



Empirical relationships describing benthic impacts of salmon aquaculture

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ABSTRACT: Benthic organic enrichment due to sedimentation of waste feed and fecal matter released from salmon and other marine finfish aquaculture facilities has traditionally been measured by observing changes in benthic macrofauna assemblages. Sediment oxygen consumption, dissolved nutrient fluxes and variables such as redox potentials (normalized to hydrogen potential, $E_{h_{NHE}}$) and dissolved 'free' sulfides (ΣS^{2-} , HS^- , H_2S) (S) are also sensitive chemical indicators of benthic enrichment effects. Hypoxic or anoxic sediments are formed when high rates of organic matter (OM) sedimentation stimulate anaerobic metabolic processes such as sulfate reduction. General changes in $E_{h_{NHE}}$, S, OM flux and indices of macrofauna diversity in sediments as a result of increased organic enrichment around salmon aquaculture sites have been described in numerous studies. Some of the results are summarized here in empirical regressions that relate changes in sediment chemical and benthic biological variables to increased OM supply. The equations are descriptive of the data for salmon aquaculture sites where the studies were performed and further investigations are required to determine if the relationships provide general quantitative expressions for changes in sediment geochemical conditions and macrofauna community structure due to benthic organic enrichment.

KEY WORDS: Sediment organic enrichment · Redox potentials · Sulfides · Sulfate reduction · Macrofauna · Diversity

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INTRODUCTION

Giles (2008) summarized frequently observed negative impacts on benthic macrofauna communities due to sedimentation of waste feed pellets and fish fecal matter produced during marine finfish aquaculture. Depending on substrate type and current velocities sedimentation of waste products in the vicinity of netpens can result in increased sediment organic matter (OM), organic carbon (OC), nitrogen (N), dissolved 'free' porewater sulfides (ΣS^{2-} , HS^- and H_2S) (S), particulate acid-volatile sulfides (AVS), bottom cover by white sulfur bacterial (*Beggiatoa* spp.) mats and sediment-water exchanges of dissolved oxygen and ammonium while apparent redox potential (normalized to hydrogen potential, $E_{h_{NHE}}$) discontinuity (RPD) depth and benthic macrofauna biodiversity are reduced.

These general changes in sediment chemical properties and numbers, biomass and major macrofauna taxa

due to benthic organic enrichment are often represented by a conceptual model (P-R) (Pearson & Rosenberg 1978). Hypoxic or anoxic conditions are formed in surface sediments as a result of increased OM sedimentation, and macrofauna requiring oxygen for respiration cannot survive (Rosenberg 2001). Significant changes in species composition and community structure occur, since only taxa tolerant of suboxic conditions can survive (Bagarino 1992, Vaquer-Sunyer & Duarte 2010). The general effects of reduced diversity and altered macrofauna community structure due to increased benthic organic enrichment around salmon aquaculture facilities represented in the P-R model have been confirmed in many studies (Gowen & Bradbury 1987, Weston 1990, Black 2001, Brooks & Mahnken 2003, Kalantzi & Karakassis 2006, Kutti et al. 2007, Giles 2008).

Studies over the past decade have shown that geochemical methods can also be used as cost-effective measures of impacts of sedimentation of aquaculture-

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derived waste on surface sediments (Wildish et al. 1999, 2001, 2004, Brooks 2001, Brooks & Mahnken 2003, Holmer et al. 2005). Hargrave et al. (1997) compared different variables measured in surface sediments around salmon farms in the southwestern Bay of Fundy and found that S and sediment-water fluxes of O₂ and CO₂ were more sensitive to benthic organic enrichment than biological indicators such as macrofauna biomass or the proportion of deposit and suspension feeders. Giles (2008), using more recent data, concluded that sediment biogeochemical properties and sediment-water O₂ and NH₄⁺ fluxes were more sensitive to sediment organic enrichment than variables associated with macrofauna biomass and diversity.

Holmer et al. (2005) described the formation of hypoxic or anoxic conditions and the accumulation of particulate and dissolved S in marine surface sediments that can occur when high rates of OM sedimentation at salmon aquacultures sites stimulate sulfate reduction and other anaerobic metabolic processes. The impact of excessive benthic organic enrichment has been described using different terminology in the past depending on whether chemical or biological variables were used as the basis for classification. When enrichment classes are scaled according to S and Eh_{NHE}, 5 common categories can be identified that describe the gradient from normal to grossly polluted conditions described by the P-R model (Table 1).

Many of the negative benthic effects associated with high OM deposition are due to the formation of sub-oxic conditions. Brooks (2001) and Brooks & Mahnken

(2003) presented data showing relationships between reduced species numbers and diversity, increased S concentrations and decreased Eh_{NHE} potentials in response to higher OM sedimentation measured around salmon farms in coastal British Columbia. Hargrave et al. (2008a) used these and other published observations to construct a nomogram to show changes in inter-related variables with organic enrichment. The 2 axes formed by Eh_{NHE} and S provided scales for variables represented conceptually for an organic enrichment gradient in the P-R model although explicit empirical functions between variables were not presented. The quantitative relationships represented by the alignment of Eh_{NHE} and S scales with other variables in the nomogram are reported here. The calculated functions are only descriptive of the datasets on which they are based and further studies will be required to determine if the relationships are sufficiently general for application in other locations.

MATERIALS AND METHODS

Variables in the benthic enrichment nomogram.

Variables used to construct the nomogram (see Table 2) were determined for 18 fixed values of S (logarithmic scale: 100 to 10000 µM) and Eh_{NHE} (linear scale: +225 to -210 mV) representative of the range of sediment oxic categories described in Table 1. The ranges encompass observations from previous studies cited in the table caption. Although the data are from

Table 1. Nomenclature for gradients in benthic organic enrichment based on previously published descriptions. Values for 'free' dissolved sulfides (ΣS^{2-} , HS⁻, H₂S) (S) and redox potentials (Eh_{NHE}) with thresholds for transitions between oxic sediment categories (**bold**) from Hargrave et al. (2008a)

Benthic condition ^a	Geochemical status ^b	Oxygen stress ^c	Sediment condition ^d	Geochemical category ^e	Macrofauna diversity ^f	Oxic category ^g	'Free' S (µM)	Eh _{NHE} (mV)
Normal	Oxic	Pre-hypoxic	Very good	Normal	High	Oxic A	100	225
							150	200
							250	175
							400	150
							625	125
						Oxic A/B threshold	750	100
Normal	Post-oxic	Aperiodic	Good	Oxic	Good	Oxic B	875	75
							1250	25
							Oxic B/ hypoxic A threshold	1500
Transitory	Sulfidic	Moderate	Less good	Hypoxic	Moderate	Hypoxic A	1750	-25
							2500	-75
						Hypoxic A/B threshold	3000	-100
Polluted	Sulfidic	Severe	Bad	Hypoxic	Poor	Hypoxic B	4000	-150
							5000	-175
						Anoxic threshold	6000	-185
Grossly polluted	Methanic	Persistent anoxia	Very bad	Anoxic	Bad	Anoxic	7000	-195
							8500	-200
							10000	-210

^aPearson & Rosenberg (1978), ^bBerner (1981), ^cDiaz & Rosenberg (1995), ^dHansen et al. (2001), ^eWildish et al. (2001),

^fRosenberg et al. (2004), ^gHargrave et al. (2008a)

different locations in all cases it was possible to compare values of specific variables with measurements of $E_{h_{NHE}}$ and S made at or near salmon aquaculture sites in shallow coastal areas with relatively soft bottom in northern temperate latitudes where cores or grabs were collected for geochemical and faunal analysis. Values for variables could differ in other areas where sediments are more coarse grained or at lower latitudes where bottom deposits may be rich in carbonates (Holmer et al. 2005).

Determination of variable values. pH values shown in Table 2 were extrapolated from observations in Hansen et al. (2001) and Schaanning & Hansen (2005) where $E_{h_{NHE}}$ and pH were measured in surface sediments (0 to 2 cm) in cores or grabs collected in Norwegian fjords. Measurements of sulfide activity were made by inserting a Ag^+/S^{2-} electrode directly into sediments (i.e. there was no extraction with an alkaline antioxidant buffer solution) and calculating S concentrations from pH as pS^{2-} ($-\log[\Sigma H_2S]$). S concentrations reported in Table 2 were derived using an alkaline buffer extraction of sediment where S was measured as a concentration (μM). Soluble S concentrations may be expressed on a sediment volume or weight basis (Hargrave et al. (2008a,b) but units of μM are used here for comparison of data from different studies on a standard basis.

