example, if one wished to factor out site-to-stie variation in testing for long-term successional patterns, or to factor out geological effects if the focus is on species responses to anthropogenic stress. [emphasis added] The variables to be factored out are known as 'covariables.' "

Their method may provide a sensitive indicator of change in community structure, but their change in community structure may only consitute a minor portion of the variation in community structure. If wave exposure, grain size and organic carbon concentration are major determinants of cobble & gravel community structure, then the first two dimensions of an ordination might only explain 10% of the total variation in community structure, rather than say 60%. One could regard these external variables as merely adding to the "noise-to-signal" ratio, reducing the



power of statistical tests, or one could regard these variables as major determinants of community structure that must be included explicitly in the analysis rather than removed statistically. These apparent weaknesses in the inferential arguments in **Gilfillan et al. (1995)** could have been easily remedied by presenting the proportion of total community variation explained by the two-dimensional snapshot of community structure shown in Figure 16.

Despite the weaknesses in the analysis by **Gilfillan et al. (1995)**, the goal was admirable. It **is** important to deal with covariates in an analyses of community structure. It **is** important to reach conclusions on the basis of multivariate analyses. It **is** important to couple the results of multivariate analyses to applied research problems, e.g., "What percentage of the area of Prince William Sound was still affected by oil in 1990?"

In a remarkable report, **Coats (1995)** developed detrended principal components analysis as a modified version of Gallagher's PCA-H method (described in **Gallagher et al. 1992**, **Trueblood et al. 1994**). Both used detrending, which probably wasn't necessary or even recommended for either analysis. **Wartenberg et al. (1987)** showed that detrending has little theoretical justification and often destroys the underlying structure of multivariate data, making interpretation difficult. Both developed methods to remove the variation in community structure due to grain size and organic carbon concentration (although Coats chose to use clostridium spores as a covariate instead of TOC). Both developed test criteria based on the bivariate normal confidence ellipse to classify sites as either being similar to a set of reference sites or



**Figure 18**. **A.** Linear response model in PCA and RA. **B**. Unimodal response model in (D)CA and CCA. Figure 3.1 and 3.2 from ter Braak & Šmilauer (1998).

significantly different from reference sites. Both methods gave clear answers to problems, and both methods allowed - calculation of the statistical power to assess changes in community structure.

**Coats'** (1995) method differs from Gilfillan et al. in a number of ways. Gilfillan et al. (1995) used correspondence analysis while Coats used principal components analysis. **Coats (1995)** analyzed the variation in CNESS faunal distances among sampling sites, while Gilfillan et al. (1995) analyzed variation in chi-square distances among sampling sites (this is not stated explicitly in the paper, but correspondence analysis is a partitioning of chi-square distances). ter Braak & Prentice (1988) argued that CA and PCA differ theoretically in the underlying models of species distributions with correspondence analysis assuming a unimodal response model and principal components and redundancy analysis models following a linear response model. Figure 18, from ter Braak & Šmilauer (1998), shows the linear and unimodal response models. Since the unimodal response model, shown in Fig. 18B seems to correspond to standard views of the distribution of species in nature (the Gleasonian continua model), it might appear that the





correspondence analysis model is superior theoretically. This is not the case. Legendre & Gallagher (2001) show that correspondence analysis, principal components analysis, and redundancy analysis can be solved with the same eigenanalysis or singular value decomposition algorithm. The methods differ only in the transformation of the underlying sample x species matrix. The unimodal response model in correspondence analysis is due to the simultaneous double standardization of species abundances by both total species abundance in each sample and by sample abundance. PCA-H also standardizes by all species data in each sample, normalizing by the Expected Species Shared, a diversity index (described first in Grassle & Smith 1976, and used explicitly as a diversity index by Smith 1989). One motivation behind normalizing by diversity is that faunal similarity should reflect turnover in species and not change in the number of species. PCA-H also standardizes by species, dividing each normalized species frequency by the mean of the species column. One benefit of the PCA-H data transformation is that rare species do not need to be dropped. The simultaneous double standardization used in correspondence analysis is akin to normalizing species frequencies by the variance in frequencies across samples. Thi can often produce the anomalous result that the major contributors to distances among samples in ordination space are rare species, especially if these species are found only in sparse samples (Nov-Meir et al. 1975). PCA-H also scales scores across samples, by simply centering abundances. By choosing a large random sample size, PCA-H like the NESS and CNESS faunal association measures on which it is based, is sensitive to rare species but the method isn't dominated by these rare species. To avoid the rare species effect, Gilfillan et al. (1975) dropped the rarest 20% of species from their data. One might make the argument that these rare species in a region are the ones most likely to show a long-term effect from an oil spill. Abundant species might recruit in rather more rapidly. One telling difference between the CA and PCA-H models is that ecologists almost never perform a chi-square clustering of samples – it doesn't make ecological sense. Ecologists have developed faunal association indices that match their understanding of community ecology. Benthic ecologists often use NESS, and more recently, CNESS. Both these indices are often highly correlated with many more common association indices. The PCA-H method is a partitioning of an ecologically meaningful faunal association index; but the CA and CCA methods partition chi-square distances.

#### The GEEP workshop: analyzing benthic samples from a Norwegian fjord

John Gray convened some of the top applied benthic ecologists to a GEEP workshop (Group of Experts on the Effects of Pollution) from around the world to compare methods with a pair of benthic data sets. The results are described in a series of papers from the same volume of Mar. Ecol. Prog. Ser. (Bayne *et al.* 1988, Clarke & Green 1988, Gray *et al.* 1988, Heip *et al.* 1988, Underwood & Peterson 1988, Warwick 1988). The first set of data was the species data from twenty-four grab samples from six stations along a putative pollution gradient in a Norwegian fjord. The second set of data was from a mesocosm experiment designed to assess the effects of copper on benthic community structure. A variety of methods were used to analyze both sets of data. None were really successful, but the most successful of the lot was Bob Clarke's non-metric multidimensional scaling of species composition among sites.

Lauren Cleary, in her UMASS/Boston M.Sc., reanalyzed the GEEP data with PCA-H and Sanders rarefaction. The metric scaling of CNESS m=20 is shown in Fig. 19. This figure shows



that the within station variation was relatively low. The biggest pattern is the triangle formed by the E, A and B-C groupings. Each of these endpoints on the triangle are about  $\sqrt{2}$  CNESS units apart, indicating that these three endpoints share virtually no species. Station B was similar to C, and the combined group B-C was similar to group D. Station A, from a sandy site outside the harbor, was very different from the remaining stations. However, this station was more similar to the fused cluster B-C-D than to the E and G stations. Unfortunately, Figure 19 by itself says nothing about which stations might be impacted by pollution.

The Gabriel Euclidean distance biplot, shown in Fig. 19 sheds more light on the pollution gradient. The shallow water, mesohaline capitellid polychaete *Heteromastus filiformis* (Hf) is the most important species contributing to CNESS distances among stations. *Heteromastus filiformis* accounts for 9% of the total CNESS variation among samples.



**Figure 19**. Sanders Hurlbert-rarefaction curves for the GEEP data.



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The GEEP experts calculated Shannon's diversity and evenness for the 24 samples and concluded that diversity was a poor indicator of the pollution gradient (Their problem in interpreting the results was due to the mistake of calculating half the diversities with Shannon's formula with log base 2 and the other half with natural logs). The Sanders-Hurlbert rarefaction curves, shown in Fig. 20 reveal that diversity was informative. Site A clearly has the highest species diversity of the 6 sites and site C the lowest. The rarefaction curve shows that sample C4 has the lowest diversity of the samples, despite its having a total number of species close to the median. It is



**Figure 20**. Sanders Hurlbert-rarefaction curves for the GEEP data.

difficult to discern clear differences between sites B, D, and E, and G in terms of the rarefaction curves.





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Figure 21 shows the 24 non-dimensional diversity curves produced by dividing the Sanders-Hurlbert rarefaction curve by the log-series expectation. John Lambshead at the British museum has found that the departures from the log-series is indicative of recent disturbance. Using this criterion then, samples B4, C2, C3, C4, E3, and D1 may have been recently disturbed. All of the samples from sites B, C, D, and E exhibit distributions of individuals among species that are considerably less even than the log series expectation, except for sample C1 and D3. These two samples had the lowest total number of species (Fig. 20), but after

**Figure 21**. A non-dimensional diversity graph, produced by rarefaction they appear to have species dividing the log-series expectation by the rarefaction curves diversity comparable to or higher than the (shown in Fig. 20. The horizontal dashed lines at 0.75 and other samples.

1.25 are rough benchmarks for severe departures from logseries expectation.

