



Response of Benthic Fauna and Changing Sediment Redox Profiles over a Hypoxic Gradient

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Received 3 November 2000 and accepted in revised form 17 April 2001

The Koljöfjord is an enclosed, stratified fjord on the Swedish west coast with hypoxic/anoxic bottom water during most of the year. In the winter 1999/2000, the water in the entire fjord was re-oxygenated after a period of stagnation, but the following summer oxygen concentrations declined to below 1 ml l^{-1} between 20 and 40 m depths. The objectives of this study were to investigate the structure of benthic communities along a depth gradient of declining oxygen concentrations and the impact of fauna on sediment redox conditions. The vertical distribution of the fauna in the sediment was restricted to the upper few centimetres. Dominant species at most stations were the burrower *Capitella capitata* and the tube-builder *Pseudopolydora antennata*. The species found in the fjord are probably not particularly tolerant towards hypoxia, but they have life-history traits that facilitate a rapid colonization following improved oxygen conditions. The depth of the Redox potential discontinuity (RPD) layer, a recognizable division zone between oxidized (sub-oxic) and reduced chemical conditions, is dependent on infaunal activity, e.g. burrows, tubes and feeding voids. Measurement of apparent RPD (aRPD) from sediment profile images (SPIs) compared well to electrode measurement of RPD. We conclude that a digital analysis of aRPD from images has many advantages compared to RPD measurements by electrodes.

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Keywords: RPD; sediment profile imaging; fjord; *Capitella*; *Pseudopolydora*

Introduction

Disturbance gradients elicit varied responses from the benthos depending upon the source of stressor in combination with temporal and spatial factors. As benthic communities are changed, biologically mediated geochemical cycles are also altered. Systems stressed by organic matter have received the most attention with many having a well documented fit to the response model developed by Pearson and Rosenberg (1978), e.g. Heip (1995) and Nilsson and Rosenberg (2000).

Dissolved oxygen is a key factor in regulating both benthic community complexity and many biogeochemical cycles, such as sulphur and nitrogen (Aller, 1979; Yingst & Rhoads, 1980; Jenkins & Kemp, 1984). In many marine and estuarine systems, the flux of dissolved and particulate substances across the sediment-water interface is regulated by benthic organisms. These organisms mix and irrigate surface sediments and by this activity create a thin layer of oxidized sediments between the water column and deeper anaerobic sediments. During periods of

hypoxia ($<2 \text{ ml l}^{-1}$) changes in community structure and behaviour lead to altered geochemical profiles in the sediments as bioturbation declines from lack of oxygen to support macrofaunal activity.

Initially it is the behaviour of organisms that is changed. This leads to first order reductions in bioturbation rates, which are reversible if hypoxia is not severe or long-term. When hypoxia leads to mortality, then second order changes in bioturbation rates occur that are not reversed until community structure is restored.

To investigate the degree to which benthic communities and geochemistry are correlated, their relationship was examined along a hypoxic gradient in the Koljöfjord, located on the west coast of Sweden (Figure 1). The Koljöfjord is part of the fjordic system around the island of Orust. To the west it is connected to the Skagerrak by an 8 m sill and to the east by a 12 m sill with the adjoining Havstensfjord. A halocline that fluctuates around 15 m stratifies the Koljöfjord and prevents mixing of surface and bottom waters, which makes Koljöfjord prone to development of hypoxia. Salinity is 22–25 above the halocline and about 28 below. Hypoxic conditions are alleviated by

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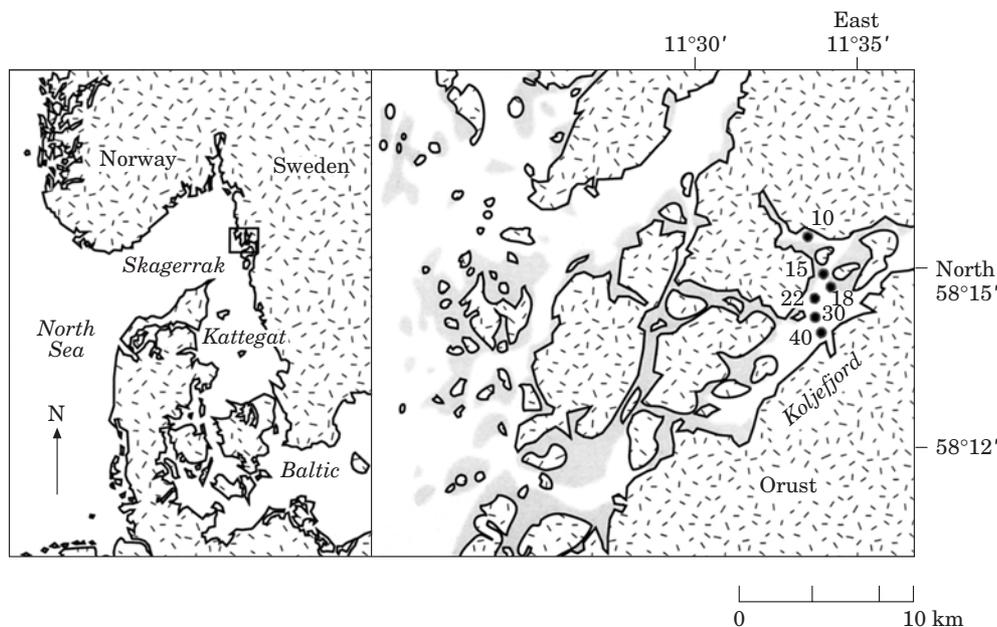


