

Towards a classification of organic enrichment in marine sediments based on biogeochemical indicators

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Abstract

A nomogram is developed to show that pH, redox potentials ($E_{h_{NHE}}$) and measures of dissolved sulfides ($H_2S + HS^- + S^{2-}$) (total free S^{2-}) can be used to classify organic enrichment impacts in marine sediments. The biogeochemical cycle of sulfur in marine sediments is described to show that changes in macrobenthic infauna community structure associated with high levels of organic matter supply result from stress due to oxygen deficiency (hypoxia and anoxia) and toxic effects of S^{2-} . The changes reflect enhancement of microbial sulfate reduction under conditions of high organic matter sedimentation and the progressive formation of hypoxic–anoxic conditions measured by decreased $E_{h_{NHE}}$ and increased concentrations of S^{2-} . The nomogram provides a basis for classification of the oxic status of marine sediments based on changes in inter-related biological and biogeochemical variables along an organic enrichment gradient. © 2008 Elsevier Ltd. All rights reserved.

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1. Introduction

The response of benthic communities and sediments to increased organic matter input is well known and determined in large part by the physical nature of the substrate, the availability of dissolved oxygen and the composition of the biological community (Pearson and Rosenberg, 1978; Snelgrove and Butman, 1994; Gray et al., 2002). Despite this general understanding there is no commonly shared quantitative scale for defining organic enrichment effects. Since oxygen supply is limited by physical and biological factors that control exchanges across the sediment–water interface, hypoxic and anoxic conditions are created in surface sediments if rates of oxygen consumption exceed supply. Changes in oxic conditions in surface sediments affect the size and taxonomic composition of both microbial and faunal communities in all benthic habitats (Nilsson et al.,

1991; Diaz and Rosenberg, 1995; Nilsson and Rosenberg, 2000; Gray et al., 2002; Diaz et al., 2004).

This general understanding of how physical and biological factors affect marine benthic communities through oxygen availability provides the basis for a comprehensive scale for measuring organic enrichment effects in sediments. Such a unified model would be useful for quantifying eutrophication in coastal waters (Cloern, 2001), to evaluate benthic habitat quality (Ferreira, 2000; Diaz et al., 2004), and to serve as a basis for decisions regarding cost effective methods for monitoring organic waste discharges from rapidly growing industries such as marine aquaculture (Fernandes et al., 2000; Kalantzi and Karakassis, 2006; Giles, 2008).

The following review briefly describes the biogeochemical cycle of sulfur in marine sediments that is basis for the formation of oxic–anoxic conditions. With increased organic matter loading sulfate reduction becomes the major metabolic pathway predominating over oxic (aerobic) respiration. The aim is to show how biogeochemical variables used to measure these processes are linked to

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changes in marine benthic community structure along an organic enrichment gradient continuum. Methods used to measure effects, as reflected in qualitative indices previously proposed to describe organic enrichment impacts in marine sediments, are compared on a common quantitative scale in the form of a nomogram to classify enrichment zones based on different biogeochemical variables.

2. The sulfur cycle

An understanding of how macrobenthic infauna respond to and are affected by increased organic matter supply caused by eutrophication requires consideration of the sulfur cycle. The microbiological structure and biogeochemical transformations involving sulfur are well known (Fig. 1) and pool sizes and transformation rates between compounds have been measured (Fenchel, 1969; Jørgensen, 1977, 1982; Fenchel and Blackburn, 1979; Chanton et al., 1987; Thode-Andersen and Jørgensen, 1989; Heilskov and Holmer, 2001; Gray et al., 2002; Holmer et al., 2005; Otero et al., 2006; Preisler et al., 2007).

Inorganic sulfur compounds that accumulate in suboxic sediments are utilized by sulfate-reducing bacteria and removed through chemical oxidative processes (Berner, 1971; Jørgensen, 1982; Canfield, 1989; House, 2003; Holmer et al., 2005; Preisler et al., 2007). Transformations of inorganic sulfur occur through a cyclic series of coupled oxidation–reduction (redox) processes overlapping vertically within the sediment (Jørgensen, 1977; Berner, 1981; Canfield et al., 1993). Aerobic respiration occurs in the surface oxic layer while in subsurface hypoxic and anoxic sediments sulfate-reducing bacteria reduce sulfate to sulfide. When sulfate is depleted methanogenesis becomes the dominant microbial metabolic process in anoxic sediments.

Other electron acceptors (e.g. NO_3^- or FeO_2H) may be utilized during anaerobic metabolic processes in suboxic layers at depths determined by the degree of organic enrichment (Holmer and Kristensen, 1992, 1996; Canfield et al., 1993; Thamdrup, 2000; Jensen et al., 2003; Holmer et al., 2005; Preisler et al., 2007).

Some sulfides produced during sulfate reduction are complexed with metal ions such as iron to form FeS and pyrite (FeS_2) (Howarth, 1979; Aller, 1980; Berner, 1971, 1984; Howarth and Jørgensen, 1984) (Fig. 1) but these solid phase forms of S^{2-} are not toxic to benthic fauna. However, total dissolved sulfides (free $\text{S}^{2-} = \text{H}_2\text{S} + \text{HS}^- + \text{S}^{2-}$) that accumulate in sediment layers where sulfate reduction occurs (Thode-Andersen and Jørgensen, 1989; Holmer and Kristensen, 1992, 1996) are highly toxic (Grieshaber and Völkel, 1998; Gray et al., 2002). Reduced S^{2-} compounds also strongly influence biogeochemical conditions in sediments since they arise from energy flow through anaerobic bacterial metabolism associated with inorganic mineralization and organic matter decomposition (Berner, 1980; Fenchel and Blackburn, 1979).

Berner (1981) suggested that redox (E_{hNHE}) potentials could be used as the basis for a geochemical classification system in sediments. The subscript NHE refers the normal hydrogen electrode corrected potential determined after mV measured with a Pt electrode are normalized for the electrolyte in the reference electrode. As progressively less favourable electron acceptors are used to oxidize organic matter during diagenesis, E_{hNHE} potentials decrease reflecting different coupled biogeochemical reactions. Oxygen reduction in surface aerobic (oxic) sediments is replaced by nitrate and metal oxide reduction in post-oxic sediments at deeper depths where sulfate reduction pre-

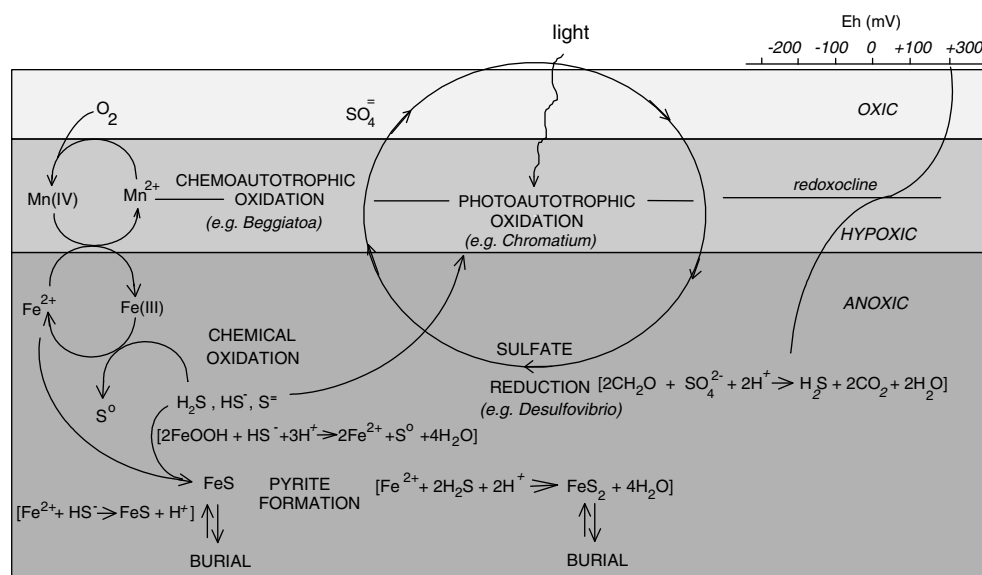


Fig. 1. Major geochemical reactions in the sulfur cycle and an illustrative profile of redox (E_{h}) potentials in marine sediments in oxic (light grey), suboxic or hypoxic (medium grey) and anoxic (dark grey) sediment zones (modified from Fenchel, 1969; Blackburn et al., 1975; Jørgensen, 1977; Berner, 1984; Brooks and Mahnken, 2003; Preisler et al., 2007).

dominates. If oxygen supply from the water column is sufficient, a surface oxic layer of sediment of variable thickness will always be present with reduced sediments at deeper depths.

