Organic carbon content of sediments as an indicator of stress in the marine benthos

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ABSTRACT: While organic matter in sediments is an important source of food for benthic fauna, an overabundance can cause reductions in species richness, abundance, and biomass due to oxygen depletion and buildup of toxic by-products (ammonia and sulphide) associated with the breakdown of these materials. Moreover, increasing organic content of sediment is often accompanied by other chemical stressors co-varying with sediment particle size. In the present study, synoptic data on the structure of macroinfaunal communities and total organic carbon (TOC) content of sediment were obtained from 951 stations representing 7 coastal regions of the world: the northern Black Sea (Crimean and Caucasian coasts); eastern Mediterranean Sea (Greece); North Sea (Ekofisk oil field); Firth of Clyde and Liverpool Bay, UK; Seto Inland Sea, Japan; Boston Harbor and Massachusetts Bay, USA and estuaries of the southeastern USA. Macroinfaunal and TOC data were examined to look for patterns of association consistent with conceptual model predictions and to identify TOC critical points corresponding to major shifts in the benthic data. Species richness, Hurlbert's $E(S_n)$, was selected as the primary response parameter. Results suggested that risks of reduced species richness from organic loading and other associated stressors in sediments should be relatively low at TOC concentrations less than about 10 mg g^{-1}, high at concentrations greater than about 35 mg g^{-1}, and intermediate at concentrations in between. Predictive ability across these ranges was high based on results of re-sampling simulation. While not a measure of causality, it is anticipated that these TOC critical points may be used as a general screening-level indicator for evaluating the likelihood of reduced sediment quality and associated bioeffects over broad coastal areas receiving organic wastes and other pollutants from human activities.

KEY WORDS: Marine benthos · Total organic carbon · TOC · Benthic–TOC relationships · Ecological indicators · Pollution impacts · Benthic species richness

INTRODUCTION

A common approach to assessing risks to ecosystem health is the characterization of stressors and corresponding effects through the use of indicators (Fisher et al. 2001). An ecological indicator is an attribute of the ecosystem, either biological, chemical, or physical, that is sufficiently correlated with an endpoint of concern to serve as a surrogate measure of that endpoint (Cairns et al. 1993). For an indicator to serve as a valid measure of condition, there must be a conceptual link between the presence/absence of the indicator and the state of the ecological function at risk. Secondly, a good indicator should be amenable to measurement

and preferably easy to measure. Most importantly, the expression of the indicator should convey information that is meaningful to decision-making with respect to the risk of concern (Fisher et al. 2001). Accordingly, an important function of indicators is the identification of stressor–response relationships and corresponding thresholds for management action. As noted by Fisher et al. (2001), because of the complexity of most stressor–response relationships in nature, it is usually impractical if not impossible to completely characterize all contributing variables; thus, a common approach in the use of an indicator is to focus on a select set of factors that are pivotal to understanding the targeted risk and that involve some degree of uncertainty.

The benthos is an effective place to look for indicators of human-induced stress in coastal marine ecosystems. Benthic fauna are important components of these systems, playing vital roles in detrital decomposition, nutrient cycling, and energy flow to higher trophic levels. Moreover, benthic fauna live in close association with bottom substrata, where organic pollutants and chemical contaminants tend to accumulate and where low-oxygen conditions are typically the most severe. Because of their relatively sedentary existence, it is difficult for these organisms to avoid exposure to pollutants and other adverse conditions in their immediate surroundings. Measures of the ambient benthic community reflect the sensitivities of multiple species and life stages to pollutants that may have been building up in the sediment and affecting the fauna over many generations (Hyland et al. 1999).

Organic matter in surface sediments is an important source of food for benthic fauna (Sanders 1958, Gray 1974, Pearson & Rosenberg 1978, Lopez & Levinton 1987, papers in Lopez et al. 1989, Snelgrove & Butman 1994). However, an overabundance may lead to reductions in species richness, abundance, and biomass due to oxygen depletion and buildup of toxic by-products (ammonia and sulphide) associated with the breakdown of these materials (Pearson & Rosenberg 1978, Diaz & Rosenberg 1995, Gray et al. 2002). Increases in the organic content of sediment also may be accompanied by increases in chemical contaminants that are co-varying in relation to a common environmental factor (e.g. increasing proportions of finer-grained sediment particles that would provide greater surface area for sorption of both organic and other chemical pollutants) (Landrum & Robbins 1990, Lamberson et al. 1992, Thompson & Lowe 2004). Thus, benthic fauna, especially those in muddy depositional environments, must often cope with multiple, co-occurring stressors.

Pearson & Rosenberg (1978) developed a graphic model (Fig. 1A) to describe a generalized pattern of response of benthic communities in relation to organic enrichment. A modification of this conceptual model is

presented here in Fig. 1B to demonstrate the relationships between organic enrichment, benthic response, and other related environmental factors, including oxygen depletion and presence of other co-varying, sediment-associated stressors (e.g. ammonia, sulphides, chemical contaminants). Similarly, in a recent review of models of benthic responses to eutrophication, Gray et al. (2002) expounded on the importance of such factors, further suggesting that major effects on the benthos in relation to organic enrichment result from hypoxia rather than eutrophication per se. Thompson & Lowe (2004), who observed a close association between presence of impaired benthic assemblages and high levels of both chemical contaminants and organic matter in sediments of the San Francisco estuary, California, also used a modification of the Pearson–Rosenberg (P–R) model to characterize benthic responses to such combined stressor gradients.

In accordance with this conceptual model, benthic faunal variables would be expected to increase in rela-
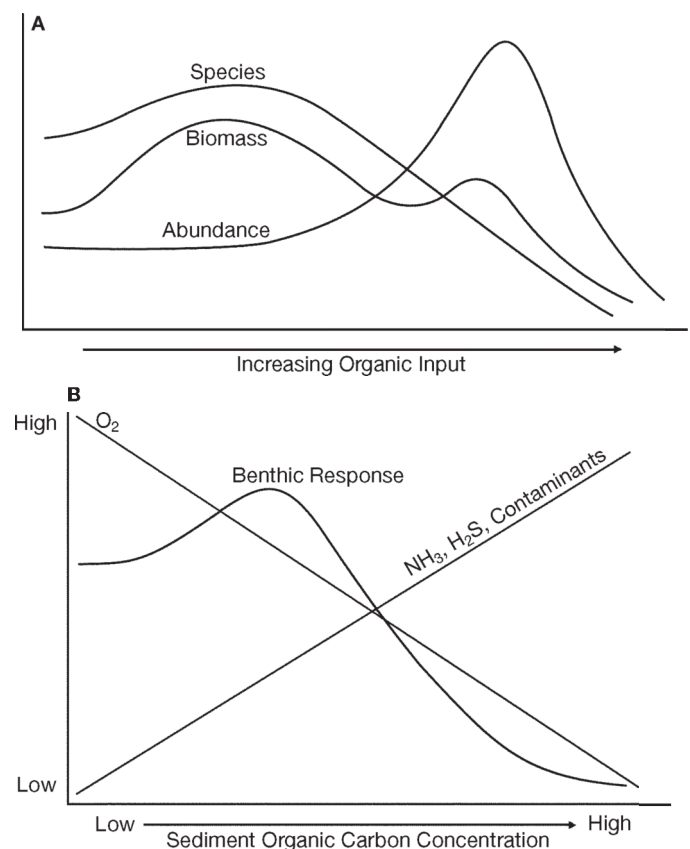