Values of organic carbon sedimentation (CS) represent measures of particulate matter deposited in moored sed-

iment traps combined with results from application of the DEPOMOD model to predict sedimentation around salmon aquaculture sites in coastal British Columbia (Chamberlain & Stucchi 2007). Benthic macrofauna data was available at sampling sites where CS and S were measured for calculation of 2 biodiversity indices: the Shannon Index (H'), and the Infaunal Trophic Index (ITI). The Benthic Habitat Quality (BHQ) index is derived from sediment profile images to determine 3 scores related to surface and subsurface structures and mean depth of the apparent Redox Potential Discontinuity (RPD). Representative values were determined using data in Nilsson & Rosenberg (1997) and Rosenberg et al. (2004). Values for the number of macrofauna taxa (NT), Benthic Enrichment Index (BEI, calculated as the product of OC [$mol\ C\ m^{-2}$] in surface sediment [upper 1 cm] $\times E_{h_{NHE}}$) and the Hulbert Index (ESn) were determined from the studies indicated in Table 2 and as described in Hargrave et al. (2008a). The Benthic Quality Index (BQI) provides a measure of benthic macrofauna species composition and abundance based on expected number of species among 50 individuals which has been shown to be related to BHQ in a description of faunal succession following the P-R model (Rosenberg et al. 2004).

Although sediment grain size is an important variable affecting oxygen penetration in sediments (House 2003), it was not included in data summarized by Hargrave et al. (2008a) in the nomogram nor is it

Table 2. Variables used to construct the benthic enrichment nomogram described in Hargrave et al. (2008a). S: dissolved 'free' porewater sulfides (ΣS^{2-} , HS^- , H_2S); Eh: $E_{h_{NHE}}$, electrode potential compared to the normal hydrogen electrode; CS: organic carbon sedimentation; NT: number of macrofauna taxa (parentheses: percent reduction in number of taxa from a mean of 51.5 for reference sites with S < 100 μM); BEI: Benthic Enrichment Index; BHQ: Benthic Habitat Quality; BQ: Benthic Quality Index; I: Shannon Index; ESn: Hulbert Index; ITI: Infaunal Trophic Index

S ^{a,b,c} (μM)	Eh ^{a,b,c} (mV)	pH ^d	CS ^e (g C m ⁻² d ⁻¹)	NT ^f	BEI ^g	BHQ ^h	RPD ^h (cm)	BQI ^h	H' ^e	ESn ^d	ITI ^e
100	225	8.00	0.1	51 (1.9)	1600	15.0	5.59	20	3.60	30	75
150	200	7.97	0.2	48 (7.7)	1500	14.0	5.52	20	3.55	30	74
250	175	7.95	0.3	42 (19.2)	1400	12.0	5.17	19	3.50	29	70
400	150	7.92	0.5	38 (26.9)	1300	11.0	4.82	18	3.45	28	62
625	125	7.90	0.7	32 (38.5)	1100	9.5	3.98	17	3.40	26	55
750	100	7.87	1.0	29 (44.2)	900	9.0	3.61	16	3.35	25	50
875	75	7.85	1.3	27 (48.1)	700	8.5	3.22	15	3.30	23	45
1250	25	7.80	2.0	23 (55.8)	250	7.0	2.05	13	3.10	20	35
1500	0	7.75	2.5	21 (59.6)	0	6.5	1.72	12	3.00	18	30
1750	-25	7.70	3.0	18 (65.4)	-300	6.0	1.42	11	2.80	17	25
2500	-75	7.58	4.0	13 (75.0)	-1000	4.5	0.81	9	2.40	13	16
3000	-100	7.50	5.0	10 (80.8)	-1400	4.0	0.68	8	2.10	11	12
4000	-150	7.35	7.0	6.0 (88.5)	-2000	3.0	0.50	6	1.60	9	9
5000	-175	7.15	8.5	5.5 (89.5)	-2500	2.5	0.44	5	1.30	7	6
6000	-185	7.00	10.0	5.0 (90.4)	-2800	2.0	0.39	4	1.00	6	5
7000	-195	6.85	11.5	4.5 (91.3)	-3000	1.5	0.36	3	0.80	5	4.5
8500	-200	6.70	13.0	4.0 (92.3)	-3300	1.0	0.33	2.5	0.60	4.5	4
10 000	-210	6.55	15.0	3.5 (93.3)	-3500	0.5	0.31	2	0.40	4	3.5

^aWildish et al. (2001), ^bBrooks (2001), ^cBrooks & Mahnken (2003), ^dHansen et al. (2001) and Schaanning & Hansen (2005), ^eCromey et al. (2002) and Chamberlain & Stucchi (2007), ^fBrooks (2001) and Brooks & Mahnken (2003), ^gHargrave (194) and Hargrave et al. (1997), ^hRosenberg et al. (2004) with Redox Potential Discontinuity (RPD) depth calculated using a regression derived from data in Nilsson & Rosenberg (1997) (see Fig. 4a)

considered here. Levels of OM in marine sediments are highly dependent on sediment grain size and although differences in concentrations are often detected at increasing distances from a farm (Brooks & Mahnken 2003, Kalantzi & Karakassis 2006), between-location variability often leads to non-significant relationships with other variables (Giles 2008). Dell'Anno et al. (2002) suggested that sediment OM biochemical composition could be used to indicate the trophic status of coastal benthic habitats and Hyland et al. (2005) proposed that OC in sediment be used as an indicator of stress in marine sediments. In general, however, OM, OC and N are not correlated with other measures of benthic enrichment (Hargrave et al. 1997, Brooks & Mahnken 2003, Giles 2008). Thus data for sediment grain size and OM, while important for considering enrichment effects, are excluded from the present analysis.

Borja et al. (2000, 2009) have described the AZTI (Marine and Food Technology Center, Bizkania, Spain) Marine Biotic Index (AMBI) for benthic quality assessment. Fleischer et al. (2007) and Grémare et al. (2009) examined relationships between AMBI and BQI in various marine and estuarine areas. Although high values of AMBI were sometimes associated with low values of BQI there was no consistent pattern in different locations. AMBI is based on computations using assigned values for sensitivity or tolerance of macrobenthic species to disturbance, but responses of indicator species may differ between locations (Bustos-Baez & Frid 2003, Rosenberg et al. 2004). Fleischer et al. (2007) recommended that the BQI with a modified scaling term be used as an index for marine benthic habitat quality rather than the AMBI index. No data exists for comparing AMBI with Eh_{NHE} and S so the index could not be considered in the present analysis.

Statistical methods and data presentation. SlideWrite Plus v7.0 (Advanced Graphics Software) and SigmaStat v2.0 (SPSS) were used to perform least-squares regression analyses (Gauss-Jordan method for linear approximation) between Eh_{NHE} and S and 10 dependent variables (Table 2). Values for each variable associated with corresponding redox potentials and S represent nominal values observed in previous studies. Linear, exponential, nonlinear exponential and sigmoidal functions (Table 3) were tested for goodness-of-fit by comparison of correlation coefficients and homogeneity of variance. A multiple linear regression was then used with or without ln-transformations of variables to derive a single function describing the combined effects of S and Eh_{NHE} on dependent variables. The multiple regressions form the basis for the structure of the 2-dimensional nomogram where linear and logarithmic scales for Eh_{NHE} and S are aligned to allow approximate values of dependent variables sensitive to organic enrichment to be determined

Table 3. Equations used to describe relationships between variables listed in Table 2. Constants (a_0) and fitted parameters (a_1 , a_2 , a_3) were calculated using least squares regression methods as described in the text. Equation type G was assessed with and without logarithmic (ln) transformation of dependent (y), and Eh_{NHE} and S as independent variables (x_1 and x_2)

Equation type	Function	Linear form
A	Linear	$y = a_0 + a_1 \times x$
B	Linear	$y = a_0 + a_1 \times \ln(x)$
C	Exponential	$\ln(y) = a_0 + a_1 \times x$
D	Exponential	$\ln(y) = a_0 + a_1 \times \ln(x)$
E	Nonlinear exponential	$y = a_0 + a_1 \times e^{-x/a_2}$
F	Sigmoidal	$y = a_0 + a_1/[1 + e^{-(x-a_2)/a_3}]$
G	Multiple linear	$y = a_0 + (a_1 \times x_1) + (a_2 \times x_2)$

from the intersection of a straight line connecting measured values of the 2 variables (Hargrave et al. 2008a). Constants were added to Eh_{NHE} (+250) and BEI (+3000) to calculate positive values for ln-transformations. Nonlinear curves used the Levenberg-Marquardt Algorithm with coefficients determined iteratively by minimizing the chi-squared function (least squares criterion). Multiple linear regressions were performed with an alpha value of 0.05 for inclusion of variables. Empirical relationships are referred to by equation number in parentheses.