The redoxcline, also referred to as the redox potential discontinuity (RPD) (Fenchel, 1969; Fenchel and Riedl, 1970), reflects the depth of oxygen penetration into surface sediments. It represents the depth where $E_{h_{NHE}}$ potentials change rapidly from positive to negative values (Fig. 1). Surface aerobic sediments may range from a few mm's up to 10 cm in depth depending on the balance between oxygen penetration and consumption (Revesbech et al., 1980; Reimers, 1987; Cai and Sayles, 1996; Preisler et al., 2007) and will generally be deeper in sandy sediments (1–2 cm) than in more fine-grained organically rich mud deposits (Andersen and Hilder, 1987). It is possible for S^{2-} and oxygen to coexist within the surface oxic layer in subtidal sediments (Wit et al., 1989) and in sediments colonized by seagrasses due to active transport of oxygen into plant rhizomes (Pedersen et al., 2004). Air-channels that transport oxygen into sediments are an adaptation of seagrasses allowing growth and enhanced organic matter mineralization in reduced sediments (Holmer et al., 2005). If sediments with an oxic layer only a few mm thick are sampled to a deeper depth (e.g. 0–2 cm), the mixed 'surface' sediment will contain both dissolved O_2 and S^{2-} .

It has been recognized that $E_{h_{NHE}}$ -pH conditions in marine sediments are primarily controlled by photosynthesis, respiration and oxidation–reduction reactions between Fe and S (Zobell, 1946; Baas Becking et al., 1960; Fenchel, 1969; Berner, 1963, 1980). As more reducing conditions are formed through sulfate reduction, both pH and oxidation–reduction ($E_{h_{NHE}}$) potentials decrease. The characteristic relationship between these variables is the basis for the MOM environmental monitoring system developed and applied in Norway (Ervik et al., 1997) using pH, $E_{h_{NHE}}$ and S^{2-} as principal variables to identify acceptable and non-acceptable benthic conditions associated with organic enrichment due to salmon farms (Fig. 2).

Changes such as those that occur in surface sediments and benthic microbial and macrofaunal communities when sulfides accumulate and hypoxic (low oxygen) or anoxic (no oxygen) conditions are created have been reviewed by Holmer et al. (2005). Sulfide accumulation is stimulated by high rates of organic matter sedimentation that increase oxygen consumption by aerobic bacteria. However, when respiratory oxygen uptake rates exceed oxygen supply by diffusion and advective processes, anaerobic metabolic pathways and sulfate reduction become the predominant processes for mineralization of organic matter in marine sediments (Jørgensen, 1977; Findlay and Watling, 1997; Gray et al., 2002; House, 2003).

Many types of bacteria representing both aerobic and anaerobic transformation processes are involved in cycling of sulfur in sediments (Fig. 1). *Beggiatoa*, for example, is a mat-forming, filamentous sulfur bacteria that undergoes chemoautotrophic growth. Oxygen from internally stored

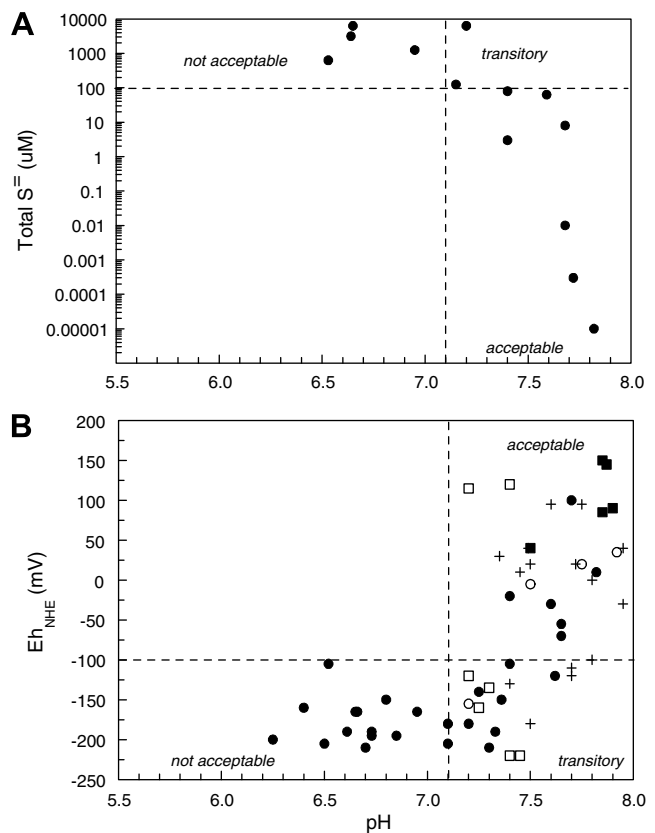


Fig. 2. Relationships between (A) pH and total S^{2-} and (B) pH and $E_{h_{NHE}}$ in 0–2 cm sediments around salmon aquaculture farm sites in coastal Norway. Vertical dotted lines represented suggested boundaries for acceptable, transitory and unacceptable conditions based on the geochemical variables. Data for pH- S^{2-} from below and along the edges of a fish farm and for pH- $E_{h_{NHE}}$ from various station categories – below net pens (filled circles), abandoned sites (open circles), transition zone (crosses), exposed reference (filled square) and sheltered reference (open square) locations. Redrawn from Schaanning and Hansen (2005).

NO_3^- is used to oxidize H_2S to S^0 which accumulates inside cells as white granules (Møller et al., 1985). Since both oxygen and H_2S are required for metabolism, *Beggiatoa* occurs at oxic/anoxic interfaces with a preference for sediment layers where both O_2 and S^{2-} are absent (Preisler et al., 2007). When oxygen concentrations in bottom water become low due to respiration in the water column or in upper sediment layers, white *Beggiatoa* mats are visible on the sediment surface indicating that reducing conditions have reached the sediment/water interface. Cells of *Beggiatoa* are motile and demonstrate chemotactic movements away from high S^{2-} concentrations along steep S^{2-} and O_2 gradients (Fenchel, 1969; Fenchel and Riedl, 1970; Preisler et al., 2007). Extensive *Beggiatoa* mats occurred on sediments around salmon farms when total S^{2-} concentrations were between 800 and 1200 μM (μmol) (Hargrave et al., 1993; Brooks and Mahnken, 2003). *Desulfovibrio* is another example of a chemoautotrophic, sulfate reducing bacteria but this taxa is strictly anaerobic and oxidizes H_2 by reducing sulfate. It occurs at a greater sediment depth than *Beggiatoa* in sub-oxic sediments with negative $E_{h_{NHE}}$ potentials (Fig. 1).

3. Sulfide measurements

Although present in higher concentrations, total S^{2-} in sediments is more difficult to determine than in the water column since exposure to oxygen will lower concentrations. Various types of microsensors (e.g. Clark-type polarographic and ion-specific electrodes) have been developed for *in situ* use to overcome this problem allowing gradients in dissolved oxygen and various inorganic ions to be measured as vertical profiles in surface sediment layers (Reimers, 1987; Archer and Devol, 1992; Luther et al., 1998; Preisler et al., 2007). However, dedicated equipment (e.g. benthic landers to place equipment on the bottom without sediment disturbance) is required to position and move electrodes vertically over small (<1 mm) distances across the sediment–water interface for *in situ* measurements. An additional constraint for use of microelectrodes such as Ag^+/S^{2-} electrodes for total S^{2-} determinations is the need for precise pH measurements to allow calculations of H_2S concentrations in pore water. The equilibrium between H_2S , HS^- and S^{2-} is shifted towards S^{2-} in marine sediments because of pH values between 7 and 8 (Jørgensen, 1982; Schaanning and Hansen, 2005). Pore water sulfides also can be assessed by various spectrophotometric methods (Cline, 1969). The methods require separation of pore water from sediments using *in situ* dialysis bags or in the laboratory by centrifugation or squeezing.