Fig. 1. Conceptual models of benthic response to organic enrichment. (A) The Pearson & Rosenberg (1978) (P–R) model of species, abundance, and biomass patterns in relation to increasing organic input (note that the original P–R figure showed organic matter decreasing from left to right along the x-axis). (B) A modification of the P–R model showing a generalized pattern of benthic response in relation to total organic carbon and other potential co-varying sediment-associated stressors

tion to increasing organic matter (expressed here as total organic carbon, TOC) up to a certain point, and then begin to decline (Fig. 1B). For simplicity, we have used a single curve to characterize this generalized response, though it is recognized that benthic species richness, abundance, and biomass may follow somewhat different paths (as presented in the original P–R model). The biotic-response curve in Fig. 1B most closely resembles the curve for species richness in the original P–R model (Fig. 1A). Species richness typically will be at its peak at low to slightly moderate TOC levels, due to a combination of the nutritional value of organic matter available as food, a low incidence of environmental stressors, and the co-existence of species with varying tolerance levels and recruitment strategies. As TOC increases toward the higher end of the scale, the benthos is exposed to increasing amounts of physiological stress from oxygen depletion (due to higher biological oxygen demand, BOD) and related by-products of the organic decomposition process (ammonia and sulphides). Concurrently, higher levels of TOC often correlate with increasing concentrations of other potential co-varying stressors (e.g. chemical contaminants). Species richness typically will show a gradual decline over the intermediate TOC range, as increasing numbers of sensitive species fail to survive. In contrast, in accordance with the P–R model, other benthic variables may continue to increase throughout the intermediate range (abundance), or exhibit secondary peaks (biomass), due to the presence of heartier opportunistic species that are able to flourish under the increasingly harsh conditions and reduced competition, as the more sensitive species decline. At very high TOC concentrations, associated environmental stressors will exceed the physiological tolerance limits of a large percentage of species, leading to a sharp decline in most benthic variables. Typically, benthic assemblages under such conditions will be dominated by a few pollution-tolerant, r-selected opportunistic species. Disturbances that are too severe may eliminate even the heartiest species, resulting in azoic conditions. The P–R model (Pearson & Rosenberg 1978) of highest species richness at slightly moderate levels of organic enrichment is also supported by the broader 'intermediate disturbance hypothesis' (Grime 1973, Horn 1975, Connell 1978, review by Wilkinson 1999), which invokes alternative theoretical mechanisms to explain the same phenomenon.

Given these patterns, it should be possible to identify TOC critical points indicative of low to high risks of related adverse environmental conditions leading to stress in the benthos. Desirable attributes of such an indicator are linkage to a conceptual framework, high predictive ability, ease of use, and broad management applicability. In this paper, we present results of our efforts to develop such an indicator, using test data sets from 7 different locations around the world (Fig. 2). Synoptic measurements of macro-infauna, concentrations of TOC, and other environmental variables were examined across the various data sets to look for consistent patterns of association and to identify TOC critical points corresponding to major shifts in the benthic data. We must caution that it is not our intention for these critical points to serve as measures of causality (i.e. to imply that the observed bioeffect was caused by TOC itself). Rather, our premise is that because TOC tends to correlate with factors causing ecological stress (e.g. low dissolved oxygen, high ammonia and sulphide, chemical contamination of sediments), then TOC, in turn, may serve as a simple screening-level indicator, or symptom, of such stress.

MATERIALS AND METHODS

Data were obtained from 951 stations from 7 coastal regions on 3 different continents (Fig. 2, Table 1). General features of these data sets are as follows:

Northern Black Sea: 72 stations from multiple sampling efforts conducted along the Crimean and Caucasian coasts, in locations ranging from non-polluted
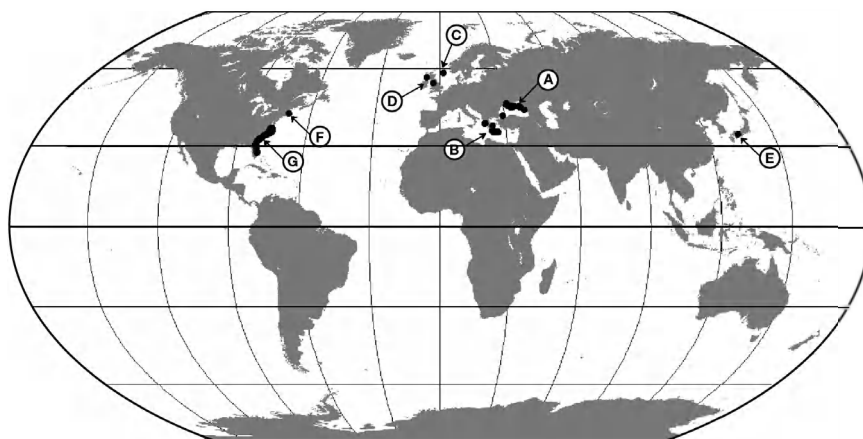

Fig. 2. Study areas: (A) northern Black Sea (along Crimean and Caucasian coasts); (B) eastern Mediterranean Sea (along the coast of Crete); (C) North Sea (near Ekofisk oil rig); (D) Firth of Clyde and Liverpool Bay, UK; (E) an estuary of the Seto Inland Sea, Japan; (F) Boston Harbor and Massachusetts Bay, USA; and (G) estuaries of the SE USA (Cape Henry, Virginia, to St. Lucie Inlet, Florida)

Table 1. Sources of data used to investigate the relationship between organic carbon and benthic species richness. Letters next to study areas refer to location codes in Fig. 2. TOC: total organic carbon (measured on a CHN analyzer); OM: organic matter content (measured by mass loss on ignition). In cases where carbon was measured as OM, values were multiplied by a factor of 0.33 to estimate TOC (Leong & Tanner 1999). All samples were taken from the upper surface layer of sediment (<5 cm)

Study Area	No. samples	Sampling period (years)	Sampler (m^2)	Sieve (mm)	Carbon method
Northern Black Sea (A)	72	1976–1977, 1979–1986, 1988–1989, 1992	0.25	1.0	TOC
Eastern Mediterranean Sea (B)	199	1986–1987, 1993, 1995–1997	0.10	0.5	TOC
North Sea (C)	39	1987	0.10	1.0	OM
Firth of Clyde and Liverpool Bay, UK (D)	31	1981, 1983, 1991	0.10	1.0	TOC
Estuary of Seto Inland Sea, Japan (E)	18	1994–1995	0.04	1.0	TOC
Boston Harbor and Massachusetts Bay, USA (F)	303	1991–1999	0.04	0.3	TOC
Estuaries of southeastern USA (G)	289	1994–1997	0.04	0.5	TOC

sites within boundaries of marine reserves and other protected areas to sites severely polluted from organic enrichment and petroleum contamination. Samples are from sites with water depths of 5 to 92 m and a salinity range of 16 to 24 practical salinity units (PSU) (most sites < 18 PSU) (Mironov 1992, Petrov 2000a,b). Present study contact was A. Petrov.