#### ECOTOXICOLOGY

#### Introduction

Benthic community structure changes in response to pollution gradients. Species diversity and species composition change in response to changes in pollutant loads. But how do pollutants affect the benthic infauna and can we predict the effects of pollutants at the community-level? In particular, can we establish sediment quality criteria (SQC) for pollutants that will predict whether a given concentration of pollutant in the sediments will cause a change in community structure? It is now well established that the total concentration of a potentially toxic substance is a poor predictor of effects at the community level. Much of the pollutants in sediments are not bioavailable. For example, PAHs may be bound in relatively inaccessible charcoal-like soot particles. Heavy metals may be bound to sulfides or organic compounds, rendering them relatively non-toxic.

#### Predicting pollutant effects at the community level

There are three major approaches being used to define Sediment Quality Criteria for heavy metals and hydrophobic organic pollutants:

- ERM & ERLs
- Equilibrium partitioning for nonionic hydrophobic pollutants
- SEM/AVS ratios for divalent heavy metals



The Long & Morgan (1990), Long et al. (1995) ERM & ERL approaches are an atheoretical approach to assessing toxicity. ERM stands for Effects Range Median and ERL stands for Effects Range Low. These authors have compiled a large database including studies of chronic toxicity using amphipod tests, bioaccumulation, and alterations in community structure. Studies that include both a pollutant concentration and an effect are eligible for inclusion in the database. All effects are assumed equal. Thus, a study documenting a dramatic change in community structure associated with increased concentrations of a variety of heavy metals and hydrophobic organic pollutants would count as 1 effect. A study with a single compound showing bioaccumulation relative to a control sediment would count as another effect. Hundreds of studies are compiled in the database. For each pollutant (e.g., copper), the records in the database are sorted from highest to lowest concentrations of the pollutant. The pollutant concentration at the point at which 50% of the studies have shown one effect or another is marked as the ERM concentration. The pollutant concentration below which only 10% of the studies showed some kind of effect is marked as the ERL concentration. The ERM and ERL values are expressed as the weight of pollutant over the dry weight of sediment. Since organic carbon concentration is often not measured in studies used in the database, there is no normalization by organic carbon.

#### **Bioavailability**

#### Metals & the SEM/AVS ratio

It is well established that the free-ion activity determines the toxicity of a metal. In both sediments and the water column, metals that are complexed with ligands are not toxic. Heavy metals, like copper, can be complexed with organic ligands and as metal-sulfide complexes. DiToro *et al.* (1989, 1992) have argued persuasively that acid-volatile sulfides (AVS) can effectively bind to and detoxify heavy metals in sediments. Acid volatile sulfides are usually found as FeS or iron sulfides. DiToro *et al.* (1989) showed that in the presence of unbound divalent cationic heavy metals, like Cd, Cr, Cu, Hg, Ni, Pb, Zn, the Fe is displaced from the FeS complex by the heavy metal, which forms an insoluble Me-S complex. Metals bound as insoluble sulfide complexes are not bioavailable and are not toxic.

DiToro *et al.* (1989, 1992) have argued that there are a variety of sulfide phases in natural sediments. The 'reactive' sulfide phase can be extracted using cold 0.5 M hydrochloric acid. DiToro *et al.* (1989, 1992) argue that the cationic heavy metals should be measured using the same cold HCl extraction. Metals extracted in this way are called the SEM, for simultaneously extractable metals. If the molar ratio of SEM to AVS, or SEM/AVS, is less than 1.0, then none of the divalent cationic heavy metals are toxic. If the SEM/AVS ratio is greater than 1.0, then the sediments may or may not be toxic. Even if SEM>AVS, the metals may be bound by organic ligands and not bioavailable.

#### Nonionic hydrophobic organic compounds

Like heavy metals, it is only the bioavailable fraction of potentially toxic organic compounds that controls toxicity. In general, only the dissolved unbound form of potentially toxic organic compounds that controls toxicity and bioaccumulation. **DiToro** *et al.* (1992) proposed an





equilibrium partitioning approach to predict the SQC for nonionic hydrophobic organic pollutants. Their proposal has the following components:

- Only the unbound, dissolved form of organic pollutants is toxic.
- The concentration of the dissolved form in the porewater is inversely proportional to the sediment organic carbon concentration.
- The fraction of unbound and bound organic pollutants can be predicted if the octanol water partition coefficient is known and if the concentration of organic carbon in the sediment is known.
- It is assumed that the major route of exposure is via the porewater.
- An analysis of benthic and pelagic organisms indicate similar chronic toxicity to the unbound dissolved forms.
- If this is true, then water quality criteria (WQC) can be extended to the sediments if the octanol-water partition coefficients are known.



Figure 22 Some routes of exposure of toxic pollutants to benthic organisms. The dissolved, unbound form of the pollutant, shown in red, is the major toxic form, and the most likely route of exposure is via porewater and overlying water used for respiration. Animals can also be exposed to toxic substances via their food: for deposit feeders this is indicated by ingestion of deposits and predation. The kinetics and partitioning of bound and unbound pollutants in the gut is largely unknown. Pollutants bound in pellets and soot particles are not readily bioavailable.

Figure 22 shows a schematic diagram showing the two major modes of exposure to benthic organisms: respiration and food. Campfens & Mackay (1997) modeled the process of biaccumulation and bioconcentration in benthic and pelagic organisms. Respiration is a major route of exposure for all organisms. Organisms will acquire pollutants in direct proportion to the partition coefficient between the organism and the concentration of the dissolved form in the water used for respiration. In essence, animals are modeled as if they are bags of lipids. In nature, organisms can also acquire pollutants from their food. This can include both the sediments, associated organic matter and pollutants and other organisms. Without these trophic pathways, organisms would come to a chemical equilibrium with the water used for respiration. Benthic organisms, which can use the overlying water for respiration, will have a lower pollutant concentration than one that uses sediment interstitial water for respiration, since interstitial water has a higher pollutant concentration.



Eugene Gallagher



umb

#### What is the route of exposure?
A benthic organism that eats other benthic organisms can receive higher pollutant loads, if the prey contains a higher body burden. The organism can come to a steady-state pollutant concentration, even though its body burden is not in chemical equilibrium with the surrounding porewater. Biomagnification refers to the accumulation of a pollutant in excess of that expected from equilibrium partitioning. **Campfens & Mackay (1997)** model a food web in which two fish species, with identical lipid contents (an important parameter in modeling the partitioning of hydrophobic pollutants) could have drastically different pollutant loads. The fish could differ even though they respire with the same water if one feeds on benthic organisms with a high pollutant concentration and the other feeds on pelagic organisms with a lower pollutant load. The trophic pathways of fish are an important component in modeling bioaccumulation and biomagnification.

Deposit feeders pose a challenge for equilibrium partitioning theory. These organisms ingest sediments with a high concentrations of pollutants, and they respire using interstitial water (and the immediately overlying water). **DiToro** *et al.* (1991, p. 1568) argue that the route of exposure could be either the deposits or the porewater, but pragmatically it makes little difference. If the sediments are in chemical equilibrium with the porewater (at equifugacity), then the partitioning from the particles to the organism via the gut should be similar to the partitioning between the porewater and the organisms respiratory surfaces (*e.g.*, gills, branchiae, or body walls). The unknown feature involves the digestive process. Presumably, the proteolytic enzymes in a deposit-feeder's gut would make pollutants more bioavailable, increasing the importance of this mode of exposure.

### Colloids, fecal pellets, and soot

Brownawell & Farrington (1985, 1986) and Farrington (1985) have argued that it is insufficient to consider sediments as a two-phase system: porewater and sediment particles. They provide persuasive evidence that colloids, which are organic-rich particles which pass through conventional 0.4-µm sieves must be considered as well. This organic colloid phase is often indistinguishable from the dissolved organic phase in sediments. Hydrophobic organic pollutants will partition onto this organic colloid phase. **DiToro** *et al.* (1991) argue that this organic colloid phase is not bioavailable.

This colloid phase can affect the distribution of hydrophobic organic pollutants in sediments. Pollutants in the colloidal phase will diffuse in the porewater and can be moved by bioirrigation from the benthic infauna. Particle-bound heavy metals and particulate-bound organic compounds would not be moved by bioirrigation.

Fecal pellets can be an important phase in polluted marine environments. For example, up to 75% of the weight of sediments in some areas of Boston Harbor are bound into fecal pellets. Karichoff was the first to model the effects of pellets on pollutant profiles. Pellets tend to be organic-rich and anoxic particles. Both nonionic hydrophobic pollutants and heavy metals can be sequestered in pellets, and are not readily available for chemical partitioning into the porewater. Pollutants in pellets are not bioavailable for two reasons: they are generally bound to organic matter, and organisms rarely ingest fecal pellets.