Commercially available specific ion electrodes (e.g. Orion Sure-Flow™ Combination Ag^+/S^{2-} Electrode) can also be used to measure total S^{2-} without simultaneous measurements of pH (Wildish et al., 1999; Thermo Electron Corporation, 2003). The method requires removal of sediments from cores or grabs, ensuring protection from prolonged exposure to air and mixing samples with a similar volume of alkaline antioxidant buffer solution (SAOB). The buffer containing NaOH, EDTA and ascorbic acid prevents S^{2-} oxidation and increases sample pH to ~12 to convert H_2S and HS^- in pore water to S^{2-} . SAOB and wet sediment are mixed immediately before measurements and concentrations are expressed on a sediment volume basis as $\mu M S^{2-}$. Since S^{2-} measured by the electrode is dissolved in pore water concentrations can be expressed as $\mu M mL^{-1}$ if sediment water content is measured.

Long extraction times (>5 min) after mixing SAOB and sediment must be avoided since solid phase metal–sulfide complexes may be solubilized in the alkaline buffer solution (Wildish et al., 1999). S^{2-} standards in a concentration range of 100, 1000 and 10,000 μM can readily be measured using commercially available Ag^+/S^{2-} electrodes and stable mV potentials are usually obtained within 1–2 min, so measurements can be made rapidly. The minimum sensitivity (lowest detectable concentration) using the Orion electrode is in the range of 1–10 μM . In practice, however, it is often difficult to achieve accurate standardization at concentrations <50 μM because low S^{2-} concentrations are unstable. Potentials formed using ion-specific electrodes are also temperature sensitive and

the temperature of calibration standards and extracted samples must be similar.

Different pools of component ions of total S^{2-} in sediments can also be measured relative easily on samples brought to the laboratory. Sediments are fixed by addition of zinc acetate after which sulfides are extracted by distillation (Fossing and Jørgensen, 1989). Zinc acetate precipitates pore water sulfides and “reactive” iron-sulfides (amorphous FeS and Fe_3S_4) as ZnS due to a lower precipitation product for Zn compared to Fe. Pyrite (FeS_2) remains in its original form. The sediment is distilled either in a one-step method combining acidic and chromium reducible conditions, where all sulfides are liberated as H_2S in a N_2 stream and trapped as ZnS, or in a two step procedure where acid volatile sulfides (AVS = H_2S , HS^- , FeS, Fe_3S_4) are separated from the chromium reducible sulfur (CRS = S^0 , FeS_2) and quantified spectrophotometrically (Cline, 1969). The same principle is used for measurements of sulfate reduction where the only modification is incubation with a sulfate tracer ($^{35}S-SO_4^{2-}$) before sectioning (Fossing and Jørgensen, 1989; Kallmeyer et al., 2004). Tracer accumulation as sulfides in both AVS and CRS fractions (total reducible sulfur) (TRS) is then quantified by determining radioactivity using a scintillation counter.

The variety of methods used to measure different forms of sulfur in sediments creates problems when comparing data from various studies. For example, AVS and CRS represent different compounds within the sulfur cycle and it is difficult to directly compare results of spatial and temporal variability in the measurements with biological observations such as macrofauna biomass or community biodiversity (Brooks and Mahnken, 2003; Brooks et al., 2003). Importantly, although Ag^+/S^{2-} electrodes respond selectively to dissolved S^{2-} and at known pH the concentration of H_2S ($\sum[S^{2-}] + [HS^-] + [H_2S]$) can be calculated (Preisler et al., 2007), the measure is less accurate than other chemical methods (Schaanning and Hansen, 2005). They suggest expressing total S^{2-} as pS ($= -\log[\sum H_2S]$) and reporting measured values of rest potentials (Es) corrected for the reference electrode potential in untreated sediments (i.e. without use of a strong alkaline buffer). In our review, where most measures of total S^{2-} were derived using electrodes in an alkaline buffer solution, concentrations are reported as μM (sediment volume basis) to compare data from different studies and to provide a common scale for expressing levels of sediment organic enrichment.

4. Sulfide toxicity

The negative effects of organic enrichment and resulting total S^{2-} accumulation operate on benthic infauna at individual, population and community levels of organization. Fauna respond to both hypoxic effects of low dissolved oxygen concentrations that inhibit respiration as well as to direct toxicity of total S^{2-} formed during sulfate reduction (Theede et al., 1969; Miron and Kristensen, 1993a,b; Diaz and Rosenberg, 1995; Julian et al., 2001; Gray

et al., 2002). As mentioned above, iron monosulfides (included in the AVS pool), elemental sulfur (S^0) and complexed particulate iron-sulfides (e.g. pyrite) produced during sulfate reduction are generally non-toxic to macrofauna (Brooks and Mahnken, 2003), but S^{2-} compounds are highly toxic (Bagarino, 1992; Grieshaber and Völkel, 1998).

Total S^{2-} brought into contact with oxic surface sediments or oxygenated water is rapidly oxidized (chemical oxidation) (Fig. 1). Chemical oxygen demand can often account for all benthic oxygen uptake when organic matter sedimentation is very high (Hargrave et al., 1993). Approximately equal amounts of organic carbon in coastal sediments can be consumed by oxic respiration and sulfate reduction (Jørgensen, 1982; Canfield, 1989). Jørgensen (1977) calculated that 90% of sulfide produced by sulfate reduction in a shallow Danish estuary was reoxidized by oxygen at the sediment surface. Sulfate was estimated to have a turnover time of 4–5 months, whereas H_2S in pore water, with a smaller pool size, had a faster turnover time (1–5 days). FeS and pyrite accumulated at 5–10 cm depth and being stable under these conditions had very long turnover times of about 10 years.

The formation and stable nature of S^0 , FeS and pyrite during sulfate reduction in coastal sediments is well known (Howarth, 1979; Aller, 1980; Berner, 1971, 1984; Howarth and Jørgensen, 1984). Of three major factors responsible for pyrite accumulation (concentration and reactivity of iron compounds, availability of dissolved sulphate and concentration of organic matter utilized by sulfate-reducing bacteria), Berner (1971) considered that the availability of metabolizable organic matter was the most important. Preisler et al. (2007) concluded that most of the S^{2-} flux into the suboxic layer in coastal sediments was removed chemically by precipitation with Fe^{2+} and oxidation by Fe(III). While rapid oxidation of AVS has been observed in biodeposits under mussel rafts (Otero et al., 2006), pyrite, representing ~60% of total reduced sulfides in the sediments, was relatively stable and resistant to oxidation as found in previous studies.

With the exception of salt marshes and deep sea vents natural concentrations of dissolved total S^{2-} in the water column are generally low (<10 μM) due to rapid oxidation (Powell and Somero, 1986; Otero et al., 2006). Because of the importance of sulphate reduction in organic matter decomposition in marine sediments and restricted movement of pore water, concentrations in coastal and estuarine sediments are usually much higher. Values of >5000 μM total S^{2-} can occur in sediments in areas of intensive finfish aquaculture (Brooks and Mahnken, 2003; Wildish et al., 2004; Holmer et al., 2005; Schaanning and Hansen, 2005) but such high concentrations are seldom found naturally. Concentrations >1000 μM in sediments from coastal areas with industrial and urban development may be caused by increased organic matter loading through discharge of waste effluents or other sources organic of enrichment, but levels are seldom as high as have been observed in sediments near

salmon farms (Wildish et al., 2001; Brooks and Mahnken, 2003; Brooks et al., 2003). Because of the long turnover times concentrations of pyrite buried in subsurface sediments in areas where high rates of organic matter sedimentation have persisted can be up to an order of magnitude greater than in surface sediments (Jørgensen, 1977; Fenchel and Blackburn, 1979; Howarth, 1979; Sørensen and Jørgensen, 1987; Boesen and Postma, 1988; Otero et al., 2006).