Eastern Mediterranean Sea: 199 stations from multiple sampling efforts conducted along the upper continental shelf of Crete (Karakassis & Eleftheriou 1997), in Heraklion Harbor (Lampadariou et al. 2000), and in the Aegean and eastern Ionian Seas (Karakassis et al. 1999, 2000). Samples are from sites with water depths of 10 to 190 m and salinity >38 PSU. Present study contact was I. Karakassis.

North Sea: 39 offshore stations radiating from an active drilling platform at the Ekofisk oilfield (Gray et al. 1990). Stations are in fully marine areas (salinity > 34 PSU), with depths of about 76 m. Present study contact was R. Warwick.

Liverpool Bay, Firth of Clyde: Liverpool Bay samples are from 7 offshore stations (4 replicates each) along a transect extending across a dredging disposal site following the 10 m depth contour (Somerfield et al. 1995). Firth of Clyde samples are from 24 offshore stations, consisting of 12 from each of 2 transects extending across the Garroch Head sewage-sludge dumping ground, at depths of 64 to 194 m (Pearson & Blackstock 1984). All stations are in fully marine areas (salinity >34 PSU). Present study contact was R. Warwick.

Seto Inland Sea (Japan): samples are from 3 stations sampled 6 times within an estuarine subtidal zone. Low-tide water depths ranged from 4 to 8 m, with a near-bottom salinity range of 31 to 34 PSU (Magni 1998). Present study contact was P. Magni.

Boston Harbor, Massachusetts Bay: 303 stations from Boston Harbor, a highly contaminated, shallow, urban estuary in Massachusetts, USA, and from more pristine coastal locations nearby in Massachusetts Bay. Stations are from depths of 3 to 50 m, with a salinity range of

20 to 33 PSU. (Blake et al. 1998). Present study contact was J. Shine.

SE US estuaries: 289 subtidal stations sampled during the summers 1994 to 1997 in estuaries from Cape Henry, Virginia, to St. Lucie Inlet, Florida. Samples are from depths of 0.5 to 16 m, with a salinity range of 0 to 39 PSU. These estuaries receive a wide range of organic and chemical stressors originating from multiple sources. However, co-occurrences of impaired benthic condition and adverse exposure condition (sediment contamination and/or toxicity) are limited to a relatively small percentage of the region's total estuarine area (estimated at less than about 25%, Hyland et al. 1998). Present study contact was J. Hyland.

All stations were represented by similar matching sets of macroinfaunal and TOC data. There were some differences in methods used to generate the data among the various studies (e.g. variations in sieve sizes, surface area of sampling gear, method of organic matter determination; Table 1); however, steps were included in the present analysis to account for such differences. For example, as described in more detail below, the primary measure of biological response was based on a variable that is relatively independent of sample-size differences caused by variations in sieve sizes and gear type. Also, in the few cases (39 of 951 samples) where organic carbon was measured as organic-matter content by mass loss on ignition (MLOI), rather than TOC by a CHN analyzer, these values were reduced by a factor of 3 to convert to TOC and correct for the overestimation of organic carbon associated with the MLOI methodology (Leong & Tanner 1999).

A major objective of the study was to compare data across the various locations to describe the overall pattern of benthic response in relation to increasing TOC and to identify TOC critical points indicative of low versus high risks of impaired benthic condition. There is no doubt that benthic species can vary in relation to a complexity of other interacting environmental

factors (see 'Discussion'). However, in order to make maximum use of the various data sets, no attempt was made to exclude samples to partition out the influences of such factors, as much of this knowledge was unattainable for one thing. For example, while it is understood that factors related to the quality, bioavailability, fluxes, and utilization (ingestion and assimilation) of organic matter as a food source are particularly strong determinants of benthic species distributions (Gray 1974, Tenore et al. 1982, Lopez & Levinton 1987, papers in Lopez et al. 1989, Snelgrove & Butman 1994), the present analysis was conducted with data from prior field studies that did not include such measurements, and thus it was impossible to go back and account for their effects. Moreover, for some other determinants, partitioning the data sets to account for their effects would interfere with the underlying goal of examining benthic responses across broad geographic regions and TOC concentration ranges. For example, excluding stations with chemically contaminated sediments would also exclude many stations with high TOC (given that both are highly inversely correlated with grain size). The intention here was to examine patterns of benthic response in relation to increasing TOC, without controlling for such differences, thereby testing the robustness of TOC as a screening-level indicator (or symptom) of stress over as broad of a range in conditions as possible.

Numbers of individuals of each benthic species (or lowest practical taxon) in a sample were recorded by station and study region. Though a variety of benthic variables were calculated from these count data, species richness, based on Hurlbert's $E(S_n)$ (Hurlbert 1971), was selected for further analysis of benthic– TOC relationships. $E(S_n)$ is the expected number of species present in an increasingly rarefied sample of n individuals randomly selected (without replacement) from a finite collection of N individuals and S species. With this measure, meaningful comparisons of species richness among collections of different sizes can be made by adjusting the collections to a common size (n). Thus, this measure was especially suitable for the present study in which we sought to examine species richness in relation to TOC among samples collected with varying types of sampling gear. Note, however, that $E(S_n)$ is not sample-size independent when $N < n$; thus, a low value of n ($n = 10$) was chosen so that low-density samples (especially from the Black Sea) could be included in the analysis. In addition to its conceptual basis for sample-size independence (Hurlbert 1971), $E(S_n)$ at $n = 10$ was shown to be highly independent of sample-size differences in computer simulations run on a variety of diversity indices with data from this study.