**Chin & Gschwend (1992)** and **McGroddy et al. (1996)** have modeled the role of soot in controlling the distribution and bioavailability of PAHs in Boston Harbor sediments. After running three phase models — dissolved PAH, colloidal PAH, and particulate PAH — it was found that far too much PAH remained bound to the particulate phase. These authors have argued that the PAHs are bound in soot particles and the PAHs are not available for partitioning into the dissolved and colloidal phases. Wang et al. (2001) also argued that soot plays a role in controlling the partitioning between dissolved, colloidal and particulate phases, but they also noted that Boston Harbor sediment PAHs are sorbed within *Capitella* fecal pellets.

# **Terms & concepts**

**ANOSIM** A technique developed by **Clarke & Green (1988)**, based on Dietz' permutation tests and ultimately on Mantel's work on cancer clusters. Are two similarity matrices more similar than chance alone would indicate?

half-change unit defined by Woodwell (1967), quote from Westman (1978): "Woodwell (1967) calculated percentage similarity in measuring changes in an oak-pine forest exposed to chronic gamma irradiation. He noted, however, that species richness was a more uniformly varying index of community change to chronic gamma irradiation than was percentage similarity. Using the level of irradiation at which species richness is reduced by 50%, Woodwell's studies permit comparison of the inertia of several

# **Outlines**

## ASSIGNED

Grassle, J. F. and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. J. Marine Research 32: 253-284. {5, 6, 20, 45}

Species that rapidly respond to open environments:

- opportunistic, colonizing, or r-selected
  - Characteristics

plant assemblages."

- lack of equilibrium population size
- density independent mortality
- ability to increase rapidly or high r
- high birth rate
- poor competitive ability
- dispersal ability
- None of these features alone can define an opportunist
- Wilson & Bossert (1971): (r-strategist): a species "adapted for life in a short-lived unpredictable habitat."
  - discovers habitat quickly
    - reproduces rapidly
    - disperse in search of new habitats as the existing one grows unfavorable.
- Grassle & Grassle propose to use high mortality as a measure of the degree of opportunism



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- Succession following an oil spill and filed experiments.
  - IV: muddy sand station. *Capitella* grew most quickly followed by *Microphthalmus aberrans*, *Polydora ligni*, *Syllides verrilli* and *Streblospio benedicti*.
  - P. 261> After the spring increase, the decline resulted from any one of a combination of resource depletion, predation, an possible accumulation of toxic metabolites.
- Definition of opportunistic species:
  - We propose defining degree of **opportunism** both in terms of ability to respond to unpredictable events and the mortality rates sustained by the species.
  - Thus high abundance, high reproductive rate and high mortality rate are all part of the life history of the opportunist.
  - There are 2 major life history patterns in marine benthic opportunists. Each of the most opportunistic polychaetes are both able to disperse widely by means of planktonic larvae or rapidly exploit local resource through direct development or a brief planktonic existence.
- Opportunists and community characteristics.
  - Most predictable environments should have more specialized (less opportunistic) species and less predictable environments should have more opportunistic species.
  - Communities with higher diversity generally have smaller average population size
- Mortality and Demand-to-Resources ratio.
  - the low demand-to-resources ratio and high productivity to biomass ratio found in communities characterized by species with high reproductive capacity are the product of a high turnover of individuals.
  - A direct consequence of the longer life spans of the species.
  - The poor competitive ability of the polychaete opportunists may result from a shortage of the most labile food components. A species such as *C. capitata* may digest only the parts of the sediment that may be most readily converted to tissue to sustain the high growth rate.
- Summary:
  - Species with the most opportunistic life histories increased and declined at the 2 stations with the greatest reduction in species diversity
  - Initial response to disturbed conditions, ability to increase rapidly. Large population size, early maturation, and high mortality are all features of opportunistic species.
  - The most opportunistic species live in environments of low predictability. According to our definition of predictability, adaptation to unpredictable environments is through short-term selection. The ability to survive depends on the variety of larval genotypes rather than the physiological tolerance of an average individual
  - Since adaptation is based on short-term selection, emphasis is placed on large population size.
  - 2 types of benthic opportunists:
    - mixed strategy variety has obligate planktonic dispersal
    - Ind type includes *Capitella*. The larvae are not lost to the subpopulation or swamped by larvae from surrounding areas since they are ready to settle shortly after release from brood structures.
  - Community characteristics such as diversity and ratio of productivity to biomass in unpredictable vs predictable environments are directly related to the spectrum of life histories or degree of opportunism of the component species. Species diversity indicates the spectrum of population sized and the productivity/biomass ratios are related to total mortality.

#### Rhoads, D. C., P. L. McCall, and J. L. Yingst. 1978. Disturbance and production on the estuarine seafloor. American Scientist 66: 577-586. {6, 6, 23, 40, 54, 58}

- 1. Introduction
- 2. disturbance important
- 3. theories linking succession and production
- 4. disposal of dredged sediment and sludge
- 5. can be managed to improve production
- 6. The estuary
- 7. definition of estuary and Long Island Sound
- 8. sources of disturbance
- 9. Odum's 1969 model modified Table 1





One can rank most colonizing species according to their time of appearance in succession, their temporal and spatial persistence, and their rates of population growth and decline (Table 1):

 Table 1 Characteristics of early and late stages of soft-bottom benthic succession from Rhoads

 et al. (1978)
 Many of these predictions are consequences of allometric relationships and body

 size, which increases with succession..

Characteristic	EARLY STAGES	MATURE STAGES
Organism size	small	large
Life cycles of species	short	long
Growth of individuals and populations	rapid	slow
gross production to standing crop (P:B)	high	low
feeding mode or strategy	suspension & surface deposit feeding	subsurface d feeding
Use of buried detritus	less important	more important
Symbiosis within system	undeveloped	developed
Nutrient conservation	poor	good

Table 2 Colonizing species from Rhoads et al. (1978)		
SUCCESSIONAL GROUP	Species	
	Streblospio benedicti	
Group 1	Capitella	
	Ampelisca abdita	
~ •	Nucula annulata	
Group 2	Tellina agilis	
	Nephtys incisa	
Group 3	Ensis directus	

#### 10. **Two experiments:**

- a. McCall's (1977) tray experiment
- b. Dredge spoil experiment
- 11. Recovery to ambient
- **Fig. 4:** The Bray-Curtis Faunal similarity index indicates similarity in faunal composition between an experimental site and its ambient environment. Convergence =1... the faunal composition of the dump will not match the ambient assemblage until the dump site has passed through earlier successional stages and the climax stage has had a chance to develop. This may require several years.
  - a. tray experiment converged after 240 d.
  - b. dredge site only ate 20% similarity after 480 d.



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#### 12. Succession and productivity

- a. disturbed bottoms dominated by fast growing species.
- b. Pioneering species have a negligible effect on sedimentary properties below the surface of the bottom
- c. A kind of microbial garden results.
- d. Development of a microbial garden probably requires a period of several years.
- e. Estimates of production

#### 13. Managing disturbance.

a.

- don't put in communities that are already disturbed
  - i. they already have high productivity
  - ii. storms make management difficult
- b. system-specific pulsing frequencies.
- c. deep-water sites hold the greatest potential for production enhancement
- d. cap the material
- e. poor understanding of what a mature benthic community is
- f. Long Island sound changed from Sanders 1956.

## SUPPLEMENTAL

Pearson, T. H. and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Ann. Rev. 16: 229-311 {6, 13} What are the patterns & processes

- 1. Fluctuations in organic input may be considered to be one of the principal causes of faunal change in near-shore benthic environments p. 229
- 2. Experimental studies have been few, relatively unsophisticated and normally associated with -and dependent upon-field sampling programs.
- 3. Bias toward boreo-temperate areas in the data available.
- 4. Despite these limitations, even a cursory glance at the data suggest that there is a consistent pattern to the faunal changes observed along a gradient of increasing organic input to marine sediments.
- 5. Goals

a.

8.

- a. to describe and analyze the pattern
- b. to interpret it in terms of accepted tenets of benthic ecology
- c. to expose parts that are poorly understood
- 6. Organic gradient effects can be discerned through variation in space, or more relevantly, in time.
  - a. seasonal studies: Bagge, Boesch 1973
  - b. years: Dean & Haskins, Pearson, Rosenberg, Lie & Evans, Grassle & Grassle
- 7. They follow Mills' definition of a community

#### Changes in numbers of species, abundance and biomass in response to organic enrichment

- a. A benthic community in a fairly stable environment undergoes only small-scale quantitative and qualitative changes with time.
- b. Abnormal environmental variability in either space or time disturbs community stability and gives rise to changes in the basic parameters.