FIGURE 1. Map of the Koljöfjord with the six stations labelled by depth. Shaded areas are shallower than 10 m.

exchange of the bottom water that takes place during the winter at irregular intervals of 1 to 8 years (Gustafsson & Nordberg, 1999).

In several fjords along the Swedish Skagerrak coast, annual minimum oxygen concentrations in the bottom water declined significantly in the period 1951 to 1984 (Rosenberg, 1990). As a consequence, the benthic fauna has been reduced, particularly in the deeper parts of the fjords where hypoxia/anoxia is most frequent (Josefson & Rosenberg, 1988; Nilsson & Rosenberg, 1997; Gustafsson & Nordberg, 1999). However, historical data on the commercially important shrimp, *Pandalus borealis*, indicated that it was abundant in the Koljöfjord in 1909, but in 1910 only few shrimp were caught (Björck, 1913). Björck (1913) suggested that the decline in shrimp was due to low dissolved oxygen, but no measurements were made.

The oxygen concentrations in the Koljöfjord have a variable pattern (Figure 2). In early 1999, the oxygen concentrations were high at 10 and 15 m, but zero at 40 m depth. In September oxygen dropped to below 1 ml l^{-1} even at a depth of 10 m. In the winter 1999/2000, the water in the fjord was re-oxygenated with gradually greater concentrations in the shallowest depths. Shortly after this, a steep decline occurred at all depths. As an example, at 22 m depth the oxygen concentration peaked in March at 6.2 ml l^{-1} and declined to 0.7 ml l^{-1} at the time of sampling in early August. During the steepest decline from March to May at this depth, the declining rate was $0.08 \text{ ml l}^{-1} \text{ d}^{-1}$. During sampling in August, the

oxygen concentration was 1.0 ml l^{-1} at 15 m depth and less deeper down.

The objectives of this study were to investigate the structure of benthic communities along a depth gradient of declining oxygen concentrations and the impact of the fauna on redox conditions in the sediment. The six stations investigated in the Koljöfjord were located along a depth gradient from 10 to 40 m, with the 40 m station being the close location of the

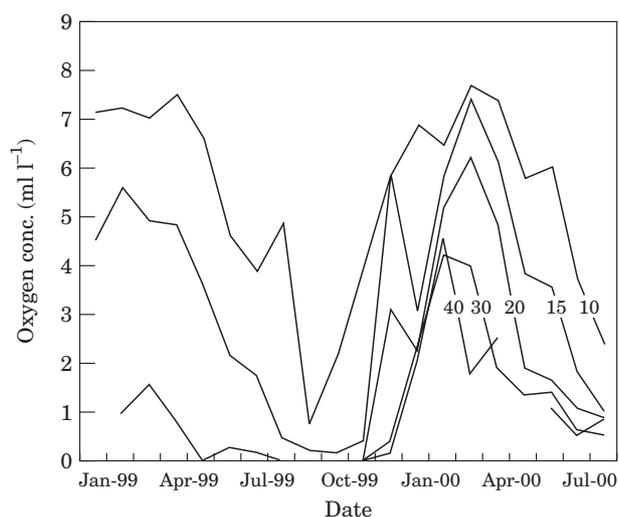


FIGURE 2. Dissolved oxygen concentrations (ml l^{-1}) from January 1999 to August 2000 at the water depths 10, 15, 20, 30 and 40 m. The recordings were made close to station 40 (courtesy of Bohusläns Vattenvårdsförbund).

long-term dissolved oxygen monitoring. The depth of the redox potential discontinuity (RPD) layer is a recognizable division zone between oxidized (sub-oxic) and reduced chemical conditions in the sediment (Fenchel, 1970; Lyle, 1983; Santschi *et al.*, 1990). The oxidized part appears as rust-brown, and the reduced layer below this is generally grey-green or black. In the present study we compared two methods to assess the depth of the RPD in the sediment. Measurements were made by electrodes and by digitally analysing the depth of RPD in sediment profile images (SPIs). The SPI technique has proven useful in this context in a number of studies (e.g. Rhoads & Germano, 1986; Nilsson & Rosenberg, 2000).