Simple x–y plots of benthic species richness versus TOC concentration were generated as a tool for exam-

ining basic patterns in the data and comparing them against the conceptual model. TOC concentration (mg g^{-1}, plotted on the x-axis) was divided initially into 10 discrete intervals as follows: ≤ 2.5, $>2.5–5$, $>5–10$, $>10–15$, $>15–20$, $>20–25$, $>25–30$, $>30–35$, $>35–40$, and >40. Mean species richness among stations within a specific TOC interval, and the 95% confidence intervals, were plotted across each of the TOC intervals. The resulting curve was examined to look for obvious breakpoints in the data. The inflection points of greatest concern with respect to evaluating potential adverse effects in relation to increasing TOC are the lower TOC critical point at which species richness starts to decline and the upper TOC critical point at which the decline starts to level out. Thus, for the identification of TOC critical points, we have used graphic models that ignore the initial increase in species richness at low TOC levels below the lower inflection point in the conceptual model.

Two quantitative methods were used to determine the location of these 2 critical points where changes in TOC were associated with the largest changes in species richness. In the first approach, we used ANOVA as an exploratory tool to identify TOC critical points that maximized differences in species richness among the 3 TOC ranges resulting from various combinations of upper and lower TOC values. Upper and lower TOC critical points were derived by selecting the 2 values that produced the highest F-statistic (Sokal & Rohlf 1981). In the second approach, a standard sigmoid dose–response curve was fitted to the data using non-linear, least-squares regression (Bates & Watts 1988). The function was of the form:

$$f(x) = a_0 + a_1 / (1 + e^{a_2 + a_3 x}) \tag{1}$$

where x is TOC (mg g^{-1}) and a_0, a_1, a_2, and a_3 are parameters selected by the regression procedure to minimize the sum of squared deviations from the fitted curve. Upper and lower TOC critical points were derived from the inflection points of the fitted curve. The inflection points were calculated by determining minima and maxima of the second derivatives.

The regression method was applied again using a modification of the above equation that included categorical site variables to test for variation in species richness related to geographical location. The form of this function was:

$$f(x) = a_0 + a_1 / (1 + e^{a_2 + a_3 x}) + a_4 L_1 + a_5 L_2 \ldots + a_9 L_6 \tag{2}$$

where x and a parameters are defined as before, and the terms L_1 to L_6 are categorical values (either 0 or 1) used to describe location of the data (i.e. northern Black Sea, eastern Mediterranean Sea, etc.). Curves were fitted to the combined data sets multiple times, each time allowing a different individual data set to

serve as a reference location and the remaining ones to exert their influence relative to the reference location. This latter modification of the regression function provided a test as to whether any single geographic location unduly influenced the derivation of TOC critical points.

The 2 TOC critical points determined from each analysis were used to separate samples into 3 groups of low, medium, and high levels of TOC. To evaluate the predictive ability of these critical points as indicators of change in benthic species richness, a re-sampling simulation (Lunneborg 1999) was used to estimate the probability of observing reduced species richness with increasing TOC across these 3 ranges. Simulations consisted of 10 iterations of 250 pairwise comparisons of randomly selected samples (with replacement) from each group. Probabilities of reduced species richness were computed for the following combinations: $E(S_{10})$ in low TOC range > $E(S_{10})$ in medium TOC range; $E(S_{10})$ in low TOC range > $E(S_{10})$ in high TOC range; $E(S_{10})$ in medium TOC range > $E(S_{10})$ in high TOC range. These probabilities, which can range from 0.5 to 1.0, are a measure of the power of a critical point in separating samples with higher and lower species richness. Probabilities closer to 1.0 are indicative of critical points with higher discriminatory power, while probabilities close to 0.5 indicate that TOC alone has no explanatory power with respect to reductions in species richness. Type I error probabilities were computed as a basis for testing the null hypothesis that when comparing samples taken from 2 groups, the probability of observing reduced species richness in the higher TOC range is equal to 0.5 based on 1-sided t-tests.

All statistical tests were conducted using either SAS (SAS Institute) or S-Plus (Math Soft).

RESULTS

TOC-species richness patterns and critical points

The overall pattern of species richness in relation to TOC was consistent with conceptual-model predictions, with a

maximum in the low TOC range, a gradual decline over the intermediate TOC range, and a minimum in the high TOC range (Fig. 3A). This was a suitable pattern for identifying ranges in TOC that could be used to assess low, moderate, and high risks of an impaired benthos. Total faunal abundance, which we also looked at initially, was much less appropriate for such a purpose, because of the absence of a lower-end inflection point at which the curve begins to show a gradual decline. Instead, abundance increased over a much broader TOC range, as would be predicted by
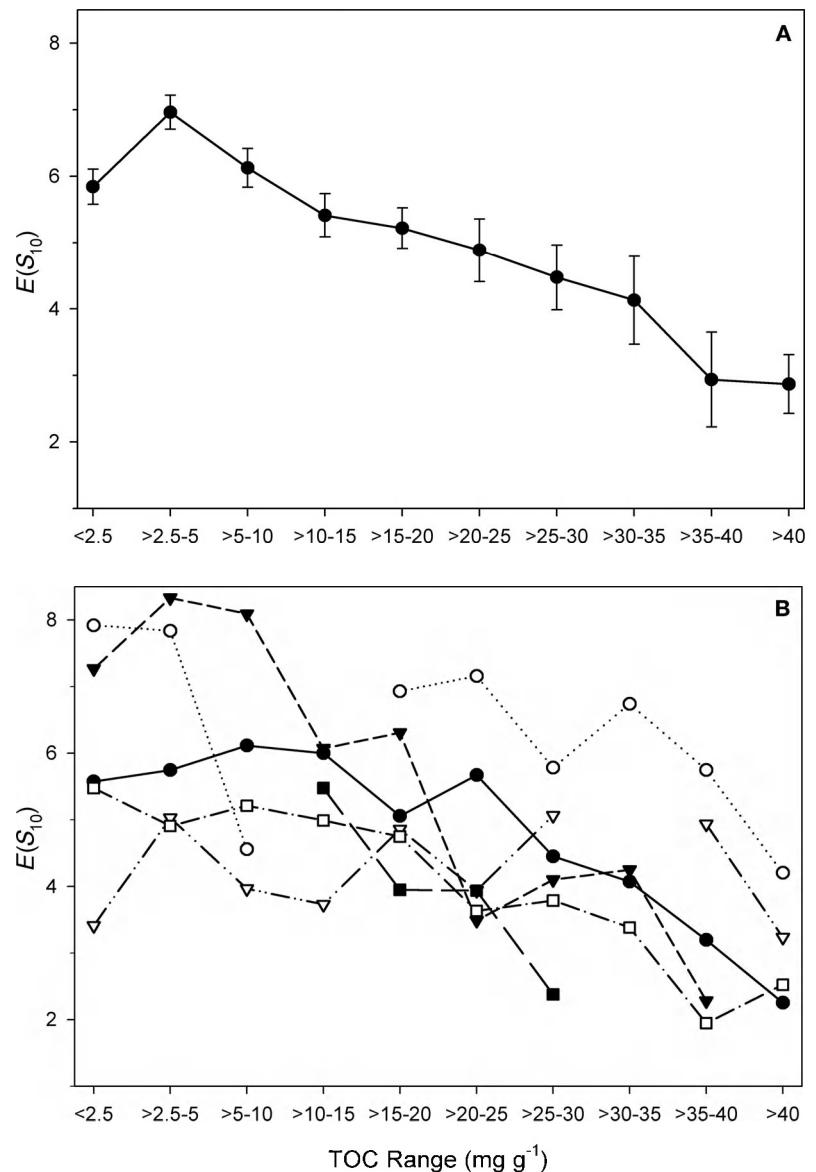