#### 9. Spatial changes along a gradient of organic enrichment

- Saltkallefjord, a 5 km long, narrow fjordic estuary on the Swedish coast.
  - the wood pulp fibre from a sulphite pulp mill.
- b. SAB curves:
  - i. summarize the changes in the basic faunal parameters occurring along transacts originating at the effluent discharge points and culminating in areas beyond the effects of the discharge material
  - ii. Sediments in the vicinity of the discharge point are devoid of benthic macrofauna.
  - iii. **ecotone point**: a transition zone within which is a community poor in species, abundance, and biomass. On the polluted side of this point, the community is composed of a few pollution-tolerant opportunistic species. On the less polluted side of the ecotone point the different transitory assemblages gradually approach the composition of the community in the unpolluted environment. The community at the ecotone point consists of species from both adjacent communities.





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iv. Biomass: there is an initial small peak in biomass corresponding to the maximum abundances of small opportunistic species, followed by a decline to the ecotone point, Beyond this, the biomass increases to a second higher maximum as a greater variety of larger species are encountered,, and finally stabilizes at a somewhat lower level as the normal non-polluted communities develop. The secondary biomass maximum probably occurs in that area of the gradient where organic enrichment of the sediments is sufficient to proved a rich food source but not yet high enough to case serious oxygen depletion.

#### Fig. 2. Generalized SAB diagram.

Sanders Grassle & Hampson

#### 10. Temporal changes in an organically enriched environment

"The changing SAB relationship described above as taking place along a gradient in space of decreasing organic enrichment may also be shown to occur along similar gradients in time." P. 235

- a. As inputs increases species number and biomass initially increase, then decrease to the ecotone point, followed by secondary maxima of biomass and abundance associated with a few small opportunistic species which, if enrichment proceeds further, then fall off rapidly to an afaunal state.
- b. Saltkallefjord in Sweden

#### i. Pollution abatement after 1966

"The first opportunists appeared in high numbers, then rapidly decreased as more species were added to the community. This reduction was followed by a secondary increase, or `overshoot' **prior to stabilization of the successional sera**." "Although the succession of species is a smooth and continuous process, the abundance of individuals among those species changes rapidly. The bell-shaped population dominance curves from two of the stations show a complex succession of species whose interrelationships are not easily ordered into any one interpretable direction, probably resulting from rapid fluctuations in environmental conditions."

#### 11. Migrating Communities.

"the opportunists were short-lived and show vigorous seasonal variations, which suggest that the PO might be reduced or even disappear over shorter periods in response to short term environmental variations."

"Moreover, the change in `health status' of a polluted region may quite easily be assessed by recognizing changes in the PO-point with time, <u>viz.</u>, if the PO-point moves away from the discharge point during successive sampling periods then pollution is increasing and if the PO-point approaches the discharge point, pollution is decreasing."

"Thus the concept of migrating communities implies a successional replacement of one community by another, i.e., it is equivalent to the ecological process going on continuously all over the world on a long time scale in response to environmental change, but in perturbed environment the changes are of short duration and so more conveniently studied."

#### 12. Changes in diversity

b.

"Community diversity is both niche and time-stability dependent, i.e., more niches open the doors for a higher diversity, thus a heterogeneous sediment accommodates a higher infaunal diversity than a homogeneous one and environmentally stable regions demonstrate higher diversity than unstable ones."

a. Rarefaction technique

Fig. 6: No. species/1000 individuals calculated by Sanders rarefaction technique.

Shannon-Wiener function:



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

where,  $p_i = frequency \ of \ species \ i \ in \ sample.$   $p_i = \frac{N_i}{N}.$   $N_i = Number \ of \ individuals \ of \ species \ i.$   $N = Total \ individuals \ in \ sample.$   $S = Number \ of \ species.$  $\log \ could \ be \ base \ 2, \ 10, \ or \ natural \ log.$ 

Evenness:

$$J' = \frac{H'}{H_{\text{max}}}.$$
$$H'_{\text{max}} = \log S.$$

Fig. 8: Abundance and diversity (Shannon-Wiener, H, and its evenness, J) during succession following pollution abatement. diversity is maximum at the ecotone point following the peak of the opportunists. Watling: He supports Hurlbert in stressing the advisability of suiting the index to the type of information required. The information statistic should be used if the interest lies in the bits of information per individual, but if the probability of intraspecific encounters is being considered than a probability measure such as the PIE of Hurlbert should be used... Watling suggests that the scaled standard deviation (SDN) of Fager (1972) which reflects changes in dominance and the degree to which resources are being shared is a particularly suitable statistic for assessing perturbations brought about by pollution.

#### c. Concluding remarks about species diversity

- i. the use of diversity indices to assess faunal change is increasing rapidly.
- ii. make within habitat comparisons

"there is grave temptation to attribute to those figures some universal significance and assume that they are immediately comparable with any other figures similarly derived, despite inconsistences in the origin and treatment of the data. Any comparisons should be carefully qualified by a detailed examination of the basis of the data being used."

13. **The utility of similarity indices and ordering techniques in assessing response to enrichment.** The above brief survey suggests that similarity indices are useful for analyzing differences in community structure along gradients of organic enrichment

#### 14. Indicators and opportunists - species associated with enrichment.

15. The use of single species, or groups of species to characterize the degree of organic pollution of a body of water has a long history in freshwater systems.

"Thus, the capitellid polychaetes and <u>Capitella capitata</u> in particular have long been used in this context. It has frequently been pointed out, however, that as many instances of the occurrence of such species in organically poor areas can be quoted as of their occurrence in enriched areas."

- a. Nevertheless, a fuller analysis of the species common to organically enriched areas and the elements common to the observed species successions is helpful in attempting to understand the basic mechanisms of those successions.
- 16. It has previously been pointed out that species changes along a gradient of increasing organic enrichment take the form of a continuous succession rather than a series of distinct groupings.

Fig. 12 Species succession in an area of Loch Eil subject to increasing inputs of organic material over a period of years. Table Ia-Ic opportunists

"It is apparent that when the amount of organic material reaching the sediments is very high then this is the overwhelmingly important environmental factor, and the species adapted to survive in these circumstances are both few and ubiquitous"



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#### 17. **Opportunists vs. enrichment species**

"There may be some advantage... in distinguishing between what may be termed general opportunists, i.e., the initial colonizers of any denuded area irrespective of the richness of the substratum, and `enrichment opportunists, which are initial colonizers only in organically rich areas."

"On the basis of the above evidence (based admittedly on a relatively small number of studies concentrated in N. America) it would appear that the majority of species associated with the early stages of succession following gross organic enrichment of an area are those also associated with successions following any major environmental disturbance which has resulted in the elimination or significant reduction of the normal fauna. Species particularly associated with the early stages of succession in organically enriched areas, i.e., those which might be termed enrichments species, appear to be very limited in number-indeed of the species in Table I - only <u>Capitella</u> and possibly <u>Streblospio benedicti</u> and/or <u>Scolelepis</u> <u>fulignosa</u> and the dorvelleid group might be considered to belong to such a category."

#### 18. **Parallel species**

opportunists are ubiquitous or have closely related equivalents in widely separated geographical areas.

- a. *P. ligni* and *P. ciliata*.
- b. S. benedicti and Scolelepis fuliginosa

#### 19. The influence of other physical factors on response to organic enrichment

- a. Salinity
- b. Sediment grain size mentioned

#### 20. Oxygen, redox potential, and temperature.

- a. An emerging R.P.D. will force the macrofauna up towards the sediment surface and thus reduce the number of niches available.
- b. Oxygen concentration important

#### 21. Water movement and enrichment

Low currents associated with high silt-clay

"Eagle (1975) discussed the interactions of bioturbation and water turbulence in controlling population growth in the benthos of Liverpool Bay, England. The activities of deposit-feeding species in creating instability in the sediment which was subsequently washed out during storm periods was considered to be instrumental in causing the replacement of one type of association by another."

#### 22. Biological Factors Associated with the response of benthic populations to organic enrichment.

- 23. Biogenic effects on sedimentary structure.
- 24. **Trophic-group amensalism**: a term summarizing the environmental incompatibility of suspension-feeders and deposit-feeders. The activities of deposit-feeding species in creating and maintaining a level of instability in the surface structure of fine sediments were shown to play a major part in excluding the settlement and development of populations of suspension feeders.