Total S^{2-} in sediment pore water creates toxic biological effects for benthic fauna by interference with aerobic respiration (Grieshaber and Völkel, 1998). H_2S inhibits cytochrome C oxidase in the electron transport system and HS^- binds with the ferric (Fe^{3+}) ion of the cytochrome to prevent oxygen release by oxyhemoglobin. Fish such as Atlantic salmon are extremely sensitive to H_2S . While appearing to tolerate prolonged exposure to low concentrations (maximum 8 μM H_2S) without mortality, slightly higher levels (20–30 μM H_2S) result in stress with liver damage and irreparable gill necrosis (Keimer et al., 1995). Although H_2S released into the water column from anoxic sediments would be expected to be rapidly oxidized (Brooks and Mahnken, 2003), even brief exposure of fish to concentrations <10 μM S^{2-} may result in physiological stress and interfere with growth (Black et al., 1995). Fish health problems in cultured Atlantic salmon have been indirectly linked to H_2S out-gassing from sediments (Keimer et al., 1995).

Macrofauna have a higher tolerance to total S^{2-} than fish and taxa inhabiting mud bottoms where concentrations may be higher are less sensitive than those on hard or sandy substrates (Bagarino, 1992). Gray et al. (2002) reviewed published literature and concluded that fish are more sensitive to hypoxic conditions (<0.5 mg O_2 l^{-1}) than crustaceans and echinoderms, with annelids and molluscs less sensitive, respectively. Under hypoxic conditions (10% oxygen saturation) the polychaete *Nereis diversicolor* survived exposure to ~200 μM H_2S for 16 days before suffering high mortality (Vismann, 1990). Other polychaete species have shown variable sub-lethal responses to S^{2-} depending on whether exposure is acute or chronic (Miron and Kristensen, 1993a,b; Julian et al., 2001). Decreases of up to 50% in burrow ventilation rates in different species occurred over a range of concentrations (100–500 μM S^{2-}) with acute exposure, but effects were reduced or absent with prolonged exposure to lower (<50 μM) concentrations. The polychaete species used in these studies were from intertidal areas where there were natural daily and tidal-frequency variations in sediment S^{2-} concentrations. For example, short-term fluctuations (1–200 μM) at 0.5 cm depth occurred in North Sea beach sediment as a function of changing light conditions (Wit et al., 1989). Variations in irrigation rates within the range of 100–500 μM S^{2-} show adaptations by polychaetes to brief periods of increased exposure (Julian et al., 2001).

The broad range of resistance in macrofauna to toxic effects of hypoxia and H_2S exposure has been reviewed (Theede et al., 1969; Bagarino, 1992; Diaz and Rosenberg,

1995; Gray et al., 2002; Brooks and Mahnken, 2003). The varied responses within S-tolerant taxa have made these useful indicator species for organic enrichment (Pearson and Rosenberg, 1978; Nilsson and Rosenberg, 1997, 2000). Opportunistic species that colonize organically rich sediments are in almost all cases those that display either physiological or behavioral adaptations allowing some degree of resistance to S^{2-} toxicity. They are generally of small body size and have short life cycles allowing rapid colonization of sediments once less S^{2-} -tolerant species have disappeared.

There are, however, limits to the ability of even opportunistic S^{2-} -tolerant fauna such as some nematodes and polychaete species to exist at higher concentrations (Hargrave et al., 1993; Duplisea and Hargrave, 1996; Miron and Kristensen, 1993a,b; Grieshaber and Völkel, 1998; Brooks and Mahnken, 2003; Brooks et al., 2003). *Capitella*, one of the most tolerant species and a commonly used indicator of excessive sediment organic enrichment, disappeared from sediments under salmon pens at concentrations $>7200 \mu\text{M}$ S^{2-} (Hargrave et al., 1993; Brooks and Mahnken, 2003). Although moderate levels of organic matter may stimulate colonization and growth of tolerant fauna, due to the combined effects of progressive oxygen depletion and S^{2-} accumulation, high amounts of organic matter input are always associated with decreases in biodiversity and biomass. Small sized opportunistic infauna that increase in abundance in response to higher S^{2-} levels are often not the preferred prey species for bottom feeding fish (Pearson and Rosenberg, 1978; Weston, 1990; Wildish and Pohle, 2005). Hypoxic conditions in near-bottom water may also result in avoidance of organically rich sediments by fish. Thus, although numbers of benthic prey may be higher for bottom feeding fish, the increased food supply may not be consumed due to this avoidance response. This may be an explanation for the occurrence of high numbers of polychaetes in organically rich sediments with relatively high levels of S^{2-} (Pocklington et al., 1994; Brooks and Mahnken, 2003; Tomassetti and Porrello, 2005).

5. Transitions from aerobic to anaerobic benthic metabolism

All aerobic bacteria and benthic fauna utilize O_2 and produce CO_2 during organic matter respiration and changes in dissolved O_2 and CO_2 in water held in cores over undisturbed sediment have been used in different studies to estimate total benthic metabolism due to aerobic and anaerobic processes (e.g. Hargrave et al., 1993; Grant et al., 1995; Findlay and Watling, 1997; Nizzoli et al., 2006). The methods require corrections for oxygen consumption due to chemical oxidation of reduced sulfides and dissolution of carbonates. The techniques were applied to sediments collected under salmon farms and at reference sites (>500 m away) in southwestern Bay of Fundy and coastal Maine waters (Findlay and Watling, 1997; Hargrave et al., 1997) (Fig. 3). Results showed that Eh_{NHE} and S^{2-} were inversely correlated and that both aerobic (O_2 uptake)

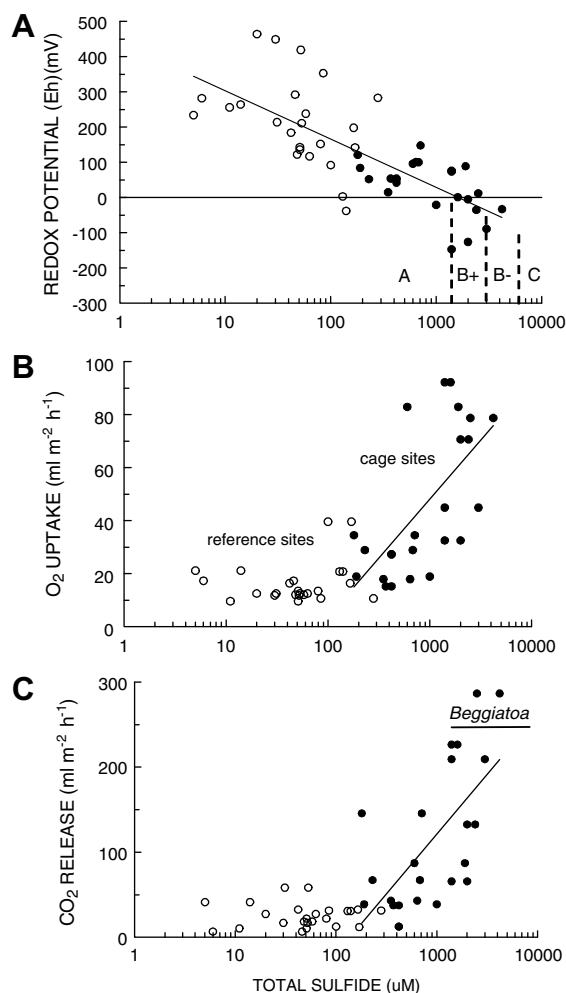


Fig. 3. Relationships between (A) Eh_{NHE} and S and sediment/water fluxes of (B) dissolved O_2 and (C) CO_2 under salmon pens (farm sites) and at reference sites (>500 m away) in southwestern Bay of Fundy from Hargrave et al. (1997). Least squares regression lines (A) $y = 440 - 59.5 \ln(x)$, $r^2 = 0.559$, A, B+, B-, C indicate organic enrichment zones based on S concentrations, (B) $y = -85.3 + 19.3 \ln(x)$, $r^2 = 0.418$, (C) $y = -300.3 + 61.0 \ln(x)$, $r^2 = 0.423$. Horizontal line in (C) indicates S^{2-} concentrations $>1000 \mu\text{M}$ where white sulfur bacteria mats (*Beggiatoa* spp.) appear on the sediment surface and sulfate reduction is the predominant microbial metabolic process.

and total (CO_2 release) respiration increased in sediments in proximity to farms. S at reference locations away from fish pens was $<300 \mu\text{M}$ while concentrations at farm sites varied from ~ 150 to $5000 \mu\text{M}$. Variability in benthic respiration was also greater at farm sites than at reference locations as might be expected because of higher rates of sedimentation of fish feces and waste feed and benthic metabolism was correlated with organic carbon sedimentation. Organic matter deposited at reference sites would be supplied from a variety of natural sources and lower sedimentation rates would be expected to be more uniform than those occurring under more heterogeneous conditions for sedimentation within farm leases.