RESULTS

Eh_{NHE} , pH and S

S and Eh_{NHE} , the 2 variables to which other measures of benthic organic enrichment are compared in the nomogram, are inversely related (Fig. 1a). The nonlinear exponential function showed the asymptotic nature of the relationship over the full range of values (Eq. 1) (Table 4). High redox potentials (+100 to +300 mV) occur in oxic sediments ($S < 750 \mu\text{M}$) with lower values (-100 to -200 mV) under hypoxic and anoxic conditions ($S > 1500 \mu\text{M}$).

Wildish et al. (1999) linearized the negative relationship between S and Eh_{NHE} for data from salmon farms and reference areas in southwestern Bay of Fundy with a logarithmic transformation of S concentrations (Eq. 2). Eh_{NHE} potentials observed in the same area in 2002 (data from Wildish et al. 2004) and those from the nomogram (Table 2) generally fall above this regression line when S is $< 750 \mu\text{M}$ and below the line at higher S concentrations (Fig. 1a). Similar regressions for the 2002 data from the Bay of Fundy (Eq. 3) and data from Table 2 (Eq. 4) have higher intercept and slope coefficients and while not being significantly different from each other ($p < 0.05$) are different from Eq. (2) ($p > 0.05$).

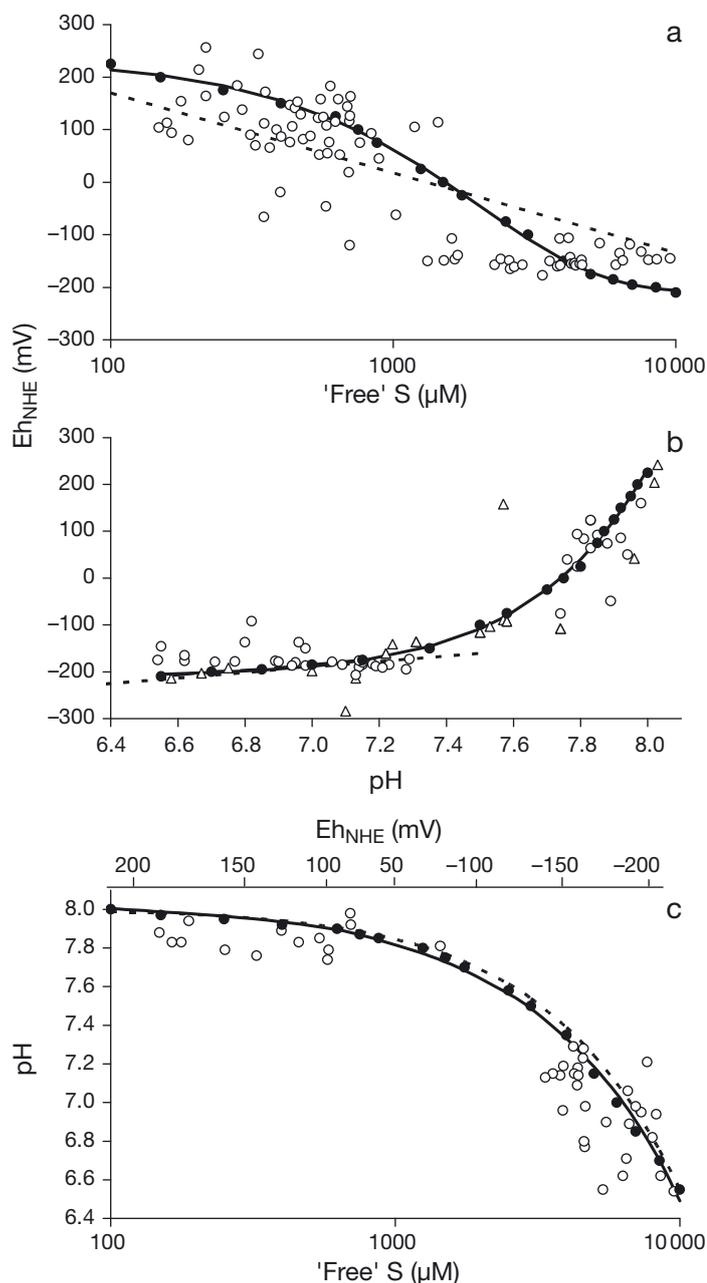


Fig. 1. Empirical relationships between (a) dissolved 'free' sulfides (ΣS^{2-} , HS^- , H_2S) (S) and redox potentials ($E_{h_{NHE}}$), (b) pH and $E_{h_{NHE}}$ and (c) S, $E_{h_{NHE}}$ and pH in surface (0 to 2 cm) sediments. ●: Values are data shown in Table 2. ○: data from Letang Inlet, Bay of Fundy in 2002 described in Wildish et al. (2004). Δ: median, minimum and maximum pH values measured below occupied and abandoned farms and non-farm reference areas of coastal Norway from Schaanning & Hansen (2005). Solid and dashed lines: empirical equations described in Table 4

The sigmoidal function described the relationship between pH and $E_{h_{NHE}}$ (Eq. 5) (Fig. 1b). The calculated curve describes the relationship between the variables observed in surface sediments from salmon farm sites

in southwestern New Brunswick (Wildish et al. 2004) and in Norway (Schaanning & Hansen 2005). The median pH in surface sediments from under net-pens in Norwegian salmon farms was lower (7.22) than in non-farm reference areas (7.85).

The dashed line in Fig. 1b with a slope coefficient of 59 (Eq. 6) represents the theoretical linear relationship for the reversible half-cell reaction $HS^-(aq) \rightleftharpoons S^{\circ} \text{ rhomb} + H^+(aq) + 2e^-$ in sediments containing H_2S when pS^{2-} , pH and $E_{h_{NHE}}$ are used to calculate pH from pS^{2-} (Berner 1963, Whitfield 1969). Predicted $E_{h_{NHE}}$ potentials from the sigmoidal curve and the theoretical relationship converge for pH values between 6.5 and 7.2 and are characteristic of sediments where redox potentials are controlled by sulfate reduction. The linear regression between $E_{h_{NHE}}$ and pH between 6.55 and 7.15 (Table 2) had a slope coefficient of 50 (Eq. 7) similar to but slightly lower than the theoretical value. In less reduced and oxic sediments $E_{h_{NHE}}$ potentials are positive and the relationship between pH and Eh becomes weaker as reflected in the data from coastal Norway and the Bay of Fundy where positive potentials increase rapidly between pH 7.8 and 8 (Fig. 1b).

The relationship between S and pH is represented by an exponential function ($r^2 = 0.996$) (Eq. 8) (Fig. 1c). Due to the high degree of collinearity between the independent variables the multiple linear regression between pH, S and $E_{h_{NHE}}$ resulted in a minor increase in the correlation coefficient over the regression between pH and S (Eq. 9 vs. Eq. 8).

CS, $E_{h_{NHE}}$ and S

The nonlinear exponential function described the relationship between CS measured by deployment of sediment traps near aquaculture sites in southwestern Bay of Fundy and $E_{h_{NHE}}$ potentials (Eq. 10) (Fig. 2a). A logarithmic linear function was used previously to describe this relationship (Eq. 11). When data in Table 2 was used to calculate a similar function (Eq. 12) the correlation coefficient was slightly lower ($r^2 = 0.955$) than obtained using the exponential function. Both expressions show decreases in $E_{h_{NHE}}$ with increasing CS. $E_{h_{NHE}}$ potentials approached asymptotic values near -200 mV as CS increased to >5 g C $m^{-2} d^{-1}$ (Fig. 2a).