"As the amount of organic material reaching the sediments increases, the larger species and deeper burrowing forms are gradually eliminated and replaced by greater numbers of lamellibranch suspension- and surface deposit feeders. ... The resulting elimination of such species may well be due to a combination of factors arising from both the physical space restrictions resulting in a reduction below the "critical space value" for the species, and the direct effect of an increasingly adverse chemical environment. Those species surviving at this stage tend to be much smaller than those of the earlier, stages, although abundances may increase if conditions are not too severe."

"Changes along the gradient of increasing organic enrichment may thus be regarded as involving a progressive reduction in the complexity of the community structure and in the degree to which the sediment is reworked by the fauna. At the low input end of the gradient there is a complex physical and faunal structure made up of a mosaic of interrelated micro-environments which are largely maintained by the activities of animals which, in this area, encompass a wide range of physical size, with large individuals often forming the dominant component in the physical structure of the whole community (<u>cf</u>. the 'keystone' or foundations species' concepts of Paine 1969 and Dayton 1973.)...Although the sequence of the



progressive elimination of species can be followed, the reasons for the success and failure of particular species at any one stage or often obscure. The dominants in the higher input areas of the gradients are progressively smaller in physical size, confined to an increasingly narrow band of surface sediment, and the trophic structure is progressively simplified as the number of species is reduced."

#### 25. Changes in trophic structure:

- 26. Surprisingly few studies of changes in benthic communities have included a full consideration of trophic structure
- 27. the percentage of deposit feeders increases in response to increasing organic inputs "This analysis suggest that as organic input increases there is a decline in the selective surface feeders and an increase in the non-selective sub-surface feeders. Selective sub-surface feeders do not form a significant element of the fauna at any stage and are entirely eliminated under high input levels."

#### 28. **Recruitment in stressed communities**:

"most change is brought about by larval recruitment following mortality in the adult populations"

- 29. adult recruitment can be important in the colonization of a denuded area.
- 30. Rosenberg (1976a) emphasized that the time and frequency of larval recruitment should be an important factor

in determining benthic community structure, especially during the early seral stages of succession. "Species, which both as larvae and adults, can tolerate a highly organic sediment and the secondary effects of this, are naturally selectively favored. A second advantage is gained if the species can also reproduce successfully in such an environment and has low larval dispersion (non-pelagic development). Species having these characteristics among others are called opportunists (Grassle & Grassle, 1974) and have short term or -r-strategy reproductions)"

#### 31. Facilitation

b.

"<u>Capitella</u> and <u>Scolelepis fulignosa</u> are non-selective deposit feeders and have very high population densities in enriched areas. Though their activities they will have a considerable effect on the sediment structure and within a comparatively short time such populations will render the sediments suitable for the settlement of the larvae of other species which themselves further modify the structure of the substratum. Such modifications, together with the increased competition for the available resources, reduces the populations of the initial opportunist colonizers. Thus the succession proceeds and, in the absence of further excessive inputs of organic material, the community becomes increasingly complex as competition for the remaining organic material intensifies and feeding habits diversify, leading to the development of various coprophagous, bacteriophagous, and carnivorous populations."

"The first colonizers of an unexploited sediment seem to belong to the same species or genera all over the world. The composition of the transitory communities in the succession will, however, certainly show temporal variations from place to place and be highly dependent on reproductive success. It is well known that species have good and bad years...This might theoretically lead to a later establishment of multiple stable points (Sutherland 1974) during succession" (page 296)

#### 32. Stress tolerance of benthic communities

- 33. Species which tolerate low salinities dominate in polluted environments
- 34. Boesch (1972): typical species replaced by eurytolerant species.
  - a. Boesch (1974); although estuarine communities lack resistance (stability), they have high resiliency
    - Jernelov & Rosenberg (1976): features which render some species more tolerant to pollution
      - i. alternate biochemical pathways
        - ii. low genetic diversity

#### 35. General discussion and conclusions:

"If organic enrichment is of a certain magnitude it will superimpose its own gradient on the environment and induce modifications of the distribution of organisms initially controlled by, for example, salinity and temperature."

- 36. Between the 2 endpoints of Figure 20, we have defined three successional stages
  - a. the peak of opportunists, with few species in great numbers.



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- b. the ecotone point
- c. the transition zone with initially great fluctuations of the populations progressing towards the more stable normal community.
- 37. The final stage of a recovery process, *i.e.*, the `normal' community in the habitat, will naturally be habitat-dependent but is highly predictable for a region.
- 38. The ecotone point along a gradient of organic enrichment is a poorly populated area. During a recovery process much space and many niches are unoccupied...Thus, in contrast to the pioneer and `final' communities in the succession, which are highly predictable, the transitory communities are unpredictable.
- 39. Succession is equivalent to a process of accumulating information.
- 40. The ability of a community to withstand perturbations is not, in our opinion related to a community structure or diversity, but rather dependent on the ability of the individual organisms to adapt to the changed conditions.
- 41. In the absence of continued high inputs of organic material, the feeding activities of non-selective deposit feeders such as *Capitella* themselves cause rapid changes in the sedimentary micro-structure by pelletizing material and increasing the surface area available for microbial attachment. This in turn prepares the way for colonization by subsequent members of the succession.

42. **Pollution assessment** 

We have shown that definite boundaries rarely exist between pollution tolerant and non-tolerant communities, but rather that the change is gradual. Almost all studies in organically enriched areas of the world have shown that along such a gradient there is a peak of opportunists (PO) *i.e.*, a community where a few opportunist species are extremely abundant. This is suggested as an easily recognized reference point for the rapid assessment of the extent of organic pollution.

## **Web Resources**

Table 2. Web resources on pollution effects on benthic communities.			
URL	Site	Description	
http://www.nap.edu/execsu mm/0309084385.html	National Academy Press	Full html text of Oil in the Sea III: Inputs, Fates, and Effects (2003) Ocean Studies Board (OSB), Marine Board (MB), Transportation Research Board (TRB)	
http://eagle.nrri.umn.edu/p ubdefault.htm	Estuarine and Great Lakes (EaGLe) Coastal Initiative	Coastal research sites funded by EPA Star program	
http://www.savetheharbor. org/about_1.html	Save the Harbor Save the Bay	Environmental watchdog group for Boston Harbor & MA Bay	



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Underwood, A. J. and C. H. Peterson. 1988. Towards an ecological framework for investigating pollution. Mar. Ecol. Prog. Ser. 46: 227-234. [Some comments from the GEEP workshop] {31}

Underwood, A. J. 1997. Experiments in ecology. Cambridge University Press, Cambridge. 504 p.

Warwick, R. M. 1988a. The level of taxonomic discrimination required to detect pollution effects on marine communities. Mar. Poll. Bull. 19: 259-268. [Taxonomy to the species level is not needed.] {15}

Warwick, R. M. 1988b. Analysis of community attributes of macrobenthos of Frierfjord/Langesund fjord at taxonomic levels higher than species. Mar. Ecol. Prog. Ser. 46: 167-170. {15}

Warwick, R. M. 1988c. Effects on community structure of a pollution gradient -SUMMARY. Mar. Ecol. Prog. Ser. 46: 207-211. [Summary of results of GEEP workshop. Multivariate methods such as MDS and DECORANA compared. Field biomass spectra also analyzed.] {?}

Warwick, R. M. 1993. Environmental impact studies on marine communities: pragmatical considerations. Aust. J. Ecology 18: 63-80. [A very nice paper, criticizing the use of Caswell's (1976) neutral model and many other techniques for identifying disturbed communities. He advocates using meiofauna – no surprise since Warwick works with meiofauna] {70}

Westman, W. E. 1978. Measuring the inertia and resilience of ecosystems. Bioscience 28: 705-710. [Review of inertia, resilience, amplitude, elasticity, resilience, malleability. Includes a discussion of half-change units, used by Woodwell 1967] {38}

## GENERAL POLLUTION (SEWAGE; SEE ORGANIC ENRICHMENT, METALS AND OIL BELOW)

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- Armstrong, J. W., R. M. Thom, and K. K. Chew. 1980. Impact of a combined sewer overflow on the abundance, distribution and community structure of subtidal benthos. Mar. Env. Res. 4: 3-23. [Application of discriminant analysis]
- Aschan, M. 1990. Changes in soft bottom macrofauna communities along environmental gradients. Ann. zool. Fennici 27: 329-336. [3 areas were sampled, Shannon-Wiener diversity, PCA of 9 dominant species. Regression analysis to find environmental variables correlated with PCA axes. Pollution effects couldn't be discerned from natural environmental parameters]
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- Carlton, J. T. and J. B. Geller. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science 261: 78-82. [Marenzelleria viridis introduced to Germany in 1983. <u>Rangea</u> <u>cuneata</u> introduced from Southern US to New York in 1991]
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- Franz, D. R. and W. H. Harris. 1988. Seasonal and spatial variability in macrobenthos communities in Jamaica Bay New York - an urban estuary. Estuaries 11: 15-28. [Metals (Cd, Cu, Hg, and Pb) and TOC are negatively correlated with species diversity. cf., Effects of metals]