High rates of aerobic and anaerobic benthic metabolism as total S^{2-} concentrations increase above ~ 500 – $1000 \mu\text{M}$

often coincide with the appearance of white *Beggiatoa* mats on sediments (Møller et al., 1985) (Fig. 3C). The area covered becomes more extensive at concentrations $>3000 \mu\text{M}$ (Hargrave et al., 1993; Brooks and Mahnken, 2003; Crawford et al., 2006). Crawford et al. (2001) also found that white sulfur bacteria were visible in video images of sediments under salmon farms in Tasmania confirming observations in other studies (Weston, 1990; Holmer and Kristensen, 1992) to show that local benthic organic enrichment under fish pens could be detected by the presence of bacterial mats.

6. Macrofauna responses to organic enrichment

There is an extensive literature documenting changes in the size and structure of benthic infaunal communities associated with variations in organic matter supply, stress due to oxygen deficiency (hypoxia and anoxia) and toxic effects of H_2S (Theede et al., 1969; Theede, 1973; Pearson and Rosenberg, 1978; Warwick, 1986, 1987; Schwinghamer, 1988; Weston, 1990; Pocklington et al., 1994; Findlay et al., 1995; Henderson and Ross, 1995; Pohle and Frost, 1997, 1998; Nilsson and Rosenberg, 1997, 2000; Brooks, 2001; Chamberlain et al., 2001; Pohle et al., 2001; Wildish et al., 2001; Brooks and Mahnken, 2003; Brooks et al., 2003; Hartstein and Rowden, 2004; Wildish and Pohle, 2005). Other studies, however, have found either limited or no clear effects of biodeposition on sediment biogeochemical characteristics or macrofaunal community size and/or structure (Grant et al., 1995; Crawford et al., 2003; Anderson et al., 2005; Miron et al., 2005).

Hydrodynamic factors determine the local erosional–depositional nature of sediments as well as oxygen supply at any given location. These site-specific factors, among others, determine if increased organic matter sedimentation will create hypoxic or anoxic conditions at the sediment surface and to what extent total S^{2-} will accumulate in sediments (Findlay et al., 1995; Findlay and Watling, 1997; Anderson et al., 2005; Schaanning and Hansen, 2005). Observations of variability in effects of benthic organic enrichment in different studies can be attributed to complex relationships between current velocity and the nature (sediment texture and organic content) of bottom substrates (Kalantzi and Karakassis, 2006; Giles, 2008).

Despite this variability, the general pattern of effects of organic enrichment and hypoxic and anoxic conditions on macrobenthic infauna is well known (Weston, 1990; Diaz and Rosenberg, 1995; Gamienick et al., 1996; Nilsson and Rosenberg, 1997, 2000; Chamberlain et al., 2001; Gray et al., 2002; Wildish and Pohle, 2005). Where sediment oxygen depletion and total S^{2-} accumulation occur due to reduced currents and increased organic matter sedimentation patterns of changes in macrofauna community composition are similar in many different studies. Only taxa tolerant of low oxygen and relatively high S^{2-} are present under conditions of increased organic matter loading. High

rates of organic matter sedimentation, oxygen depletion and S^{2-} accumulation lead to a reduction in average body size, suspension feeders begin to disappear, deposit feeders become more dominant and the distribution of individuals is progressively restricted to sediment surface layers (Brooks and Mahnken, 2003).

These generalized changes in macrofauna community structure, size distribution and position of organisms in the sediment column in response to the formation of hypoxic and anoxic conditions are the basis for the first general description of a benthic organic enrichment gradient proposed by Pearson and Rosenberg (1978). Gray et al. (2002) concluded that it is not organic enrichment *per se* but rather the formation of hypoxic conditions within sediments that cause negative effects on benthic fauna. Small-bodied opportunistic species, including polychaetes such as *Capitella capitata* and some S^{2-} -tolerant nematodes, are often the only taxa remaining when surface sediments contain relatively high ($>5000 \mu\text{M}$) concentrations of S^{2-} (Brooks and Mahnken, 2003; Brooks et al., 2003). This is the reason why specific polychaete taxa are useful as ‘indicator’ species for sediment organic pollution (Pocklington et al., 1994; Tomassetti and Porrello, 2005). As organic matter input increases from natural to moderately high levels the presence of these species demonstrates the transition of sediments from oxic to hypoxic states. However, as levels of organic supply become higher, even these S^{2-} -tolerant taxa cannot survive and sediments become progressively azoic with respect to macrofauna and only single cell organisms such as protozoa, ciliates and flagellates capable of living in S^{2-} -rich sediments are present (Fenchel and Riedl, 1970).

Molluscs are the macrofauna phylum most sensitive to organic matter enrichment and S^{2-} accumulation, while crustaceans, echinoderms and annelids such as polychaetes show an intermediate response (Gray et al., 2002). Although there was considerable variability, at low S^{2-} concentrations, data from salmon farms in the Broughton Archipelago area showed that less- S^{2-} tolerant, non-opportunistic species (molluscs and crustaceans) decreased in numbers by 50% with each increase of $\sim 280 \mu\text{M}$ S^{2-} (Brooks and Mahnken, 2003). Observations by Sutherland et al. (2005, 2006) under and near salmon pens in the same area also showed that numbers of arthropod classes and individuals and bivalve and polychaete abundance decreased as total S^{2-} concentrations increased from 100 to 6000 μM . Only nematodes failed to show a consistent pattern of response.

Nematodes in the meiofaunal size fraction contain a variety of species that vary greatly in their sensitivity to S^{2-} toxicity and therefore respond differently to organic enrichment (Schwinghamer, 1988; Diaz and Rosenberg, 1995; Duplisea and Hargrave, 1996; Grieshaber and Völkel, 1998; Mazzola et al., 2000; Mirto et al., 2000; Nilsson and Rosenberg, 2000; Sutherland et al., 2007). The difference in abundance of nematodes (Ne) and crustaceans (copepods (Co) and ostracods) has been proposed as a sensitive indicator of organic pollution in marine sediments since in general crustaceans are more sensitive to hypoxia

than nematodes (Warwick, 1981, 1986; Amjad and Gray, 1983; Raffaelli, 1987; Sundulli and De Nicola Giudici, 1989; Gray et al., 2002). A range of Ne/Co ratios (>10 – >100) has been proposed for different types of sediments (mud-sand) to identify organic pollution thresholds, but it is unlikely that a single value can be selected for broad application. The actual S^{2-} tolerance of species and the proportions of mesobenthic (living interstitially within sediments) and epibenthic (on or close to the sediment surface) taxa reflecting different meiofauna groups in a given set of samples affects relative numbers and responses to varying S^{2-} levels. However, the pattern of decreasing numbers of nematodes and copepods as S^{2-} concentrations increase has been widely observed irrespective of sediment type (Sutherland et al., 2007).