Chamberlain & Stucchi (2007) plotted the relationship between arithmetic values of S and DEPOMOD-predicted values for CS using a logarithmic x-axis (as shown in Fig. 2b). However, regression analysis showed that for both data in Table 2 and median values of CS reported by Chamberlain & Stucchi (2007) S was linearly related to CS over the range 0.01 to

Table 4. Regression equations and r^2 values for empirical relationships between variables described (see Table 2), that are shown in Figs. indicated. Dependent variable (y) listed first followed by independent variables. Function type by letter listed in Table 3. Solid or dashed line type refers to lines plotted in Figs. 1 to 5

Variables	Function (line type)	Regression	r^2	Equation number
Fig. 1a				
Eh _{NHE} -‘free’ S	E (solid)	$y = -209 + 444 \times e^{-x/2025}$	0.999	(1)
	B (dash) ^d	$y = 473 - 66 \times \ln(x)$	0.672	(2)
	B	$y = 683 - 98 \times \ln(x)$	0.729	(3)
	B	$y = 771 - 108 \times \ln(x)$	0.966	(4)
Fig. 1b				
Eh _{NHE} -pH	F (solid)	$y = -209 + 3767 / [1 + e^{-(x-8.64)/0.32}]$	0.999	(5)
	A (dash) ^b	$y = -603 + 59 \times x$	1.000	(6)
	A	$y = -537 + 50 \times x$ ($x = 6.55$ to 7.15)	0.987	(7)
Fig. 1c				
pH-‘free’ S	C (dash)	$\ln(y) = 2.08 - 0.00002 \times x$	0.996	(8)
pH-‘free’ S-Eh _{NHE}	G (solid)	$y = 7.93 - (0.00014 \times x_1) + (0.0004 \times x_2)$	0.997	(9)
Fig. 2a				
Eh _{NHE} -CS	E (solid)	$y = -209 + 424 \times e^{-x/3.44}$	0.997	(10)
	B (dash) ^c	$y = 54.0 - 75.2 \times \ln(x)$	0.679	(11)
	B	$y = 62.3 - 95.9 \times \ln(x)$	0.955	(12)
Fig. 2b				
‘free’ S-CS	A (solid)	$y = -25.2 + 632 \times x$	0.994	(13)
	A (dash) ^d	$y = 62.2 + 487 \times x$	0.817	(14)
Fig. 2c				
CS-‘free’ S-Eh _{NHE}	G	$y = 0.535 + (0.0014 \times x_1) - (0.004 \times x_2)$	0.997	(15)
Fig. 3a				
BEI-CS	E (solid)	$y = -4174 + 5861 \times e^{-x/6.92}$	0.999	(16)
	B (dash) ^c	$y = 647 - 1428 \times \ln(x)$ ($x > 1$)	0.780	(17)
	B	$y = 1508 - 1841 \times \ln(x)$ ($x > 1$)	0.991	(18)
Fig. 3b				
BEI-Eh _{NHE}	A	$y = -94.8 + 12.3 \times x$ ($x < 100$)	0.997	(19)
BEI-‘free’ S	B (dash)	$y = 11245 - 1554 \times \ln(x)$ ($x > 750$)	0.979	(20)
BEI-‘free’ S-Eh _{NHE}	G (solid)	$y = 164 - (0.227 \times x_1) + (7.72 \times x_2)$	0.993	(21)
Fig. 4a				
RPD-BHQ	E (dash) ^e	$y = -0.28 + 0.40 \times e^{x/3.96}$	0.987	(22)
	F (solid) ^e	$y = 0.259 + 5.42 / [1 + e^{-(x-8.19)/1.68}]$	0.991	(23)
Fig. 4b				
BHQ-Eh _{NHE}	A	$y = -0.40 + 0.03 \times x$	0.977	(24)
BHQ-‘free’ S	B	$y = 30.1 - 3.24 \times \ln(x)$	1.000	(25)
BHQ-‘free’ S-Eh _{NHE}	G (solid)	$y = 26.3 - (2.70 \times \ln(x_1)) + (0.005 \times x_2)$	0.999	(26)
Fig. 4c				
BQI-Eh _{NHE}	A	$y = 11.69 + 0.042 \times x$	0.994	(27)
BQI-‘free’ S	E	$y = 2.00 + 18.79 \times e^{-x/2508}$	0.998	(28)
BQI-‘free’ S-Eh _{NHE}	G (solid)	$y = 12.6 - (0.00033 \times (x_1)) + (0.036 \times x_2)$	0.999	(29)
Fig. 5a				
NT-Eh _{NHE}	A	$y = 22.5 + 0.103(x)$	0.970	(30)
NT-‘free’ S	B	$y = 104 - 11.4 \times \ln(x)$	0.985	(31)
	B (dash) ^f	$y = 89.8 - 9.5 \times \ln(x)$	0.510	(32)
NT-‘free’ S-Eh _{NHE}	G (solid)	$y = 82.8 - (8.41 \times \ln(x_1)) + (0.028 \times x_2)$	0.987	(33)
Fig. 5b				
H'-Eh _{NHE}	B	$y = -4.60 + 1.35 \times \ln(x)$	0.994	(34)
H'-‘free’ S	C	$\ln(y) = 1.37 - 0.00022(x)$	0.996	(35)
	C (dash) ^d	$\ln(y) = 1.23 - 0.00017(x)$	0.468	(36)
H'-‘free’ S-Eh _{NHE}	G (solid)	$y = -6.15 + (0.11 \times \ln(x_1)) + (1.50 \times \ln(x_2 + 250))$	0.997	(37)
Fig. 5c				
ESn-Eh _{NHE}	A	$y = 17.8 + 0.063(x)$	0.994	(38)
ESn-‘free’ S	E	$y = 3.69 + 28.3 \times e^{-x/2313}$	0.998	(39)
ESn-‘free’ S-Eh _{NHE}	G (solid)	$y = 4.91 + (1.80 \times \ln(x_1)) + (0.079 \times (x_2))$	0.997	(40)
Fig. 5d				
ITI-Eh _{NHE}	E	$y = -45.0 + 75.4 \times e^{x/447}$	0.995	(41)
ITI-‘free’ S	E	$y = 3.79 + 78.2 \times e^{-x/1378}$	0.999	(42)
	E (dash) ^d	$y = 24.5 + 58.6 \times e^{-x/935}$	0.664	(43)
ITI-‘free’ S-Eh _{NHE}	G (solid)	$\ln(y) = -6.07 + (0.00011 \times x_1) + (1.69 \times \ln(x_2 + 250))$	0.995	(44)

Sources of equations or data used for regression calculations: ^aWildish et al. (1999), ^bWhitfield (1969), ^cHargrave (1994), ^dChamberlain & Stucchi (2007), ^eNilsson & Rosenberg (1997), ^fBrooks & Mahnken (2003)