- Grassle, J. F. and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. J. Marine Research 32: 253-284. [See outline above] {5, 6, 20, 45}
- Grassle, J. F. and J. P. Grassle. 1978. Life histories and genetic variation in marine invertebrates. Pp. 347-364. in B. Battaglia and J. A. Beardmore, eds., Marine Organisms Genetics Ecology and Evolution. Plenum Press, New York.
- Grassle, J. F., R. Elmgren, and J. P. Grassle. 1981.
  Response of benthic communities in MERL ecosystems to low level chronic additions of No. 2 fuel oil. Mar. Env. Res. 4: 279-297. [90 ppb leads to large changes in species composition of the benthic communities in the MERL tanks.
  Smith et al. (1979) later showed that species diversity was less affected] {9}
- Gray, J. S. 1971. The effects of pollution on sand macrofauna communities. Thalassia Jugoslavica 7: 79-86.
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- Nichols, F. H. 1979. Natural and anthropogenic influences on benthic community structure in San Francisco Bay. Pp. 409-426 *in* T. J. Conomos, *ed*, San Francisco Bay: The urbanized estuary. Pacific Division, AAAS, San Francisco CA.



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- Reish, D. J. 1980. Effect of domestic wastes on the benthic marine communities of southern California. Helgoländer Meeresunters. 33: 377-383. [Biological enhancement at <18 million L  $d^{-1}$ ; biomass increases but diversity decreases at >40 million l  $d^{-1}$ ]
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- Rhoads, D. C., J. Y. Yingst, and W. J. Ullman. 1978. Seafloor stability in central Long Island Sound: Part I. Temporal changes in erodability of finegrained sediment. Pp. 221-244 in M. L. Wiley, ed., Estuarine Interactions. Academic Press, New York. {?}
- 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."] {6}

#### Rhoads & Germano (1986)

- Roper, D. S., S. F. Thrush and D. G. Smith. 1988. The influence of runoff on intertidal mudflat benthic communities. Mar. Env. Res. 26: 1-18.
- Roper, D. S., D. G. Smith, and G. B. Read. 1989. Benthos associated with two New Zealand coastal outfalls. J. Mar. Fresh. Res. 23: 295-309.
- Rosenberg, R. 1972. Benthic faunal recovery in a Swedish fjord following the closure of a sulphite pulp mill. Oikos 23: 92-108. [One of the studies that led to the Pearson & Rosenberg (1976, 1978) and Rhoads et al. 1978 paradigm of the effects of organic enrichment on benthic communities]
- Rosenberg, R. 1973. Succession in benthic macrofauna in a Swedish fjord subsequent to the closure of a sulphite pulp mill. Oikos 24: 244-258.



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- Rosenberg, R. 1976. Benthic faunal dynamics during succession following pollution abatement in a Swedish estuary. Oikos 27: 414-427.
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- Shaw, K. M., P. J. D. Lambshead, and H. M. Platt. 1983. Detection of pollution-induced disturbance in marine benthic assemblages with special reference to nematodes. Mar. Ecol. Prog. Ser. 11: 195-202.
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- Sheehan, P. J. 1984b. Effects on community and ecosystem structure and dynamics. Pp. 51-99 in P. J. Sheehan, D. R. Miller, G. C. Butler and P. Bourdeau, eds. Effects of pollutants at the ecosystem level. SCOPE, John Wiley and Sons, Ltd. [A good summary of the key concepts involved, including a good bibliography of statistical methods]
- Sheehan, P. J. 1984c. Functional changes in the ecosystem. Pp. 101-145 in P. J. Sheehan, D. R. Miller, G. C. Butler and P. Bourdeau, eds. Effects of pollutants at the ecosystem level. SCOPE, John Wiley and Sons, Ltd.
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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. [Dramatic changes in community structure attributed to reduction in pollution load and the effects of the echiuran worm Listriolobus] {14, 55}

#### Stull et al. (1986)

- Swartz, R. C., D. W. Scultz, G. R. Ditsworth , W. A. DeBen and F. A. Cole. 1985. Sediment toxicity, contamination, and macrobenthic communities near a large sewage outfall. ASTM STP 865: 152-175. [Palos Verdes shelf]
- Swartz, R. C., F. A. Cole, D. W. Schults and W. A. DeBen. 1986. Ecological changes in the Southern California Bight near a large sewage outfall: benthic conditions in 1980 and 1983. Mar. Ecol. Prog. Ser. 31: 1-13. [9 stations at 60 m NW of the LA County Sewage District's Palos Verdes' outfall shows dramatic changes from 1980 to 1983. Capitella declined dramatically in abundance during this period. Reduction in discharge cited as the primary reason, but the 1982-83 El Niño and the effects of Listriolobus {see Stull et al. (1986)} also cited.]{?}
- Thrush, S. F. and D. S. Roper. 1988. The merits of macrofaunal colonization of intertidal mudflats for pollution monitoring: a preliminary study. J. exp. Mar. Biol. Ecol. 116: 219-233.
- Thrush, S. F., J. E. Hewitt, V. J. Cummings and P. K. Dayton. The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? Mar. Ecol. Prog. Ser. 129: 141-150. [Dredging simulated on 2 subtidal sandflats. Effects evident 3 mo later]
- Vitousek, P. M. 1994. Beyond global warming: ecology and global change. Ecology 75: 1861-1876.
  [Vitousek in this MacArthur award-winning lecture cites 3 major causes of global change:
  1) Atmospheric increase of CO<sub>2</sub> {will coral reefs dissolve?}, 2) Changes in Nitrogen biogeochemistry caused by fertilizer production, and 3) Land-use change. He also briefly alludes to DDT, overharvesting of fisheries, and biological invasions and introduction of exotic species. Where is the evidence that pollution of the coastal zone is a pernicious problem?]



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- Warwick, R. M. 1988b. Analysis of community attributes of macrobenthos of Frierfjord/Langesund fjord at taxonomic levels higher than species. Mar. Ecol. Prog. Ser. 46: 167-170.
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- 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 Delta is proposed]
- Word, J. Q. and A. J. Mearns. 1979. 60-meter control survey off Southern California. SCCWRP Report.
- Zajac, R. N. and R. B. Whitlatch. 1989. Natural and disturbance-induced demographic variation in an infaunal polychaete, Nephtys incisa. Mar. Ecol. Prog. Ser. 57: 89-102. [Cohort analysis of Long Island Sound dump site and sites 400m and 3 km away. Little pollution effect noted even at the 400-m site]

## ORGANIC ENRICHMENT (E.G., SEWAGE & KELP)

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- Amjad, S. and J. S. Gray. 1983. Use of the nematodecopepod ratio as an index of organic pollution.

Marine Pollution Bulletin 14: 178-181. [A critique of the ratio] {15}

- Anger, K. 1975. On the influence of sewage pollution on inshore benthic communities in the south of Kiel Bay. Helg. wiss. Meeresunters. 27: 480-438.
- Armstrong, J. W., R. M. Thom and K. K. Chew. 1980. Impact of a combined sewer overflow on the abundance distribution and community structure of subtidal benthos.
- 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. [Includes an analysis of diversity, classification and ordination and a critique of log-normal distribution.]
- Baden, S. P., L-O Loo, L. Pihl, and R. Rosenberg. 1990.
  Effects of eutrophication on benthic communities including fish: Swedish west coast.
  Ambio 19: 113-127782. [S. Kattegat, 23 m deep., No effects of flatfish. Lobsters leave burrows when d.o.<40% saturation]</li>
- Beukema, J. J. 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. Helg. Meeres. 43: 405-415.
- Beukema, J. J. 1989. Changes in composition of bottom fauna of a tidal-flat area during a period of eutrophication. Marine Biology 111: 293-301. [No multivariate analysis]
- Beukema, J. J. and G. C. Cadee. 1986. Zoobenthos responses to eutrophication of the Dutch Wadden Sea. Ophelia 26: 55-64. [As nutrient flux increases, so to does pelagic primary production and benthic secondary production. <u>Macoma</u> abundances increase under eutrophication. Eutrophication is regarded as having generally positive effects (P.62)]
- Boesch, D. F. 1982. Ecosystem consequences of alterations of benthic community structure and function in the New York Bight. Pp. 543-568 in G. F. Mayer, ed., Ecological stress and the New York Bight: Science and Management. Estuarine Research Foundation, Columbia S.C.
- Bottom, M. L. 1979. Effects of sewage sludge on the benthic invertebrate community of the inshore New York Bight. Estuar. coastal mar. Sci. 8: 169-180.