7. Carbonate vs. non-biogenic sediments

Holmer et al. (2005) discussed responses to organic enrichment of carbonate-rich, biogenic sediments common in tropical coastal ecosystems. The sediments are characterized by low OM and Fe content which could limit FeS formation and often coarse-grained which permits advective movement of pore water and result in deeper oxygen penetration into surface layers and a reduction in S^{2-} accumulation. As a result effects of organic enrichment on macrofauna in these sediments might be expected to differ from those in temperate latitudes. However, few studies have been carried out describing quantitative relationships between macrofauna community structure and sulfide accumulation in carbonate-rich sediments.

Geochemical cycles in biogenic sediments are similar to those in non-carbonate deposits. For example, benthic studies under milkfish farm netpens in the Philippines have shown rapid decomposition of organic matter in sediments by high rates of sulfate reduction and, when pore water sulfate pools were depleted, methanogenesis (Holmer et al., 2002, 2003). Although free S^{2-} in pore water was not measured, AVS accumulated in reduced sediments and the appearance of *Beggiatoa* mats indicated that dissolved S^{2-} was probably increased in surface sediments (Preisler et al., 2007). Particulate sulfide pools were generally higher in milkfish farm sediments than in surrounding pristine areas and available iron was bound as FeS, suggesting that iron was the limiting factor for sulfide burial as observed elsewhere in Fe-poor sediments (Morse et al., 2007).

The distribution of the alpheid burrowing shrimp *Alpheus macellarius* associated with milkfish farms in the Philippines showed that the shrimp was sensitive to organic enrichment. *A. macellarius* were absent from sulfide-rich farm sediments while numbers were greatly reduced in less impacted nearby areas at a fallowed farm site and a location unaffected by farming activity (Holmer and Heilskov, 2008). Since carbonate sediments are often coarse-grained macrofauna assemblages are dominated by species with a relatively large body size characteristic of climax assemblages as illustrated to the far right in the Pearson–Rosen-

berg diagram (Pearson and Rosenberg, 1978). Accumulation of free S^{2-} due organic enrichment, enhanced due to the absence of Fe, would be expected to have negative effects since the macrofauna exist in highly oxic surface sediments. In contrast, macrofauna in non-biogenic sediments, which are often fine-grained and enriched by natural processes of organic matter sedimentation, display by a broad range of body size representing both opportunistic and non-opportunistic taxa. Since sulfides are naturally present community assemblages are comprised of species with a tolerance to a broad range of hypoxic and reducing conditions. As organic enrichment and sulfide accumulation increases in these communities, enrichment effects due to sulfides and hypoxic conditions are also reduced to some degree by fauna burrowing and bioturbation activities (Heilskov et al., 2006).

8. Benthic enrichment indices

Various organic enrichment classification systems have been proposed for marine sediments based on changes in benthic macrofauna community size and structure and sediment geochemical characteristics due to alterations in organic matter and oxygen supply, sulfide accumulation and microbial metabolic processes (Table 1). Hard bottom substrates (rock, cobble and gravel) prevent using grabs or cores to collect samples, and water column sampling, underwater video or acoustic surveys are required to assess sediment and benthic community characteristics for monitoring purposes (DFO, 2004, 2005). All of the enrichment indices listed in Table 1 have been derived from observations in soft bottom areas of fine sand to mud sediments where sample collection was possible.

The classical method of macrofauna analysis, based on taxonomic descriptions and determinations of numerical abundance and biomass in different faunal size classes, requires sample retrieval. This was the basis for the qualitative description of changes in benthic infauna along disturbance and organic enrichment gradients proposed by Pearson and Rosenberg (1978). The approach has been widely applied as the traditional method for detecting disturbance in benthic macrofauna communities (Warwick, 1986, 1987; Schwinghamer, 1988; Weston, 1990; Wildish and Pohle, 2005). Biotic indices for assessing benthic habitat environmental quality range from simple metrics involving some measure of species richness to more complex multi-variate approaches (Diaz et al., 2004).

Other methods such as observations of sediment electrochemical properties (Holmer et al., 2005; Schaanning and Hansen, 2005), depth of the redox potential discontinuity (Fenchel and Riedl, 1970) or vertical profile imaging of undisturbed sedimentary structure (Rhoads and Germano, 1982; Grizzle and Penniman, 1991; Karakassis et al., 1998, 2000; Wildish et al., 2004, 2005) provide alternatives to the taxonomic approach. Analysis of macrofauna community size and structure is labour-intensive and time-consuming whereas geochemical methods provide a more direct mea-

Table 1
Correspondence of various scales for benthic organic enrichment classification based on nomenclature proposed by Berner (1981)¹, and Pearson and Rosenberg (1978)² modified by Wildish et al. (2001)³

Geochemical classification ¹	Enrichment classification	Macrofauna ²	RPD ^a (cm)	BHQ	Eh _{NHE} (mV)	S ²⁻ (μM)	BEI ^b
Oxic	Normal ²	III	>1	>10	>+100	<300	>+1000
Post-oxic	Transitory ²	II	<1	0–100	0–100	300–1300	0–1000
	Oxic ³						
Sulfidic	Polluted ²	I	<0.5	2–4	–100–0	1300–6000	–1000–0
	Hypoxic ³						
Sulfidic	Grossly polluted ²	0	0	<2	<–100	>6000	<–1000
Methanic	Anoxic ³						

Normal, transitory/oxic and post-oxic represent sediments within natural ranges of organic matter loading. RPD (redox potential (Eh_{NHE}) discontinuity depth) from Fenchel and Riedl (1970), BHQ (benthic habitat quality index) based on vertical profiles of sedimentary structures from sediment profile imaging (Nilsson and Rosenberg, 2000), geochemical variables (Eh_{NHE} and total dissolved sulfides (H₂S + HS⁻ + S²⁻)(free S²⁻) in surface (0–2 cm) sediments from Wildish et al. (2001) and Holmer et al. (2005) and BEI (benthic enrichment index) from Hargrave (1994) and Hargrave et al. (1997). Table modified from Wildish et al. (2004) and Holmer et al. (2005).

^a Nominal values. Actual RPD will be determined by local hydrodynamics, sediment texture, relative rates of organic matter input and oxygen supply and biological factors such as burrow structures and levels of bioturbation.

^b Nominal values. Actual BEI will be determined by sediment porosity, types and rates of sedimentation of organic matter characteristic for various enrichment levels.

sure of oxic or organic enrichment status where sediments are fine-grained enough to allow grab or core penetration and sample recovery (Wildish et al., 2001). Combinations of measures of Eh_{NHE}, pH and S²⁻ (e.g. Figs. 2 and 3A) have been shown to be sensitive and cost effective methods for monitoring oxic–anoxic conditions in soft sediments along enrichment gradients near salmon farms (Ervik et al., 1997; Hargrave et al., 1997; Wildish et al., 1999, 2001; Holmer et al., 2005; Schaanning and Hansen, 2005; Wildish et al., 2005; Giles, 2008). Sediment porosity (water content), organic matter and Eh_{NHE} potentials were combined to derive a benthic enrichment index (BEI) shown to be related to rates of organic carbon sedimentation (Hargrave et al., 1993, 1997). Negative values of BEI, determined by redox potentials <0 mV, occur when organic carbon sedimentation is >1 g C m⁻² day⁻¹.

9. Quantifying benthic effects of sulfides

Previous observations identifying effects of hypoxic conditions on marine benthic fauna along an organic enrichment gradient have been descriptive rather than predictive (Gray et al., 2002). The qualitative conceptual model of benthic enrichment proposed by Pearson and Rosenberg (1978) provides an example. However, as the previous discussion shows, quantitative relations between organic matter sedimentation, oxygen availability and the formation of reducing conditions in sediments have been described. As total S²⁻ accumulates Eh_{NHE} potentials become increasingly negative (0 to <–200 mV) indicating that bacterial sulfate reduction is the predominant metabolic reaction (Figs. 1 and 2). Several studies have shown that changes in inter-related sediment biogeochemical variables resulting from increased rates of organic matter sedimentation can be used to derive quantitative relationships to predict changes in benthic community structure from organic matter supply and S²⁻ accumulation.