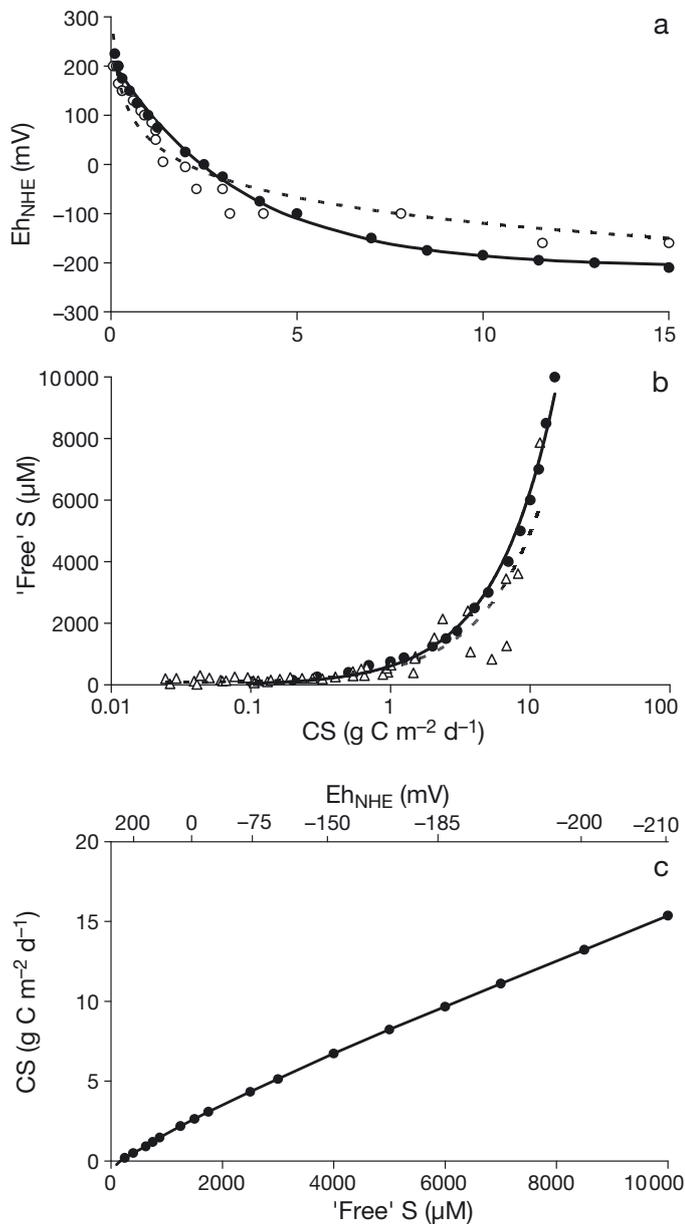


Fig. 2. Empirical relationships between (a) organic carbon sedimentation (CS) and redox potentials ($E_{h_{NHE}}$), (b) median model-predicted values for CS and 'free' dissolved sulfides (ΣS^{2-} , HS^- , H_2S) (S) and (c) S and predicted CS values. ●: data from Table 2. ○ in (a): data reported from salmon aquaculture sites in southwestern Bay of Fundy reported in Hargrave (1994). Δ in (b): measured values of S with median model-predicted values of CS from salmon aquaculture farms in coastal British Columbia presented in Chamberlain & Stucchi (2007). Solid and dashed lines: empirical equations described in Table 4

15 g C m⁻² d⁻¹ (Eqs. 13 & 14). When CS is <1g C m⁻² d⁻¹, S concentrations are low (<500 μM), but as CS increases above this threshold S increases rapidly. The multiple regression (Eq. 15) using untransformed values of $E_{h_{NHE}}$ and S resulted in a correlation coefficient

($r^2 = 0.997$) that was slightly higher than obtained using separate regressions for $\ln E_{h_{NHE}}$ (Eq. 12) and S (Eq. 13) (Fig. 2c).

CS, BEI, $E_{h_{NHE}}$ and S

Since $E_{h_{NHE}}$ is used to calculate BEI (Hargrave et al. 2008a), the inverse relationship between $E_{h_{NHE}}$ and CS (Fig. 2a) is reflected in the relationship between CS and BEI (Fig. 3a). The BEI approaches constant values when CS is <1 g C m⁻² d⁻¹ and the relationship was represented by the nonlinear exponential function (Eq. 16). Hargrave (1994) used a linear regression with log-transformation of CS to describe the inverse relationship between $E_{h_{NHE}}$ and BEI for CS > 1 g C m⁻² d⁻¹ (Eq. 17). Applying this function for CS data in Table 2 above this threshold (Eq. 18) resulted in an equation with a higher intercept but slope coefficients that were not significantly different ($p < 0.05$) (Fig. 3a).

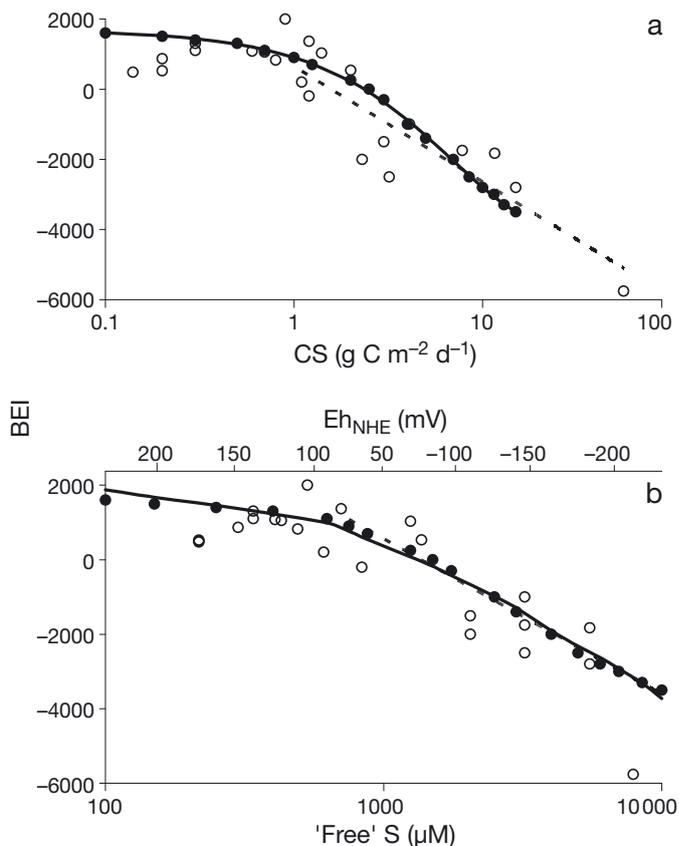


Fig. 3. Empirical relationships between (a) organic carbon sedimentation (CS) and the Benthic Enrichment Index, based on organic carbon in surface sediment (BEI) and (b) dissolved 'free' sulfides (ΣS^{2-} , HS^- , H_2S) (S) and BEI. ●: values are data in Table 2. ○: data from Letang Inlet, southwestern New Brunswick in 1994 and 1995 presented in Hargrave (1994) and Hargrave et al. (1995). Solid and dashed lines: empirical equations described in Table 4

Redox potentials and BEI should be linearly and positively related since $E_{h_{NHE}}$ is one of the variables used to calculate BEI (Fig. 3b). The linear correlation derived from the full range of values in Table 2 ($r^2 = 0.980$) was improved by only using data for potentials $>+100$ mV ($r^2 = 0.997$) (Eq. 19). This also occurred when the regression between $\ln S$ and BEI was calculated using $S > 750$ μM ($r^2 = 0.979$) (Eq. 20) compared to the full data set ($r^2 = 0.846$). The lack of correlation among $E_{h_{NHE}}$, S and BEI in oxic sediments was reflected in the multiple linear regression between S , $E_{h_{NHE}}$ and BEI (Eq. 21). High BEI values (>1000) were relatively constant in oxic sediments ($E_{h_{NHE}} > +100$ mV and $S < 750$ μM) and decreased throughout hypoxic and anoxic zones (Fig. 3b).

RPD, BHQ, BQI, $E_{h_{NHE}}$ and S

Two empirical functions described the relationship between BHQ and RPD up to maximum values of 9.5 and 3.9 (reported in Nilsson & Rosenberg 1997), respectively, equally well (Eqs. 22 & 23). Since the sigmoidal function (Eq. 23) was considered to be asymptotic for RPD at $\text{BHQ} > 10$, this was more descriptive of the RPD expected in oxic sediments. Linear correlations between BHQ, $E_{h_{NHE}}$ and S (Eqs. 24 & 25) were represented by a multiple regression (Eq. 26) (Fig. 4b).

BQI based on the ESn index of fauna diversity was linearly related to $E_{h_{NHE}}$ but the relationship with S was nonlinear with asymptotic values of S in oxic sediments for $\text{BQI} > 16$ (Eqs. 27 & 28). A multiple linear regression showed the combined effects of relationships between $\ln S$, $E_{h_{NHE}}$ and BQI (Fig. 4c) (Eq. 29) where changes in BQI are relatively small in oxic sediments and decrease more rapidly once redox potentials fall below $+100$ mV and S concentrations are >750 μM .