Fig. 3. Plot of mean species richness, $E(S_{10})$ within different ranges of total organic carbon (TOC, mg g^{-1}). (A) All data sets combined (vertical lines are 95% confidence intervals); (B) individual regions (regions are indicated by symbols — ●: Boston Harbor and Massachusetts Bay, USA; ○: North Sea/coastal UK; ▼: eastern Mediterranean Sea; ▽: northern Black Sea; ■: Seto Inland Sea, Japan; □: estuaries of the SE USA)

the conceptual model, until it finally declined at the uppermost end of the TOC scale (plot not included here). While the abundance pattern was consistent with the conceptual model prediction, the species data serve as a more sensitive measure of pollution responses addressed here. Thus, there was no further consideration of abundance, and, as noted earlier, the remaining focus was on the development of TOC critical points for evaluating risks of reductions in benthic species richness.

Mean values of $E(S_{10})$ peak at TOC concentrations between about 2.5 and 5 mg g^{-1}, begin declining between 5 and 10 mg g^{-1}, and then reach a minimum of around 35 to 40 mg g^{-1} (Fig. 3A). Thus, the desired lower and upper TOC critical points appear to be within these 2 latter intervals. As described above, 2 different quantitative methods were used to help pinpoint their location: Method 1, selecting the 2 values that produced the highest F-statistic from a series of ANOVAs performed on various combinations of upper and lower TOC values, and Method 2, calculating inflection points of a sigmoid dose–response function fitted to the original benthic–TOC data. Under Method 1, a maximum F-statistic of 172 was found at lower and upper TOC critical points of 8 and 36 mg g^{-1}, respectively. Mean differences among the resulting 3 TOC ranges defined by these 2 values were highly significant (p < 0.0001, df = 2), even after applying a Bonferroni correction to account for multiple comparisons. Method 2 produced very similar results (Fig. 4). Lower and upper inflection points along the fitted dose–response curve (based on Eq. 1) were found at corresponding TOC values of 10 and 35 mg g^{-1}. Although the variance explained by the model was modest (r^2 = 0.25) due to wide scatter in the raw data, the F-statistic from the regression analysis was highly significant (F = 107, p < 0.001), suggesting a significant overall pattern of decreasing species richness with increasing TOC (regardless of the exact mode of causality).

The modest r^2 value from the above regression model is due in part to regional differences. For example, while there is an overall pattern of decreasing species richness with increasing TOC, Fig. 3B reveals that there is variability in the paths (mostly the heights) of individual regional curves. In fact, when Eq. 2 was used in the regression analysis, thereby accounting for variations in species richness related to geographic location, the amount of variance explained by the
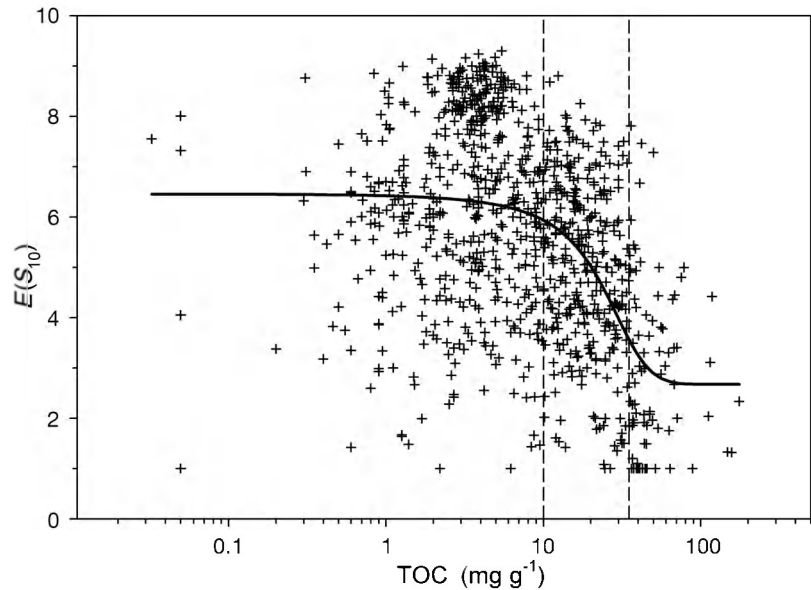

Fig. 4. Scatter plot of $E(S_{10})$ values in relation to increasing concentration of total organic carbon (TOC, mg g^{-1}, on a log$_{10}$ scale). Non-linear, least-squares regression was used to fit a sigmoidal dose–response function to the original data: $f(x) = a_0 + a_1/(1 + e^{a_2 + a_3 x})$. Major inflection points along the curve (10 and 35 mg g^{-1}, marked by the vertical lines) were calculated by determining maxima and minima of the second derivatives of the fitted equation. F-statistic of 107 is significant at p < 0.001

regression model improved substantially (r^2 = 0.62). However, an important point is that the position of inflection points derived from Eq. (2) remained the same regardless of which data sets were used as reference locations. Values of the fitted curves at the y-intercept (based primarily on the a_0 and a_1 terms) varied somewhat with each new reference-location designation; however, the positions of the TOC inflection points (based primarily on the a_2 and a_3 terms) did not change regardless of location (graphics not included here). Thus, results of the regression analysis also provided evidence that the derivation of TOC critical points from the combined data was not unduly influenced by any individual geographic location.

Given that both derivation methods (F-statistic and regression) produced very similar results, for rounding simplicity, TOC concentrations of 10 and 35 mg g^{-1} were selected as lower and upper critical points for further analysis. Thus, the likelihood of observing a decline in benthic species richness in relation to increasing TOC is expected to be relatively low at concentrations less than about 10 mg g^{-1}, high at concentrations greater than about 35 mg g^{-1}, and intermediate at concentrations in between. As a side note, substitution of H' (Shannon & Weaver 1949) for $E(S_{10})$ as a response variable gave a similar pattern as in Fig. 3A, with identical TOC critical points at 10 and 35 mg g^{-1}, thus providing further validation of the

above results. However, as explained, we have chosen to use $E(S_{10})$ as the primary response variable because of its known sample-size independence.