Sedimentation rates >1 g C m⁻² day⁻¹ resulted in the formation of hypoxic/anoxic sediments in mesocosms to which sewage sludge was added (Oviatt et al., 1987) and around salmon farms (Hargrave, 1994). Watling et al. (1995) and Findlay and Watling (1997) identified a similar threshold (1–5 g C m⁻² day⁻¹) close to salmon pens in coastal Maine where benthic microbial communities were altered and biodiversity of macrofauna reduced by sediment organic enrichment. Increased sulfate decrease around bivalve and finfish aquaculture sites occurred over a similar range of sedimentation rates (Dahlbäck and Gunnarsson, 1981; Holmer and Kristensen, 1992, 1996; Holmer et al., 2005). Observations and applications of the DEPO-MOD waste dispersion model around salmon farms in Scotland and British Columbia have also shown that proportions of benthic fauna feeding groups based on the infaunal trophic index (ITI) changed significantly when sedimentation rates increased above specific thresholds (Cromeey et al., 2002; Chamberlain and Stucchi, 2007). ITI values >50 were associated with predicted organic carbon fluxes <1 g C m⁻² day⁻¹ but values decreased rapidly (<30) as fluxes increased from 1 to 10 g C m⁻² day⁻¹. As described above, crustaceans and filter (suspension) feeding molluscs disappeared as major components of the benthic macrofauna when sedimentation rates increase to >5 g C m⁻² day⁻¹.

Observations in the Broughton Archipelago, British Columbia (BC), Canada provide additional quantitative information to directly compare S²⁻ in surface sediments and changes in macrofauna community size and structure (Fig. 4A and B). Although toxic effects of S²⁻ and hypoxia on benthic infauna have been identified, variance in the relationships shows that other variables such as biological factors of recruitment and predation can also determine macrofauna community structure. Also, as mentioned above, benthic macrofauna and meiofauna vary in their tolerance to the toxic effects of S²⁻. Despite this variability,

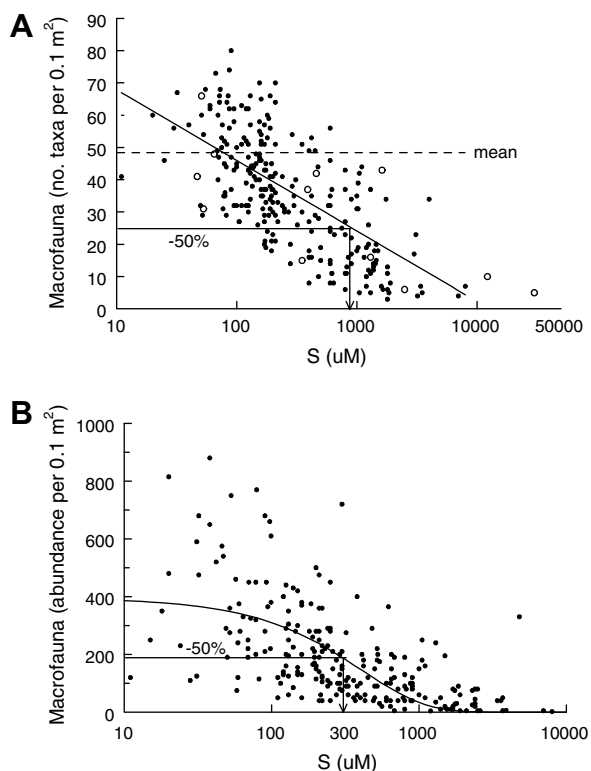


Fig. 4. (A) Relationship between S^{2-} and total number of macrofauna taxa and abundance in surface sediments observed at various distances up to 1 km away from salmon farms observed in the Broughton Archipelago (BC) (redrawn from Brooks and Mahnken, 2003). Solid points represent data from BC and open circles from southwestern Bay of Fundy (Wildish et al., 2004). Lines shows least squares regressions for data from BC between (A) numbers of taxa (mean indicated by dotted horizontal line) and S ($y = 89.8 - 21.9 \cdot \log_{10} x$, $r^2 = 0.51$), and (B) macrofauna infauna abundance (less opportunistic species) and S at the same locations ($y = 395.7 \cdot \exp(-0.00245 x)$, $r^2 = 0.38$). Arrows indicate S^{2-} levels associated with a 50% reduction in mean numbers of taxa and individuals.

the data show a continuous decrease with no apparent threshold of decreases in the number of taxa as a function of increasing S^{2-} concentrations. The number of non-opportunistic macrobenthic infauna taxa observed in the BC studies was reduced by 50% of the mean for reference stations at $\sim 1000 \mu\text{M}$ and by $\sim 70\%$ at $3000 \mu\text{M}$ S^{2-} (Brooks and Mahnken, 2003).

Observations of numbers of taxa and the Shannon–Weiner index (H') for macrobenthic infauna in southwestern Bay of Fundy and coastal Norway near salmon farms with different levels of total S^{2-} (Pohle and Frost, 1998; Pohle, 1999, 2001; Wildish et al., 2004; Schaanning and Hansen, 2005; Wildish and Pohle, 2005) show similar patterns to those in BC where there were decreases in diversity under or in close proximity (up to 100–200 m) to net pens (Fig. 4A). Exceptions can occur as, for example, at a site 50 m from a salmon farm in Norway where the diversity index indicated a highly disturbed benthic community ($H' = 0.3$) but total S^{2-} concentration was not significantly elevated. Thus, in some cases changes in benthic community structure may be a more sensitive indicator of benthic distur-

bance than geochemical measures. In general, however, there is a consistency in thresholds for various biological and geochemical variables and total S^{2-} in surface sediments along organic enrichment gradients in different studies. Benthic species richness was observed to increase at a ‘recovery’ station sampled over 5 years after re-location of salmon pens and cessation of farming operations 3 years later (Wildish and Pohle, 2005). The number of taxa increased from 5 to 25 compared to a higher total number (76) at reference sites in the same inlet, a value similar to the maximum observed in the BC studies (Fig. 4A). One salmon farm in the Bay of Fundy sampled in 2001 and 2002 showed a similar level of reduction in biodiversity (88–51%) with increased S^{2-} concentration as was observed in BC.

Three ‘sulfide regimes’ with infaunal responses beginning at 200–300 μM S^{2-} , considered to be within the ‘normal’ range ($<300 \mu\text{M}$) of concentrations in oxic coastal marine sediments, have been described (Wildish et al., 1999, 2001; Brooks, 2001). Similarly, differences in the response of the meiofauna Ne/Co ratio to biodeposition under mussel lines were thought to reflect variations in sensitivity by two opposing groups of nematodes – those more and less tolerant of anoxic conditions (Mirto et al., 2000). Also, sediment chemical remediation following removal of salmon from culture pens has been defined as the return of organic carbon and Eh_{NHE} potentials to reference levels associated with a reduction of S^{2-} to $<960 \mu\text{M}$ (Brooks et al., 2003), a threshold close to that for the transition from oxic to hypoxic sediments (between 1300 and 1500 μM S^{2-}) (Wildish et al., 2001; Cranford et al., 2006). As mentioned above, the appearance of *Beggiatoa* mats at the sediment–water interface when concentrations reached 800–1200 μM S^{2-} (Fig. 3C; Brooks and Mahnken, 2003) is an indication of the formation of hypoxic conditions in surface sediment layers.

Changes in the relative abundance of non-opportunistic and opportunistic fauna occur in hypoxic sediments between 2500 and 3000 μM S^{2-} – a threshold where most S^{2-} -intolerant taxa disappear, but colonization by more S^{2-} -tolerant species has yet to occur (Brooks, 2001; Brooks and Mahnken, 2003). Thus hypoxic sediments may be subdivided into two categories (A and B) using $\sim 3000 \mu\text{M}$ S^{2-} as a transition where the macrofauna community becomes dominated by rapidly colonizing, S^{2-} -tolerant taxa. Brooks and Mahnken (2003) found that opportunistic species increased in numbers between 2000 and 5000 μM S^{2-} but the abundance of all macrofauna, including opportunistic species, decreased significantly at higher concentrations. The observations are consistent with a threshold of 6000 μM S^{2-} proposed to characterize anoxic sediment (Wildish et al., 2001) that corresponds with the grossly polluted sediment enrichment category identified by Pearson and Rosenberg (1978) and sulfidic/methanic sediments in Berner’s (1981) classification (Table 1).