Number of taxa, biodiversity indices, $E_{h_{NHE}}$ and S

All 4 measures of macrofauna diversity (NT, H' , ESn and ITI) were positively related to $E_{h_{NHE}}$ and inversely related to S (Fig. 5). The data from coastal British Columbia used as the basis for comparing change in NT with respect to $E_{h_{NHE}}$ and S showed considerable variation but a linear regression (Eq. 30) represented the general trend. Brooks (2001) and Brooks & Mahnken (2003) used an inverse linear relationship to describe the relationship between $\ln S$ and NT, and a similar function with comparable slope coefficients was derived from data in Table 2 (slopes = -11.4 and -9.5 , respectively) (Eqs. 31 & 32). A multiple linear regression using $\ln S$ and $E_{h_{NHE}}$ showed the combined

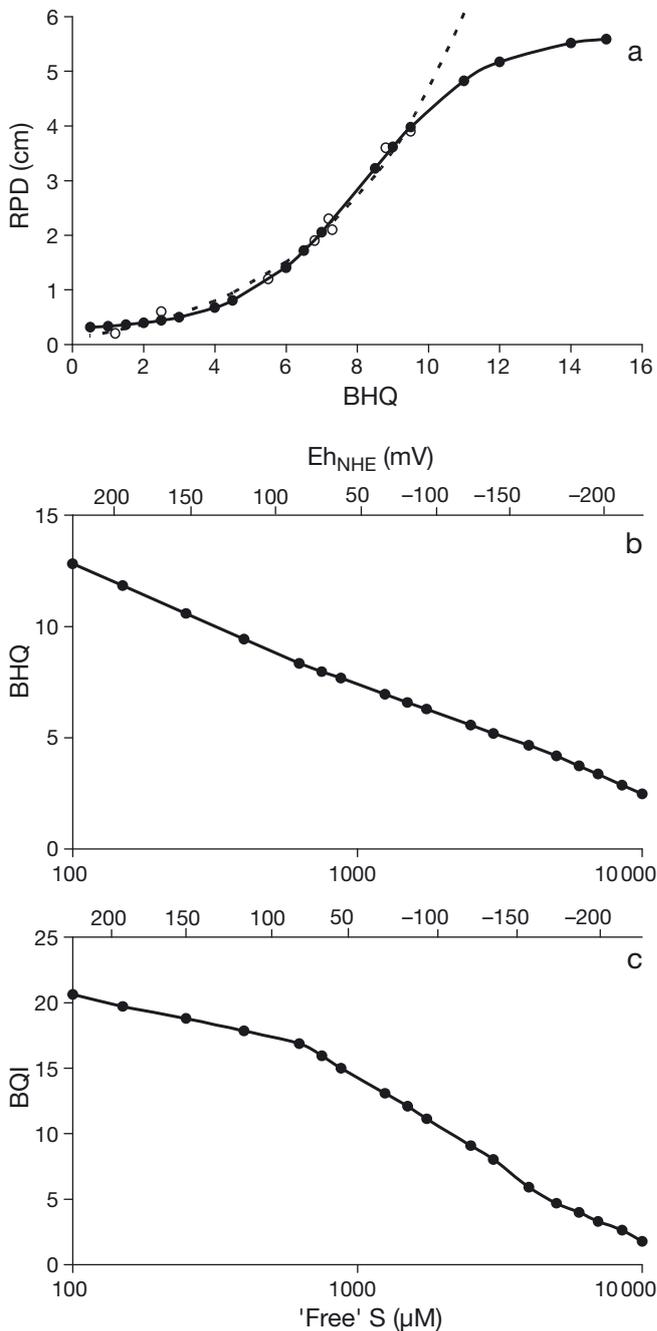


Fig. 4. Empirical relationships between (a) the Benthic Habitat Quality index (BHQ) and Redox Potential Discontinuity (RPD) depth, (b) 'free' dissolved sulfides (ΣS^{2-} , HS^- , H_2S) (S) and BHQ and (c) S and the Benthic Quality Index (BQI). ●: values based on data in Table 2. The 2 relationships between RPD and BHQ shown as solid and dashed lines (Panel a) are extrapolated from data in Nilsson & Rosenberg (1997) (○). Lines in Panels (b) and (c): empirical equations described in Table 4

effect of the 2 variables (Eq. 33). NT from locations with $S < 100$ μM (mean = 51.5) is predicted to be reduced by 50% at ~ 1025 μM S . Brooks & Mahnken

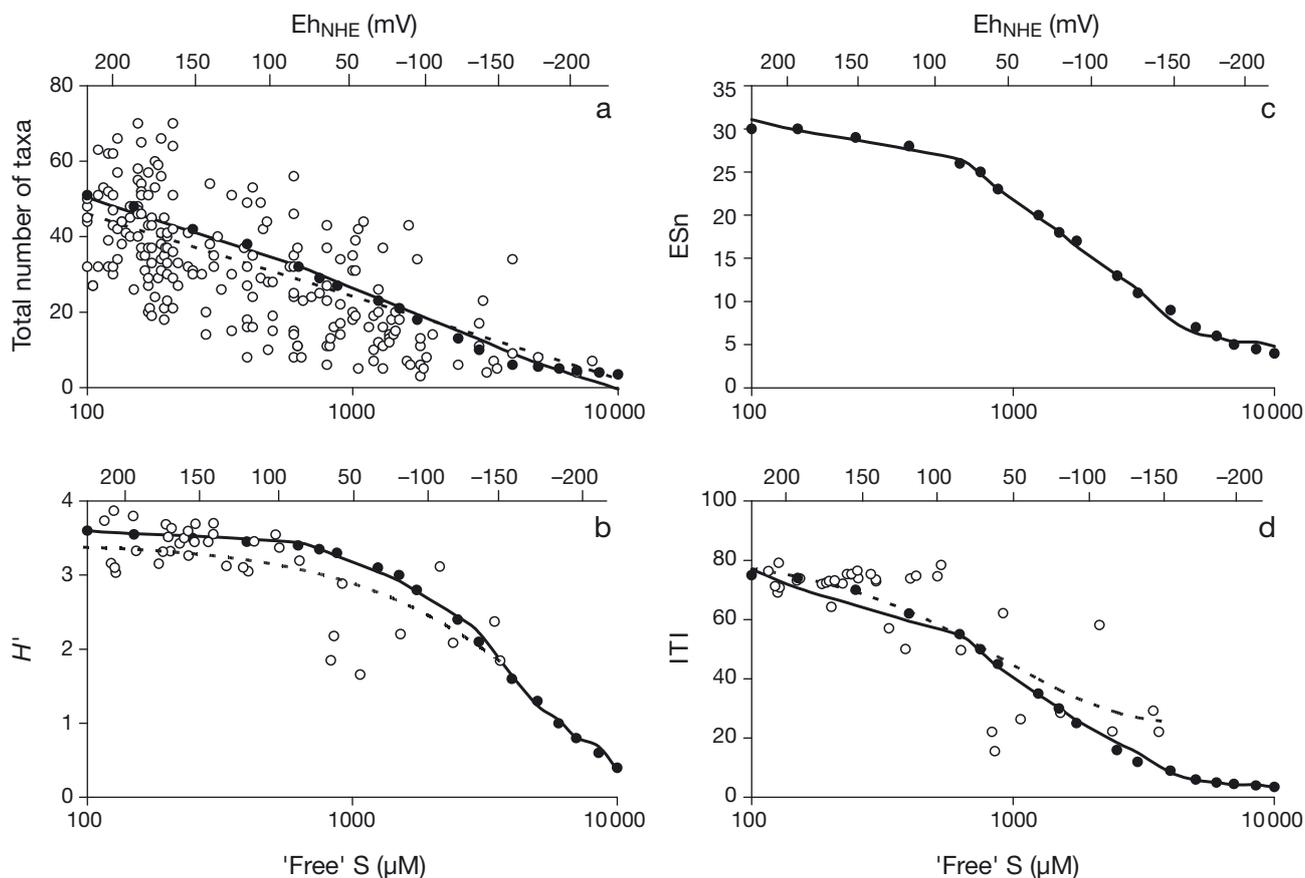


Fig. 5. Empirical relationships between (a) 'free' dissolved sulfides ($\Sigma S^{2-}, HS^{-}, H_2S$) (S) and Eh_{NHE} and total number of macrofauna taxa (O : data from Brooks & Mahnken 2003), (b) S and Eh_{NHE} and the Shannon Index (H') (O : data from Chamberlain & Stucchi 2007), (c) S and Eh_{NHE} and the Infauna Trophic Index (ESn) and (d) S and Eh_{NHE} and the Infauna Trophic Index (ITI) (O : data from Chamberlain & Stucchi 2007). ● in all panels: data from Table 2. Solid and dashed lines: empirical equations described in Table 4

(2003) calculated a 50% reduction at 964 μM S (using $NT = 49$).