Predictive ability of TOC critical points

Results of re-sampling simulation (Table 2) indicated that there is a very high probability of having high, medium, and low mean species richness within low, medium, and high ranges of TOC, respectively. The values for all group comparisons in Table 2 are significantly different from a probability of 0.5 (all p < 0.0001). These are the Type I error probabilities associated with rejecting the null hypothesis that when comparing samples taken from 2 groups, the probability of observing reduced species richness in the higher TOC range is equal to 0.5 based on 1-sided t-tests. Based on these results, it appears that there is high predictive ability across the TOC ranges defined by these critical points.

A further demonstration of the predictive ability of these TOC critical points as an indicator of benthic stress is given in Table 3, which provides a comparison of species richness and various measures of the prevalence of degraded environmental condition across the 3 TOC ranges. The comparison focuses on data from estuaries of the southeastern USA, where a benthic condition index and related sediment-quality targets have been developed for assessing prevalence of degraded benthic condition and other adverse sediment conditions (e.g. high concentrations of chemical contamination at levels likely of causing adverse effects on benthic fauna). Methods were not available to make such comparisons with the other data sets. The degraded benthic condition was evaluated using a multi-metric, benthic index of biotic integrity (B-IBI) based on the methods of Van Dolah et al. (1999). High sediment contamination was defined using guidelines presented in Hyland et al. (1999). Also, dissolved oxygen (DO) < 2 mg l^{-1} was used as a criterion for evaluating low DO potentially harmful to bottom-dwelling fauna (see review by Diaz & Rosenberg 1995). As expected, there are very low percentages of samples with degraded benthic condition and high sediment contamination (7.6 and 3.5%, respectively) within the low TOC range (≤10 mg g^{-1}) and a much higher percentage (78 and 90%, respectively) within the high TOC range

Table 2. Results of re-sampling simulation to evaluate the probability of observing high, medium, and low species richness within low, moderate, and high TOC ranges, defined by critical points at 10 and 35 mg g^{-1}. Simulations consist of 10 iterations of 250 pairwise comparisons. p-values are the Type I error probabilities associated with rejecting the null hypothesis that when comparing samples taken from 2 groups, the probability of observing reduced species richness in the higher TOC range is equal to 0.5 based on 1-sided t-tests. Subscripts 1, 2, and 3 in the group comparison column refer to low, moderate, and high ranges of TOC, respectively

Group comparison	Probability of occurrence	p-value
$E(S_{10})_1 > E(S_{10})_2$	0.70 ± 0.02	<0.0001
$E(S_{10})_1 > E(S_{10})_3$	0.91 ± 0.01	<0.0001
$E(S_{10})_2 > E(S_{10})_3$	0.81 ± 0.01	<0.0001

(>35 mg g^{-1}). An intermediate percentage of degraded condition, based on these measures, occurs within the middle TOC range. Note that the percentage of samples with low DO (<2 mg l^{-1}) in near-bottom water also increases with increasing TOC concentration, although the prevalence of this effect does not reach a very high percentage even within the highest TOC range (only 24%). Mean values of $E(S_{10})$ also show a continuous decline across the 3 TOC ranges. These results are consistent with the above conceptual model predictions, and further illustrate that the TOC critical points, while not a measure of causality themselves, may serve as a surrogate indicator of stress induced by other co-varying factors. Based on this example, the cutoff points appear to be realistic and predictive of a disturbed condition when other evidence of disturbance exists.

Table 3. Comparison of mean values of benthic species richness ($E(S_{10})$) and prevalence of degraded environmental condition (based on 3 different biological, chemical, and physical indicators) within 3 ranges of total organic carbon (TOC) in estuaries of the southeastern USA. TOC ranges are based on critical points at 10 and 35 mg g^{-1}. Values in parentheses are number of samples. B-IBI: benthic index of biotic integrity; ERM: 'effect range median' sediment quality guidelines (Long et al. 1995); DO: dissolved oxygen

| | TOC (mg g^{-1}) | | |
	≤10	10–35	>35
Mean $E(S_{10})$	5.3 (171)	4.2 (68)	2.4 (50)
Percent samples with degraded benthos (B-IBI score 3; sensu Van Dolah et al. 1999)	7.6% (170)	54% (67)	78% (50)
Percent samples with high chemical contamination of sediments (mean ERM quotient > 0.058, sensu Hyland et al. 1999)	3.5% (171)	31% (68)	90% (50)
Percent samples with low DO in near-bottom water (DO < 2 mg l^{-1}, sensu Diaz & Rosenberg 1995)	0.6% (170)	4.5% (67)	24% (50)

DISCUSSION

Regional comparisons

There was a general pattern of decreasing species richness from low to high TOC ranges (Table 4). $E(S_{10})$ for all regions combined averaged 6.3 in the low TOC range, 5.0 in the intermediate range, and 2.9 in the high range. This general pattern was consistent across most individual data sets, though as noted earlier there were some regional differences (e.g. see Fig. 3B). The main exception was the Seto Inland Sea study, which was represented entirely by stations with TOC in the intermediate range (Table 4). The narrow range in TOC concentrations for this region (12 to 29 mg g^{-1}, Fig. 5) reflects the limited number and localized nature of sampling points (i.e. total of only 18 sampling points from 3 subtidal locations in a tidal estuary). The mean value of $E(S_{10})$ for Seto Inland Sea samples, however, was similar to those calculated from samples within this same TOC range for other regions (Table 4). Another exception was the northern Black Sea, where mean $E(S_{10})$ was slightly higher within the middle than lower TOC range, though the pattern of lowest values within the uppermost TOC range was still observed.

The strongest pattern in species richness was represented by samples from the eastern Mediterranean Sea (Table 4). Mean $E(S_{10})$ for these samples was 3.5 times higher in the low TOC range than in the high TOC range. The magnitude of this change is due at least in part to the initially high level of species richness observed within the low TOC range, i.e. mean $E(S_{10})$ of 8.0, which was much larger than corresponding values for all other regions (Table 4). The fauna and flora of the eastern Mediterranean Sea are known as being highly diverse, with a large proportion of endemic species due to the region's dynamic geological past (Tortonese 1985, Fredj et al. 1992). Additionally, in this generally oligotrophic region (see discussion below) it may be that benthic species richness is more sensitive to organic over-enrichment than in other systems. Conversely, increased organic loading in a naturally eutrophic system might be less likely to cause a problem than in an oligotrophic system.