- Bridges, T. S., L. A. Levin, D. Cabrera, And G. Plaia. 1994. Effects of sediment amended with sewage, algae, or hydrocarbons on growth and reproduction in two opportunistic polychaetes. J. exp. Mar. Biol. Ecol. 177: 99-119. [Capitella responds dramatically to organic enrichment]
- Cederwall, H. and R. Elmgren. 1980. Biomass increase of benthic macrofauna demonstrates eutrophication of the Baltic Sea. Ophelia *1*: 287.
- Dauer, D. M. and W. G. Connor. 1980. Effects of moderate sewage input on benthic polychaete populations. Estuarine and Marine Science 10: 335-346. [They document dramatic increases in the abundance and biomass of many species, especially brooders, in a mudflat adjacent to a secondary treatment plant.]
- Dorsey, J. H. and R. N. Synnot. 1980. Marine soft-bottom benthic community offshore from Black Rock Sewage outfall, connewarre, Victoria. Aust. J. Mar. and Fresh Res. *31*: 155
- Dorsey, J. H. 1982. Intertidal community offshore from the Werribee sewage-treatment farm: an opportunistic infaunal assemblage. Aust. J. Mar. Fresh. Res. 33: 45-54.
- Elmgren, R. 1989. Man's impact on the ecosystem of the Baltic Sea: energy flows today and at the turn of the century. Ambio *18*: 326-332.
- Essink, K. and J. J. Beukema. 1986. Long-term changes in intertidal flat macrozoobenthos as an indicator of stress by organic pollution. Hydrobiologia *142*: 209-215.
- Ferraro, S. P., R. C. Swarz, F. A. Cole and D. W. Schults. 1991. Temporal changes in the benthos along a pollution gradient: discriminating the effects of natural phenomena from sewage-industrial wastewater effects. Estuar. Coastal Mar. Sci. 33: 383-407.
- Grassle, J. F., J. P. Grassle, L. S. Brown-Leger, R. F. Petrecca and N. J. Copley. 1986. Subtidal macrobenthos of Narragansett Bay. Field and mesocosm studies of the effects of eutrophication and organic input on benthic populations. Pp. 421-433 in Marine Biology of Polar regions and effects of stress on Marine Organisms. J. S. Gray and M. E. Christinasen, eds., John Wiley and Sons. [MERL tanks used to show communities respond rapidly to changes in food supply. Highly resilient community]

Gray, J. S. 1979. Pollution-induced changes in populations. Phil Trans. R. Soc. Lond. 286: 545-561.

#### Gray et al. (1988)

- Grizzle, R. E. and C. A. Penniman. 1991. Effects of organic enrichment on estuarine macrofaunal benthos: a comparison of sediment profile imaging and traditional methods. Mar. Ecol. Prog. Ser. 74: 249-262. [Sediment-profile imaging compared to traditional benthic sampling with multivariate statistical analysis. SPI is cheaper and faster and is adequate to describe an organic enrichment gradient]
- Holte, B.and B. Gulliksen. 1987. Benthic communities and their physical environment in relation to urban pollution down the city of Tromso, Norway. Sarsia 72: 133-141.
- Josefson, A. B. 1990. Increase of benthic biomass in the Skagerak-Kattegat during the 1970's and 1980's - effects of organic enrichment? Mar. Ecol. Prog. Ser. 66: 117-130.
- Knox, G. A. and G. D. Fenwick. 1981. Zonation of inshore benthos off a sewage outfall in Hawke Bay, New Zealand. J. Mar. Fresh. Res. 15: 417-435.
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## OIL (HYDROCARBONS) AND BENTHIC COMMUNITY STRUCTURE

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#### West Falmouth 1969 Oilspill

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#### Grassle & Smith (1976)

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  B. W. Tripp, B. Woodin and C. Phinney. 1992.
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  of fuel oil compounds and effects on animals.
  Marine Pollution Bulletin 24: 607-614. {?}

# Outer Continental Shelf (OCS) Community Structure

Carney, R. S. 2005. Zonation of deep biota on continental margins. Oceanog. Mar. Biol. Ann. Rev. 43: 211-278. [A very nice review of the ecological processes controlling beta diversity on continental margins] {?}

#### **Gulf of Mexico OCS Oil Exploration effects**

Continental Shelf Associates, Inc. 2004a. Gulf of Mexico comprehensive synthetic based muds monitoring program. Volume I. Technical. 224 pp. [Synthetic based drilling muds (SBM) are believed to be less toxic than the older oil-based muds. This study assessed SBM effects on benthic communities on the Gulf of Mexico OCS. Some minor effects noted. Maciolek & Blake wrote Chapter 12 (in Volume II) analyzes the effects of SBM on benthic community a and  $\beta$  diversity using Fisher's a, rarefaction, and CNESS] {?}

- Continental Shelf Associates, Inc. 2004b. Gulf of Mexico comprehensive synthetic based muds monitoring program. Volume II. Technical. 359 pp. [See Maciolek & Blake's Chapter 12 on analysis of SBM effects on macroinfaunal community structure] {?}
- Continental Shelf Associates, Inc. 2004c. Gulf of Mexico comprehensive synthetic based muds monitoring program. Volume II. Technical. 2158 pp. [See Maciolek & Blake's Chapter 12 on analysis of SBM effects on macroinfaunal community structure] {?}
- Continental Shelf Associates, Inc. 2006a. Effects of oil and gas exploration and development at selected continental slope sites in the Gulf of Mexico. Volume I. Executive Summary. U. S. Dept. Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study MMS-2006-044. 45 pp. [Drilling muds are used to prevent blowouts during drilling and to bring drill tailings up the drill shaft. Barium and synthetic fluids are tracers of drilling muds and are associated with changes in benthic communities in the Gulf of Mexico. Benthic communities assessed with sediment profile imaging, and analyses of macro- and meiofaunal community structure. Amphipod densities lower in areas affected by drilling mud. Figure 18 shows crude analyses of drilling effects on diversity] {?}
- Continental Shelf Associates, Inc. 2006b. Effects of oil and gas exploration and development at selected continental slope sites in the Gulf of Mexico. Volume II. Technical Report. U. S. Dept. Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study MMS-2006-045. 636 pp. [Rhoads & Germano's 1986 Organism-Sediment Index (OSI) used extensively to analyze sedimentprofile images of benthic community structure. OSI reveals that drilling produced impacted benthic communities. Effects of drilling on macroinfaunal community structure was assessed with Non-metric multidimensional scaling (See Fig. 11.18) and changes in Shannon's H' and Pielou's J] {?}



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- Continental Shelf Associates, Inc. 2006c. Effects of oil and gas exploration and development at selected continental slope sites in the Gulf of Mexico. Volume III. Appendices. U. S. Dept. Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study MMS-2006-046. 938 pp. [Appendix 12 contains a list of macroinfaunal species, without densities] {?}
- Continental Shelf Associates, Inc. 2006d. Effects of oil and gas exploration and development at selected continental slope sites in the Gulf of Mexico. Volume III. Appendices. U. S. Dept. Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study MMS-2006-046. 938 pp. [Appendix 12 contains a list of macroinfaunal species, without densities] {?}

#### Detection of North Sea Oil benthic impacts

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- Gray, J. S. 1994. Is deep-sea diversity really so high? Species diversity of the Norwegian continental shelf. Mar. Ecol. Prog. Ser. *112*: 205-209.