Changes in the 3 biodiversity indices (H' , ESn, ITI) showed a different pattern with respect to Eh_{NHE} and S with values reaching asymptotic levels in oxic sediments ($Eh_{NHE} > +100$ mV and $S < 750$ μM) (Fig. 5b–d). Relationships with H' and ESn were represented by linear and exponential functions (Eqs. 34, 35, 38 & 39) (Fig. 5b,c) but the nonlinear exponential function was required to describe the relationship with ITI (Eqs. 41 & 42) (Fig. 5d). In addition, exponential functions for H' and ITI with S calculated from data in Chamberlain & Stucchi (2007) (Fig. 5b,d) had similar intercept and slope coefficients (Eqs. 35 & 36). The regression lines for the exponential functions relating ITI to Eh_{NHE} and S (Eqs. 42 & 43) deviated at redox potentials below -100 mV and $S > 1000$ μM , but no data was provided in the Chamberlain & Stucchi (2007) study to allow extrapolation into the range of anoxic sediments ($Eh_{NHE} < -185$ mV and $S > 6000$ μM).

Multiple regressions between H' , ESn and ITI and the 2 independent variables reflected nonlinearities in

the relationships with Eh_{NHE} and S (Fig. 5b–d). Maximum correlation coefficients with H' were achieved by ln-transformations of both independent variables (Eq. 37) while ln-transformation of S and not Eh_{NHE} maximized goodness-of-fit for ESn (Eq. 40). r^2 values were highest for a multiple regression based on ln ITI, S and ln Eh_{NHE} (Eq. 44). All 3 regression curves showed inflection points to steeper gradients at $Eh_{NHE} \sim 75$ mV and $S \sim 875$ μM .

DISCUSSION

Eh_{NHE} , pH and S as indicators of benthic organic enrichment

Theoretical relationships between Eh_{NHE} , S^{2-} , HS^{-} and H_2S and in marine sediments are well known (Berner 1963, Fenchel 1969, Visscher et al. 1991) and served as the basis for selecting redox potentials and S as the primary axes for the nomogram described by Hargrave et al. (2008a). While practical problems using

Pt electrodes are known (Whitfield 1969, Sigg 2000), they can be used operationally to provide a general measure for redox conditions in sediments. The relationship between E_{NHE} and pH, proposed by Pearson & Stanley (1979) to describe different levels of sediment organic enrichment, has been used as a basis for classification of fish farm sites for management purposes under the MOM (Modeling-Ongrowing fish farm-Monitoring) system in Norway for the past decade (Hansen et al. 2001, Schaanning & Hansen 2005). Both variables decrease as sulfate reduction by anaerobic bacteria is stimulated by high rates of OM sedimentation.

Inter-related changes in the 3 geochemical variables while consistent with the theoretical relationships described by Berner (1963) and Whitfield (1969), showed deviations in oxic sediments where S concentrations are $<750 \mu\text{M}$ and E_{NHE} potentials $>+100 \text{ mV}$ (Fig. 1). E_{NHE} potentials predicted from the theoretical relationship and Eq. (7) converged when pH values were between 6.5 and 7.2, characteristic of sediments where redox potentials are controlled by sulfate reduction. The nonlinear relationship between pH and redox at higher pH values reflects the fact that when E_{NHE} potentials are positive they are not correlated with sulfide ion activity since sulfate reduction is not the predominant redox couple (Whitfield 1969).

The lack of correlation between E_{NHE} and S in oxic sediments was represented by a nonlinear exponential function (Fig. 1a) whereas Wildish et al. (1999), Brooks (2001) and Brooks & Mahnken (2003) used linear regressions between $\ln S$ and E_{NHE} to describe the relationship. Although correlation coefficients for regressions in those studies (op. cit.) were significant, as were those using a similar function for observations in 2002 from salmon aquaculture farms in the Bay of Fundy (Eq. 3), E_{NHE} and S were poorly correlated for $S < 750 \mu\text{M}$ and E_{NHE} between $+100$ and $+200 \text{ mV}$ based on data in Table 2 (Fig. 1a). This lack of correlation in oxic sediment categories means that the range of values and variability in a given set of observations will determine the form of the relationship between E_{NHE} and S.

The asymptotic nature of the pH- E_{NHE} curve showed that when pH values decrease below ~ 7.2 the slope of the line calculated from data in Table 2 (50) (Eq. 7) is close to the theoretical value (59) (Eq. 6) (Fig. 1b). Schaanning & Hansen (2005) discussed the fact that at pH values of 7.5 to 8 in marine sediments, HS^- and HCO_3^- are the predominant dissociation products of sulfide and carbonic acid. Acidification due to sulphate reduction will cause pH to decrease to values approaching 7.0 with methane-producing bacteria causing a further reduction to ~ 6.0 . They identified pH 7.1 as a critical threshold below which risk of meth-

ane gas ebullition increased from sediments under salmon pens in Norway. Based on the empirical relationships in Fig. 1, this would occur at E_{NHE} potentials between -175 and -185 mV and S concentrations of $5000\text{--}6000 \mu\text{M}$.

Benthic enrichment indicators and organic matter sedimentation

Previous descriptions and models of relationships between benthic enrichment and sedimentation of waste products from marine finfish aquaculture facilities have included measures, either qualitative or quantitative, of benthic responses to increased OM supply (Findlay & Watling 1997, Cromey et al. 2000, 2002, Silvert & Cromey 2001, Brooks & Mahnken 2003, Cromey & Black 2005, Stucchi et al. 2005, Kalantzi & Karakassis 2006, Chamberlain & Stucchi 2007, Giles 2008, Kutti et al. 2008, Brigolin et al. 2009). The range of sedimentation rates predicted within 100 m of pen arrays in many of these studies (<1 to $15 \text{ g C m}^{-2} \text{ d}^{-1}$) is consistent with values in Table 2.

Although a linear function with \ln -transformation of CS was previously used to describe the relationship between CS and E_{NHE} (Eq. 11), and a similar function described the correlation between these variables using data in Table 2 ($r^2 = 0.955$) (Eq. 12), applying the nonlinear exponential function to the data (Eq. 10) provided a higher correlation coefficient ($r^2 = 0.997$) (Fig. 2a). In contrast, a linear relationship was observed between S and CS (Fig. 2c). The logarithmic scale for the x-axis (CS in Fig. 2b), as used by Chamberlain & Stucchi (2007) for presentation of their data, reveals the asymptotic distribution of low values of S at low rates of sedimentation. Data reported by Chamberlain & Stucchi (2007) showed that S was $<569 \mu\text{M}$ when CS decreased to $<1 \text{ g C m}^{-2} \text{ d}^{-1}$. The multiple regression reflecting the linear relationships between CS, E_{NHE} and S showed a continuous increase in S up to the maximum value of CS ($15 \text{ g C m}^{-2} \text{ d}^{-1}$) presented in Table 2 (Fig. 2c). An asymptote would be expected at higher levels of organic carbon input since sulfate depletion in porewater would limit sulfate reduction, and other metabolic processes such as anaerobic chemosynthesis would then predominate (Holmer et al. 2005). Chamberlain & Stucchi (2007) identified a weak relationship between S and CS up to $\sim 1 \text{ g C m}^{-2} \text{ d}^{-1}$ with a much stronger gradient at higher sedimentation rates.

Concentrations of S below $1 \text{ g C m}^{-2} \text{ d}^{-1}$ are associated with $S < 750 \mu\text{M}$ and E_{NHE} potentials $>+100 \text{ mV}$ indicative of oxic sediments (Table 1). Hargrave (1994) identified this as a threshold for organic carbon sedimentation above which hypoxic or anoxic conditions

were formed in surface sediments around finfish aquaculture sites. Findlay et al. (1995) and Findlay & Watling (1997) quantified the relationship at salmon farms in coastal Maine by a model to compare benthic respiration (O_2 and CO_2 sediment-water exchange), OM sedimentation and oxygen supply calculated from current velocity. Aerobic conditions in surface sediments were maintained at sedimentation rates $<1 \text{ g C m}^{-2} \text{ d}^{-1}$ but at higher rates advection was insufficient to prevent the formation of hypoxic conditions.