Table 4. Comparison of mean values of benthic species richness ($E(S_{10})$) within different ranges of total organic carbon (TOC, mg g^{-1}) by study region

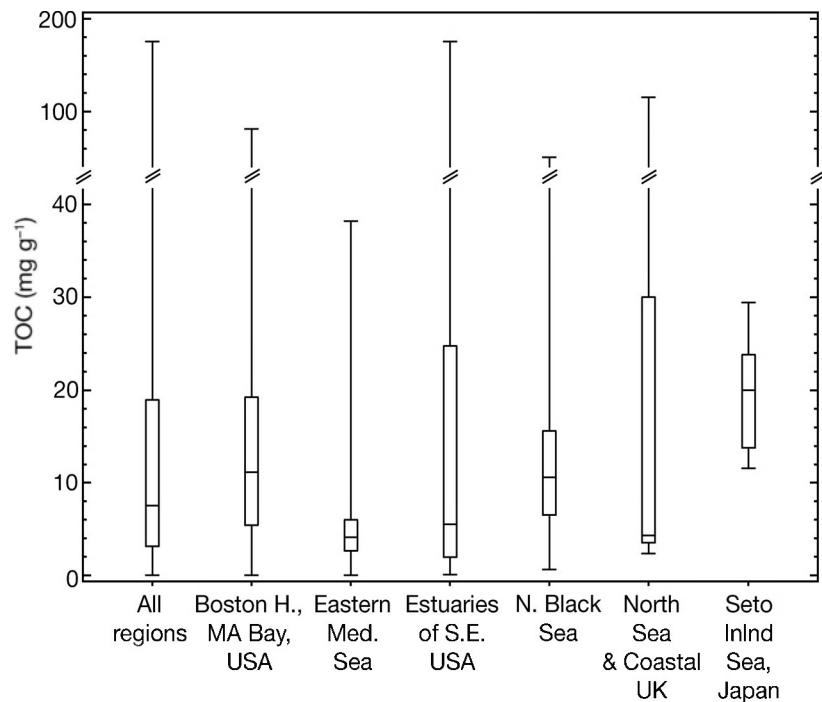| Study region	TOC ranges (mg g^{-1})		
	≤10	>10–35	>35
Eastern Mediterranean Sea	8.0	5.5	2.3
North Sea & coastal UK	7.8	6.4	4.6
Boston Harbor & Massachusetts Bay, USA	5.9	5.4	2.9
Estuaries of SE USA	5.3	4.2	2.4
Northern Black Sea	4.0	4.2	3.5
Estuary of Seto Inland Sea, Japan	–	4.3	–
All regions (pooled)	6.3	5.0	2.9

Fig. 5. Box-and-whisker plots of total organic carbon (TOC, mg g^{-1}) by study region. Boxes are inter-quartile ranges; horizontal lines within boxes are medians; whisker endpoints are high/low extremes

A comparison of TOC concentrations among regions is presented in Fig. 5. Eastern Mediterranean waters are characteristically oligotrophic (Bethoux 1981, Azov 1986). Present samples from the Cretan shelf had TOC concentrations that were consistent with this view. The inter-quartile range of TOC values among these samples was much lower in comparison to the other regions and revealed that most samples (75%) were in the low range <6 mg g^{-1}. Higher TOC levels for these waters were mostly in areas close to point-source discharges of organic wastes, e.g. beneath fish aquaculture cages (Karakassis et al. 1998). Most stations from the other regions had low to intermediate TOC levels, resulting in inter-quartile ranges between about 3 and 30 mg g^{-1}. Estuaries of the southeastern USA exhibited

the widest range in TOC concentrations, with values up to 175 mg g^{-1}.

Implications for global monitoring and data uncertainty

We have attempted here to provide a general framework for evaluating risks of reduced benthic species richness from organic loading and associated stressors in sediments within different ranges of TOC. Results suggest that the likelihood of such impairments should be relatively low at TOC concentrations less than about 10 mg g^{-1}, high at concentrations greater than about 35 mg g^{-1}, and intermediate at concentrations in between. Hopefully this framework will prove useful in sediment risk assessments over broad coastal areas that are receiving organic wastes and other co-varying pollutants associated with human activities. However, it must be understood that the TOC critical points supporting this framework are intended to be used only as a general screening-level indicator for evaluating the likelihood of reduced sediment quality and associated bioeffects, and should not be regarded as absolute criteria or measures of causality. No attempt has been made to distinguish between causes of effects directly related to TOC versus other potential co-occurring stressors within these ranges.

Predictive ability across these ranges, though reasonable based on results of re-sampling simulation (Table 2), is not free of uncertainty. This point is illustrated in Fig. 4 by the wide range in species richness values that can be observed at discrete levels of TOC. There is much scatter in the raw data. Methodological differences among the various regional data sets could be a possible source. While steps have been taken to help compensate for such differences (see 'Materials and methods'), related problems still may exist. For example, $E(S_n)$ was selected as a biological response variable to help account for sample-size differences due to different gear types (grab and sieve sizes). Yet finer sieves have been shown to retain greater numbers of small species and of juveniles of larger species retained as adults on coarser sieves (e.g. Bachelet 1990, Schlacher & Wooldridge 1996, Thompson et al. 2003). The increases could affect both the richness and evenness components of diversity and, thus, the $E(S_n)$ measure. Such potential effects are acknowledged here. However, while mesh-size variations have been shown to have strong influences on estimates of density and biomass, reports of similar effects on measures of species diversity, especially from mesh variations within the 1.0 to 0.3 mm range used in this study, are less consistent. Bishop & Hartley (1986) and Thompson et al. (2003), for example, found that few additional

species were retained with 0.5 mm sieves compared to 1.0 mm sieves. Bachelet (1970), while expounding on the significant loss of individuals with coarser sieves, also found no significant differences in number of taxa among mesh sizes from 0.5 to 0.063 mm consistently on 4 seasonal sampling occasions, nor in H' (Shannon diversity) or J' (evenness) among mesh sizes from 1.0 to 0.063 mm for most sampling occasions. Similarly, with respect to $E(S_{10})$, one of the present co-authors (I. Karakassis pers. obs.) compared values of this measure for 87 samples from the eastern Mediterranean Sea that had been sequentially sieved on 1.0 mm and 0.5 mm sieves and found no significant differences between mesh sizes. Values calculated from both fractions combined averaged 98% ($\pm$11%) of the 1.0 mm fraction alone. Moreover, while we cannot rule out the possibility of mesh-size effects, it is important to recognize the basic similarity in benthic-TOC patterns observed among the individual regional data sets in the present study (Fig. 3B). Although individual curve elevations varied, the overall pattern of decreasing species richness with increasing TOC was generally consistent among individual data sets including representatives of the various sieve sizes (e.g. 0.3 mm for Boston Harbor/Massachusetts Bay, 0.5 mm for eastern Mediterranean Sea and southeastern US estuaries, and 1.0 mm for North Sea/coastal UK).