A nomogram (Fig. 5) can be used to illustrate related patterns of changes in Eh_{NHE} potentials, pH, oxygen availability, organic enrichment and macrofauna biodiversity as

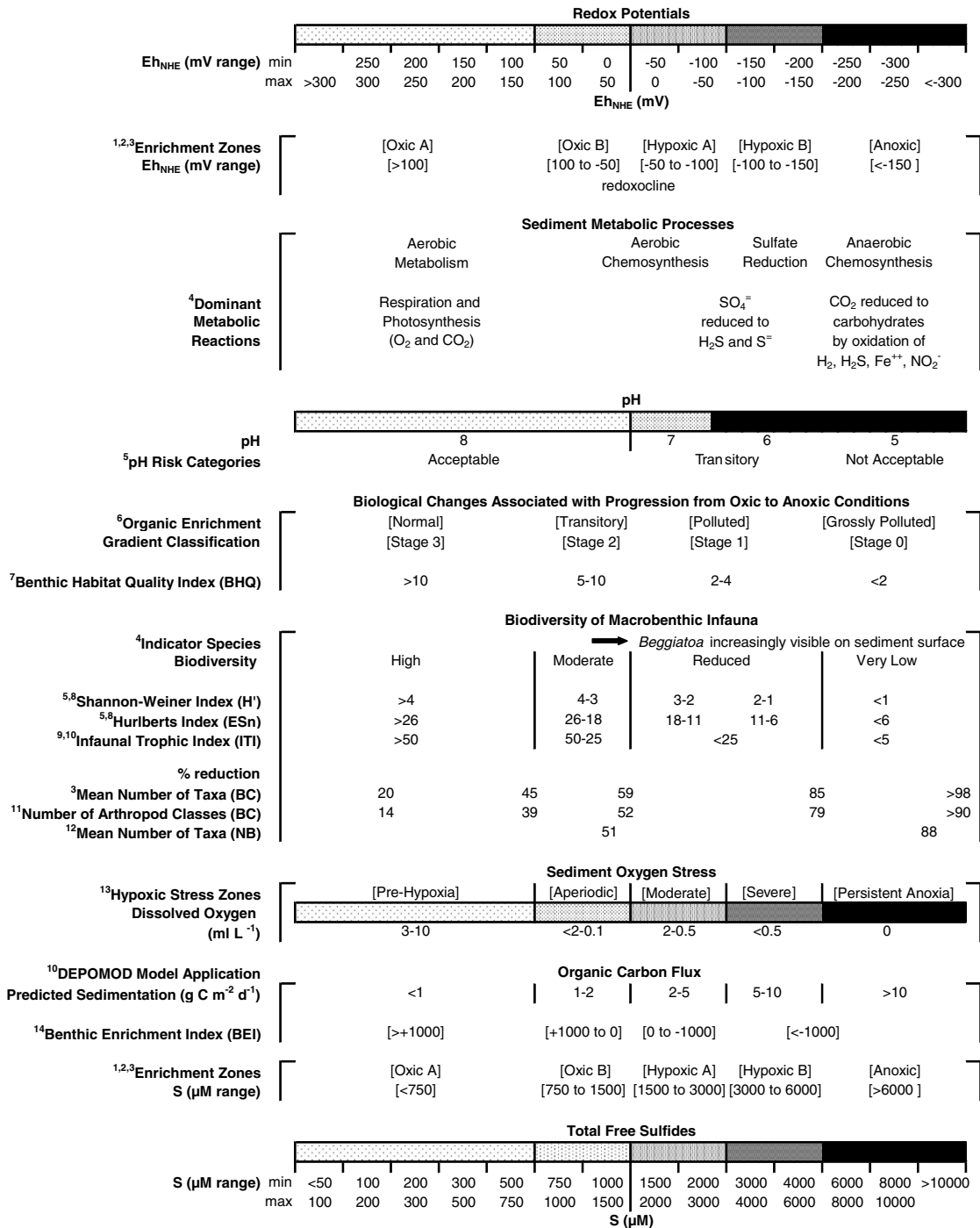


Fig. 5. Nomogram for benthic organic enrichment zonation based on $E_{h_{NHE}}$ potentials, and total free S^{2-} derived from data in Wildish et al. (2001)¹, Brooks (2001)² and Brooks et al. (2003)³. Dominant aerobic and anaerobic benthic metabolic processes in different enrichment zones as related to the sulfur cycle in marine sediments are described in Fig. 1 and Holmer et al. (2005)⁴. pH risk categories from Schaanning and Hansen (2005)⁵. The organic enrichment gradient classification is described by Pearson and Rosenberg (1978)⁶ and a benthic habitat quality (BHQ) index is based on sediment profile imaging of surface and subsurface sediment structures and mean depth of the apparent redox potential discontinuity (redoxcline) from Nilsson and Rosenberg (1997)⁷. Macrobenthic infauna biodiversity using Shannon–Weiner and Hurlberts indices are summarized from Hansen et al. (2001)⁸ and Schaanning and Hansen (2005)⁵. Infaunal trophic index values summarized from Cromey et al. (2002)⁹ and Chamberlain and Stucchi (2007)¹⁰. Reduction in macrofauna taxa expressed as percent decrease from the mean number at reference stations ($n = 49$) in the Broughton Archipelago (BC) derived using the regression [number of taxa = $89.8 - 21.9 * \log_{10}(S)$] from Brooks and Mahnken (2003)³ (data shown in Fig. 4A). Reduction in number of arthropod classes expressed as percent decrease from the calculated maximum number ($n = 6.4$) at a mean S concentration of $100 \mu M$ using the regression [number of classes = $12.07 - 2.84 * \log(S)$] from Sutherland et al. (2006)¹¹. Data from reference and farm sites in Limekiln Bay (2000) southwestern Bay of Fundy (total number of taxa in L'Etang inlet in 2000, $n = 76$) from Wildish et al. (2004)¹². Hypoxic stress zones related to dissolved oxygen concentrations are from a conceptual model of hypoxic effects on benthic community structure described in Diaz and Rosenberg (1995)¹³. DEPOMOD predicted organic carbon flux from Chamberlain and Stucchi (2007)¹⁰. Benthic enrichment index (BEI) derived from $E_{h_{NHE}}$, S, water content and organic carbon in surface (0–2 cm) sediments (Hargrave, 1994; Hargrave et al., 1997)¹⁴.

a function of increasing total S^{2-} in marine sediments. Stages in the enrichment classification system with dominant sediment metabolic processes, indices describing oxygen availability and biological structures (benthic habitat quality, hypoxic stress zones) described by Diaz and Rosenberg (1995), Nilsson and Rosenberg (1997), Nilsson and Rosenberg (2000) summarized in Table 1 are aligned with corresponding ranges of Eh_{NHE} , pH and total S^{2-} in the nomogram. Macrofauna biodiversity expressed as the Shannon–Weiner Index, total number of taxa or classes of arthropods as percentages of mean or maximum values at reference locations and infaunal trophic and benthic enrichment indices are shown relative to total S^{2-} concentrations.

Further studies are required to determine if the empirical relationships with no thresholds for reductions in numbers of non-opportunistic macrofauna taxa and classes of arthropods with increasing total S^{2-} are broadly applicable. Available data from a variety of marine coastal areas in temperate northern latitudes with varied sediment types suggest that inter-related changes in sediment biogeochemical and benthic biological variables along organic enrichment gradients are broadly similar in different locations. Additional research is needed to determine if the proposed scheme applies in carbonate-rich sediments to describe responses of macrofauna to S^{2-} and geochemical changes and where concentrations of available organic matter and Fe are generally lower than in non-carbonate deposits.

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