- Gray, J. S., T. Bakke, H. J. Beck and I Nilssen 1999. Managing the environmental effects of the norwegian oil and gas industry: from conflict to consensus. Mar. Poll. Bull. 38: 525-530. [Abstract: ... oil companies expected effects of their activities to be found to a 1 km radius round platforms ... effects were over much larger areas... roughly 10 times the area predicted by the companies. The Norwegian authorities reacted by imposing restrictions on discharges of oil-based drilling cuttings ...]
- Gray, J. S. 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf J. Exp. Mar. Biol. Ecol. 250: 23-49. [Section 8 analyzes changes in alpha and beta diversity along a Norwegian shelf pollution gradient analyzed previously by Olsgarde & Gray (1995)]
- Kingston, P. F. 1987. Field effects of platform discharges on benthic macrofauna. Phil. Trans. Roy. Soc. London B 316: 545-565. [Rarefaction curves, Pielou's J used to assess changes in diversity in sites affected by North Sea drilling muds and cuttings. Community structure strongly affected near drilling platforms]
- Olsgarde, F., and J. S. Gray. 1995. A comprehensive analysis of the effects of offshore oil and gas exploration and production on the benthic communities of the Norwegian continental shelf. Mar. Ecol. Prog. Ser. 122: 277-306. [Effects of drilling with oil-based muds assessed with multivariate analyses. Severe impacts noted near the drilling rigs] {66}
- Olsgarde, F., P. J. Somerfield, and M. R. Carr. 1997. Relationships between taxonomic resolution and data transformations in analyses of a macrobenthic community along an established pollution gradient. Mar. Ecol. Prog. Ser. 149: 173-181. [Pollutants from a Norwegian drilling rig produces drastic changes in community structure, detectable even when organisms are identified only to the level of Phylum or Class]





#### Effect of oil drilling on Georges Bank

Neff, J. M., M. H. Bothner, N. J. Maciolek and J. F. Grassle. 1989. Impacts of exploratory drilling for oil and gas on the benthic environment of Georges Bank. Marine Env. Res. 27: 77-114. [Only a small cluster diagram is provided for the extensive benthic monitoring data set collected during the Georges Bank Program. The benthic analyses are described in three large technical reports]

# $\Sigma$ PAHs, PCBs, DDT, colloids and benthos

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- Drake, D. E., R. Eganhouse and W. McArthur. 2002. Physical and chemical effects of grain aggregates on the Palos Verdes margin, southern California. Cont. Shelf Res. 22: 967-986.
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polychaete, the conveyor-belt deposit feeder *Heteromastus filiformis* (Claparde). Chemosphere 31: 3141-3152. [DDT reduces ingestion rate] {?}

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- Quensen, J. F., S. A. Mueller, M. K. Jain, and J. M. Tiedje. 1998. Reductive dechlorination of DDE to DDMU in marine sediment microcosms. Science 280: 722-724. [Mud from the Palos Verdes shelf, near the LA County Sewer outfalls, contains microbes capable of rapid rates of degradation of p,p'-DDE {the major byproduct of DDT in sediments} under methanogenic conditions {no  $O_2$  and low or no  $SO_4^{-2}$ } See also Sun et al. 2002, Sherwood et al. (2002)] {69}
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# PELLETS, BIOTURBATION & ORGANICS

Drake, D. E., R. Eganhouse and W. McArthur. 2002. Physical and chemical effects of grain aggregates on the Palos Verdes margin, southern California. Cont. Shelf Res. 22: 967-986.{?}

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## DETECTING POLLUTION EFFECTS WITH SAMPLING DISTRIBUTIONS (ABC, LOG SERIES, NEUTRAL & LOGNORMAL MODELS)

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- 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 lognormal 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]
- Gray, J. S. 1979a. Pollution-induced changes in populations. Phil. Trans. R. Soc. B. 286: 545-561. {?}
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- 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)]
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  [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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#### Lambshead & Platt (1985)

- McManus, J.W. & Pauly, D. 1990. Measuring ecological stress: variations on theme by R.M. Warwick. Mar. Biol. 108: 210-221. [58]
- Pearson, T. H., J. S. Gray, and P. J. Johannessen. 1983. Objective selection of sensitive species indicative of pollution-induced change in benthic communities. 2. Data analyses. Mar. Ecol. Prog. Ser. 12: 237-255. [Because of the break in the log-normal distribution plots, they recommend focusing on the intermediate abundance species. But, since there is no way of quantitatively separating these species, there is not much savings in time and a huge loss in potential worth of a dataset by focusing only on those intermediate abundance species.]



- Rygg, B. 1986. Heavy metal pollution and log-normal distribution of individuals among species in benthic communities. Marine Pollution Bulletin 17: 31-36. [Although frequently used as a test for detecting the effects of organic pollution impact on benthic communities, the test for fit to the log-normal distribution will be insufficient or inferior to a diversity index for detecting changes due to heavy metals.]
- Shaw, K. M., P. J. D. Lambshead, and H. M. Platt. 1983. Detection of pollution-induced disturbance in marine benthic assemblages with special reference to nematodes. Mar. Ecol. Prog. Ser. 11: 195-202. [A critique of Gray & Mirza (1979)]
- Stenseth, N. C. 1979. Where have all the species gone? On the nature of extinction and the Red Queen hypothesis. Oikos 33: 196-227. [Provides a theoretical explanation for Gray & Mirza's (1979) break in the log-normal distribution plot.] {15}
- Warwick. R. M. 1986. A new method for detecting pollution effects on marine macrobenthic communities. Marine Biology *92*: 557-562. {?}
- Warwick, R. M. 1993. Environmental impact studies on marine communities: pragmatical considerations. Aust. J. Ecology 18: 63-80. [A very nice paper, criticizing the use of Caswell's (1976) neutral model and many other techniques for identifying disturbed communities. He advocates using meiofauna – no surprise since Warwick works with meiofauna] {70}
- Warwick, R. M., T. H. Pearson, and Ruswahyuni. 1987.
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- 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.]

Warwick, R. M. and K. R. Clarke. 1991. A comparison of some methods for analysing changes in benthic community structure. J. Mar. Biol. Assoc. U. K. 71: 225-244. [Non-metric multidimensional scaling of 4th root transformed data, using Bray-Curtis similarity is their preferred option, later implemented in their PRIMER computer package] [15]

# ECOLOGICAL INDICATORS (A WORK IN PROGRESS)

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Smith, R. W.,

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### **INDICATOR SPECIES**

Ampelisca

#### Comment



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*Ampelisca abdita* is a tube-building amphipod. It has been used extensively as a test organism in chronic toxicity tests by the EPA.

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- Mills, E. L. 1967. The biology of an ampeliscid amphipod crustacean sibling species pair. J. Fish. Res. Bd. Can. 24: 305-355. [The ecology of <u>Ampelisca</u> <u>abdita</u> and <u>Ampelisca</u> <u>vadorum</u> discussed. <u>Ampelisca</u> <u>vadorum</u> tends to be found on coarser sediments] {?}
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#### Capitella

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#### Polydora & Streblospio

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#### Mediomastus

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- Grassle, J. F. and W. K. Smith. 1976. A similarity measure sensitive to rare species and its use in investigation of marine benthic communities. Oecologia 25: 13-22. [Mediomastus and Capitella abundant after the west Falmouth oilspill; NESS similarity introduced] {5, 20, 31, 65}
- Grassle, J. P. and J. F. Grassle. 1984. The utility of studying the effects of pollutants on single species populations in benthic mesocosms and coastal ecosystems. Pp. 621-642 *in* H. H. White, *eds*. Concepts in Marine Pollution Measurements. Maryland Sea Grant Program, College Park MD. *[A very nice review of <u>Mediomastus ambiseta</u> autecology and taxonomy]*

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#### Mulinia lateralis (Say, 1822)

Comment: Most of these references were obtained by a computer search on <u>Mulinia</u>. The key papers to me are the papers by Luchenbach, Grassle, Snelgrove and Virnstein on the larval recruitment and mortality of this classic opportunistic species.

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Comment: Carol Reinisch developed a monoclonal antibody to the leukemia-like neoplastic cells that can take over the hemolymph of the soft-shelled clam, <u>Mya</u> <u>arenaria</u>. She thinks the incidence of this condition may be related to pollution. As part of a study with Gallagher, Grassle, Wallace and Eganhouse, we examined the incidence of clam neoplasia on Savin Hill Cove. The incidence of neoplasia on this polluted mudflat are less than the Cape Cod Bay control sites.

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- Swartz, R. C., D. W. Schults, J. O. Lamberson, R. J.
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#### The Fugacity Approach in Toxicology

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## 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 extensions to coenoclines]{[?]}

> 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.] {15, 51, 70, 71, 86, 87}

Caswell, H. 1983. Reply to a comment by Ugland and Gray. Ecology 64: 605-606. [Rebuttal to Ugland & Gray 1983] [87] 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

Chisholm & Burgman (2004) Ecology 85: 3172



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- 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)] [85, 86, 87]
- 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.] [?]
- 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] [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]



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- 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.] {87}
- 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] {86, 87}
- May, R. M. 1984. An overview: real and apparent patterns in community structure. Pp. 3-16 in D.
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- Volkov, I, J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. Nature 424: 1035-1037. [Provides the analytical solution to Hubbell's (2001) neutral model]
- 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]
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## EMAP & CHESAPEAKE BAY

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# MASSACHUSETTS (GRAY & PEER-REVIEWED) BENTHIC LITERATURE (CHRONOLOGICAL)

**Comment**: All of the MWRA Technical Reports are available free of charge from the Environmental Quality Division at the MWRA. The MWRA web page is URL: http://www.mwra.com. You can find a listing of reports and phone numbers to call to order reports.

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