In addition to regional differences, the variability in the data could be due to a complexity of other interacting environmental factors, including season, depth, salinity, grain size, sediment hydrodynamics, particle flux, larval supply, food value of organic matter, biological interactions, or presence of other co-varying stressors (see reviews such as Gray 1974, 1981, papers in Coull 1977, Anderson et al. 1987, Lamberson et al. 1992, Snelgrove & Butman 1994). A particularly good example of this complexity is the growing realization that, in addition to the quantity of organic matter present in sediments, differences in its quality, bioavailability, fluxes, and utilization as a food source can have strong effects on patterns of distribution as well (Gray 1974, Tenore et al. 1982, Lopez & Levinton 1987, papers in Lopez et al. 1989, Snelgrove & Butman 1994).

We also mentioned earlier the importance of grain size as a correlate of TOC and other potential co-varying stressors that may be affecting the benthos. Note the direct relationship between the percent fine grains (<62 µm fraction) and increasing TOC in the present data set and the inverse pattern relative to $E(S_{10})$ (Fig. 6). Increasing proportions of finer-grained sediment particles would provide greater surface area (due to a greater surface/volume ratio) for sorption of both organic matter and chemical contaminants (Landrum & Robbins 1990, Lamberson et al. 1992). Thompson & Lowe (2004) similarly showed how changes in

benthic species composition and abundances are often linked to the interaction of fine sediments, organic material, and chemical contaminants. On a related note, a common view explaining higher abundances of deposit-feeding infauna in muddy versus sandy sediments is that there is more food associated with finer particles, due to the greater surface area for microbial growth and adsorption of organic films (Lopez & Levinton 1987). Snelgrove & Butman (1994) discuss a number of additional ways in which benthic species may vary in relation to grain size, including preferential selection of settling larvae for a particular size class, preferences for a particular grain size in feeding, exclusion of filter feeders in muddy sediments due to increased resuspension from sediment reworking by deposit feeders (i.e. trophic-group amensalism, as originally introduced by Rhoads & Young 1970), sediment stability, and the possibility that passively settling benthic larvae and sediments of similar characteristics (e.g. size, specific gravity, and gravitational fall velocity) may be hydrodynamically sorted in a similar manner within the bottom boundary-layer flow.

Thus, such inherent variability and resulting data uncertainty must be considered in future applications of the TOC critical points presented here. Low species richness does not necessarily imply that the system is under stress, or that the cause of stress, if it exists, is due to TOC per se. Low species richness might occur in sediments with low to moderate TOC for such reasons as (1) insufficient amounts of organic matter with nutritionally rich components that can be utilized as food; (2) natural influence of salinity or grain size; (3) geochemical, physical, and hydrodynamic factors restrict-

ing recruitment of larvae; (4) natural physical disturbances (e.g. sediment erosion due to bottom currents and storm events); or (5) biological interactions (e.g. competition, predation, trophic-group amensalism) (Gray 1974, 1981, papers in Coull 1977, Lopez & Levinton 1987, papers in Lopez et al. 1989, Snelgrove & Butman 1994). A variety of anthropogenic factors could contribute to such variability and potential misclassifications as well. For example, chemical contaminants could be present in toxic amounts at a particular site that was not organically enriched, even though such stressors are generally positively correlated with TOC (Landrum & Robbins 1990, Lamberson et al. 1992, Thompson & Lowe 2004). Physical disturbances of sediment caused by human activities (e.g. dredging and disposal operations, ground-fishing) also could reduce species richness independent of TOC.

Similarly, it is possible for species-rich benthic assemblages to occur in sediments with high TOC. Possible explanations for such cases include (1) the fauna were not exposed to harmful levels of stressors due to small-scale spatial variations or pollution-tolerance adaptations (Gray 1974, 1981, Pearson & Rosenberg 1978, Landrum & Robbins 1990); (2) stressors were present at high concentrations, but not in bioavailable forms (Neff 1984, Adams 1987, Reynoldson 1987, Rodgers et al. 1987, Knezovich et al. 1987, Landrum & Robbins 1990); or (3) a significant portion of the measured TOC was in a refractory form (e.g. black carbon) and not reflective of related conditions, such as hypoxia or high ammonia and sulphides, that would pose biological risks. Regarding the latter point, it has been shown that black carbon may contribute considerably to the organic matter buried in marine sediments (Middelburg et al. 1999). In the present study, which relied on the use of historical data, there was no way available to go back and identify the quality of carbon present across the various samples and thus to account for such variability uniformly across all samples.

Future research should focus on reducing such uncertainties. Of particular importance for coastal management applications is the need to differentiate between the relative contributions of multiple stressors (e.g. those related to chemical versus organic loading) that may be co-varying in relation to common environmental factors (such as the percent of fine-grained sediment). Condition of the ambient benthic community can be a sensitive indicator of anthropogenic disturbances. However,
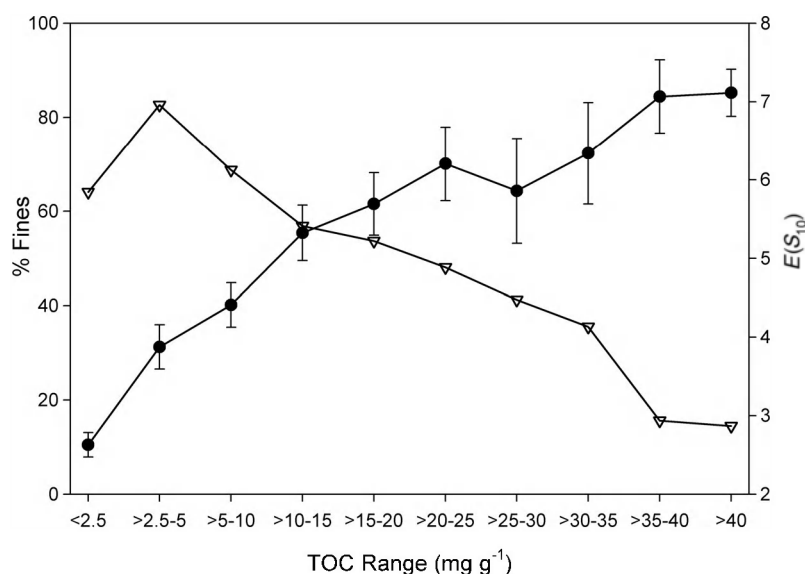

Fig. 6. Plot of the percent fine-grained sediment (<62 mm fraction) and $E(S_{10})$ versus TOC (mg g^{-1}). ●: percent fine-grained sediment; ▽: $E(S_{10})$

the incidence of a degraded benthic community in organically enriched sediments does not preclude the possibility that the observed bioeffects were due to other co-varying stressors (e.g. chemical contaminants). Where co-occurrences of high TOC levels and benthic effects are observed, detailed follow-up studies are recommended to determine exact causes and stressor sources.

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