An earlier study under blue mussel culture lines also showed that sedimentation rates $>1.7 \text{ g C m}^{-2} \text{ d}^{-1}$ were associated with increased microbial sulfate reduction and sulfide accumulation (Dahlbäck & Gunnarsson 1981). In addition, the enhancement of anaerobic metabolism and formation of hypoxic or anoxic sediments with high sedimentation rates is consistent with the relationship described by Sampou & Oviatt (1991) for a simulated eutrophication gradient where nutrients were added to experimental mesocosms. Organic carbon sedimentation $>500 \text{ g C m}^{-2} \text{ yr}^{-1}$ ($\sim 1.4 \text{ g C m}^{-2} \text{ d}^{-1}$) from salmon farms in a Norwegian fjord represented a threshold with decreases in macrofauna production at higher rates (Kutti et al. 2008).

The nonlinear exponential curve fitted to data in Fig. 3a showed that BEI is unrelated to CS below $\sim 1 \text{ g C m}^{-2} \text{ d}^{-1}$. The transition from positive to negative BEI values, based on the change from positive to negative $E_{h_{NHE}}$ potentials, occurs at $CS = 2.5 \text{ g C m}^{-2} \text{ d}^{-1}$ and $S = 1500 \mu\text{M}$ (Table 2) corresponding to the threshold for hypoxic sediment formation (Table 1). Data in Chamberlain & Stocchi (2007) showed that median values of predicted CS of 1 to $5 \text{ g C m}^{-2} \text{ d}^{-1}$ occurred at S concentrations between 388 and $2400 \mu\text{M}$. The multiple regression between $E_{h_{NHE}}$, S and BEI indicated similar low gradients in changes in the BEI with an inflection point at $E_{h_{NHE}}$ potentials $> +100 \text{ mV}$ and $S < 750 \mu\text{M}$ (Fig. 3b) corresponding to $1 \text{ g C m}^{-2} \text{ d}^{-1}$ (Table 2).

Enrichment effects on benthic quality and biodiversity indices

Depth of oxic sediment was not included as a dependent variable in the nomogram since no study provides data for the comparison with $E_{h_{NHE}}$ or S. However, RPD depth is used to derive 1 of the 3 scores forming the BHQ index (Nilsson & Rosenberg 1997) and a sigmoidal relationship between BHQ and S allowed RPD to be calculated for corresponding values of S (Table 2). The alternative nonlinear exponential function (Eq. 22) predicted excessively deep values of the RPD ($>15 \text{ cm}$) for the range of values observed in shallow coastal water (Fenchel & Riedl 1970) and in soft Norwegian fjord sediments (Nilsson & Rosenberg 1997). The upper depth

limit could reflect the fine grain sizes in the deposits at the sampling sites in Norway. More coarse-grained sediments might be expected to have a deeper oxic layer depth for a given value of S (House 2003).

Despite uncertainty associated with effects of sediment texture and the choice of function type used for calculation of RPD depth, the multiple regression for BHQ with $\ln S$ and $E_{h_{NHE}}$ (Eq. 26) shows a continuous decline as S increases and redox potentials decrease. A similar pattern exists in the multiple regression derived for NT (Fig. 5a). In contrast, multiple regressions for BQI and the biodiversity indices H' , ES_n and ITI show a different relationship where maximum values occur in oxic sediment (Figs. 4c & 5b–d). Changes in values in multiple regression curves for these dependent variables indicate inflection points with steeper gradients in Oxic B category sediments beginning close to the Oxic A/B threshold ($E_{h_{NHE}} = 100 \text{ mV}$ and $S = 750 \mu\text{M}$).

Brooks (2001) and Brooks & Mahnken (2003) in their studies of variables sensitive to benthic organic enrichment around salmon aquaculture sites in coastal British Columbia identified 3 'sulfide regimes' based on changes in macrofauna community structure: (1) oxic ($< 300 \mu\text{M S}$) with a normal range of diversity, (2) sub-hypoxic (1300 to $1500 \mu\text{M S}$) coinciding with the appearance of *Beggiatoa* mats and opportunistic fauna showing some resistance to toxic effects of S and (3) more severe hypoxic sediment types ($>3000 \mu\text{M S}$) where only the most S-tolerant fauna are present. The thresholds for transitions between oxic/hypoxic sediment at 750 and $1500 \mu\text{M S}$ ($+100$ and $0 \text{ mV } E_{h_{NHE}}$) and for the formation of hypoxic/anoxic conditions at 3000 and $6000 \mu\text{M S}$ (-100 and -185 mV) (Table 1) are consistent with these regimes. The transition from oxic to hypoxic sediments also matches the inflection point observed in BQI and other indices reflecting decreased biodiversity under increasingly hypoxic and anoxic conditions.

Wildish et al. (2004) observed high values of S (2500 to $30000 \mu\text{M}$) in sediment under a salmon farm in southwestern Bay of Fundy associated with a median BHQ value of 0 where *Beggiatoa* bacterial mats were extensive. Bacterial mats were absent at non-farm locations, S was lower (350 to $2500 \mu\text{M}$) and median BHQ values were 8 to 9 (range: 6 to 10). Values of BHQ in this range correspond to Oxic A/Hypoxic A type sediments with high to moderate levels of macrofauna diversity (Table 2). In a similar manner, Rosenberg et al. (2004) identified BQI thresholds between 'good' and 'moderate' successional stages in benthic fauna assemblages at 12.0 and 'moderate' and 'poor' at BQI = 8. These transitions are associated with S concentrations of 1500 ($E_{h_{NHE}} 0 \text{ mV}$) and $3000 \mu\text{M}$ ($E_{h_{NHE}} = -100 \text{ mV}$), respectively (Table 2).

The negative effects of excessive OM deposition on benthic macrofauna assemblages have been attributed to the formation of hypoxic conditions rather than direct effects of organic enrichment (Diaz & Rosenberg 1995, Gray et al. 2002). Rates of sulfate reduction can be stimulated by increased input of OM under aquaculture net-pens (Holmer & Kristensen 1992, Holmer & Frederiksen 2007) and the transition to more hypoxic conditions is also characterized by increased sediment oxygen consumption and sediment-water fluxes of dissolved nutrients (Hall et al. 1990, 1992, Holby & Hall 1991, Hargrave et al. 1993, Holmer et al. 2002, 2005). Increased bacterial sulfate reduction and the accumulation of metabolic by-products that form both dissolved and particle-bound sulfides such as FeS₂ (pyrite) and other metal-S complexes are underlying causes for the increase in particulate sulfides associated with benthic OM enrichment (Howarth 1979, Berner 1984, Rickard & Morse 2005, Otero et al. 2006). Particulate reduced sulfides (pyrite and other types of AVS) are in themselves not toxic to benthic fauna but oxygen consumption by these reduced compounds in surface sediments and direct toxic effects can lead to hypoxic stress on fauna (Theede 1973, Gray 1981, Rosenberg et al. 1992, Nilsson & Rosenberg 2000, Gray et al. 2002). Also, although S is toxic to many species over a range of concentrations (1 to 500 µM) and there are varying degrees of tolerance in different infauna species (Grieshaber & Völkel 1998, Vaquer-Sunyer & Duarte 2010), as concentrations increase fewer taxa are able to survive (Bagarinao 1992, Gamenick et al. 1996, Brooks & Mahnken 2003).

The presence of particulate polysulfides (pyrite and other types of AVS) has implications for measurements of S in sediment porewater using Ag⁺/S²⁻ electrodes. The electrode measurements are made after diluting wet sediment with an equal volume of an anti-oxidant buffer solution (Wildish et al. 1999), but exposure to alkaline conditions has been shown to solubilize particulate sulfides (J. Cullen pers. comm). Prolonged exposure of sediments with high concentrations of pyrite to alkaline conditions will increase apparent S concentrations if particulate sulfides are solubilized. A short exposure time (<2 min) can be used to minimize the dissolution effect but in sediments with high concentrations of metal-sulfides actual S concentrations may be over-estimated.

The data presented in Table 2 show inter-related changes in Eh_{NHE} and S and other variables, either directly measured or calculated as indices, reflecting the oxic–hypoxic–anoxic gradient represented in the P-R model of benthic organic enrichment. The changes in oxic conditions represented by decreased Eh_{NHE} and increased S are correlated along the enrichment gradient associated with increasing OM sedimentation. The

accumulation of dissolved ‘free’ S leads to toxic effects on macrofauna causing decreased abundance and diversity as concentrations increase. The empirical equations between variables presented in Table 4 provide quantitative expressions for changes in related sediment chemical and biological variables due to organic enrichment from salmon aquaculture facilities that can be tested in other locations.

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