Material and methods

Samples for infauna and sediment were taken in the Koljöfjord at the following depths: 10, 15, 18, 22, 30 and 40 m on 31 July and on 2 and 4 August 2000 (Figure 1). The depths are used as station numbers. At each station, five deployments were made with a sediment profile camera, and three samples for infauna were taken with a 0.05 m² Ponar grab. A digital CCD camera (Canon Power Shot Pro 70), took vertical *in situ* pictures through a prism (30 × 15 cm) as described in Nilsson & Rosenberg (1997). After each deployment, the sediment profile image (SPI) was transferred to a computer and stored. The contrasts in the SPIs were enhanced in Adobe Photoshop 5.0. The depth of the apparent redox potential discontinuity (aRPD) was measured in a software programme (NIH image 1.6) as the distance from the sediment surface to the borderline between rust-brown and green-grey or sometimes even black sediment. This borderline indicated the shift between ferric (Fe⁺³) and ferrous (Fe⁺²) ions (e.g. Mortimer, 1941–42). In each image, maximum and minimum depth of aRPD was measured, mean aRPD was calculated as the area of aRPD coverage divided by the width of the image, and the benthic habitat quality (BHQ) index was calculated. This index parameterises sediment structures, sub-surface structures and the aRPD. This BHQ index varies between 0 and 15 and is related to the faunal successional stages in the Pearson-Rosenberg model, where low values indicate a disturbed benthic fauna and a thin aRPD, and high values indicate a diverse fauna and deeper laying aRPD (Nilsson & Rosenberg, 1997; Nilsson & Rosenberg, 2000). The grab samples were washed on a 1-mm sieve and preserved in 70% ethanol. Biomass is ethanol wet weight.

Three sediment cores were taken at each station with a gravity corer (4.5 cm diameter). RPD

was measured with 10 different electrodes placed simultaneously and vertically through pre-drilled holes in the cores at distances of 1 cm between measurements. The electrodes were 15 cm long with a 1 mm diameter. The electrode was of platinum with a colomel electrode used as reference; the recorder was a Radiometer (Copenhagen, pH meter 22). +240 mV was added to the potential measured, which then corresponds to the shift between insoluble ferric and soluble ferrous ions (Mortimer, 1941–42; Fenchel, 1969; Lyle, 1983). At station 18, only one core was successfully analysed. The 0–1 cm of the sediment was analysed for total carbon and nitrogen with a Carlo Elba elemental analyser. The water on top of the cores was siphoned off, immediately preserved, and analysed for oxygen content by the Winkler method. Monthly records of oxygen concentrations shown in Figure 2 are from the county's monitoring programme (Bohusläns Vattenvårdsförbund).

Results

The benthic fauna in the Koljöfjord was depauperate with a dominance of polychaetes (Table 1). The total number of species collected was 12. At 18 m and deeper, only the two polychaetes *Pseudopolydora antennata* and *Capitella capitata* were found. The total abundance at stations 10 and 15 was slightly above 200 ind. m⁻² and less at greater depths. The biomass exceeded 1 g m⁻² only at station 10. Variations were generally large and indicative of patchy distributions.

In the SPIs from stations down to 30 m water depth, the top sediment appeared oxidized and benthic fauna was present (Figure 3). Tubes of *P. antennata* were seen on the sediment surface in images from 15 to 30 m depth, and one long, thin tube of *Euchone papillosa* appeared at 10 m. The rust-brown colour in the images is indicative of the oxidized (sub-oxic) zone in the sediment, and the dark colour shows the reduced zone and presence of iron sulphide. At 10 m depth, animal bioturbation has occurred, as a mean, in the upper 1.9 cm of the sediment, which is equal to the aRPD (Table 2). At station 15 and 18, polychaete tubes and burrows made the aRPD appear jagged. The greatest mean aRPD was recorded at 2.9 cm on station 15. The aRPD was variable between images at the same station (Table 2), e.g. at stations 18 and 22 the maximum aRPD in some images could be 2.7 to 2.8 cm deep in the sediment, whereas the minimum aRPD was only 0.3 cm or less. This demonstrates a patchy distribution in redox conditions at similar depths. At station 40, the sediment was black with four laminated layers, which indicate that periods of no or minor bioturbation has occurred

TABLE 1. Macrobenthic species, abundance and biomass with standard deviation ($n=3$) in the Koljöfjord in August 2000

Depth (m)	Species	Ind. m ⁻²	(SD)	Biomass m ⁻²	(SD)
10	<i>Gattyana cirrosa</i>	73	61	1.46	2.0
	<i>Pectinaria koreni</i>	47	31	0.75	0.8
	<i>Scalibregma inflatum</i>	27	23	1.25	1.3
	<i>Euchone papillosa</i>	20	0	0.02	0.0
	<i>Abra alba</i>	20	20	1.55	2.5
	<i>Microdeutopus gryllotalpa</i>	7	12	0.04	0.1
	<i>Malacoceros fuliginosus</i>	7	12	0.02	0.0
	<i>Hydrobia</i> spp.	7	12	0.04	0.1
	Total	207	169	5.15	6.8
15	<i>Pseudopolydora antennata</i>	100	122	0.05	0.1
	<i>Scalibregma inflatum</i>	33	42	0.60	0.6
	<i>Euchone papillosa</i>	33	58	0.07	0.1
	<i>Trochochaeta multisetosa</i>	27	31	0.01	0.0
	<i>Eteone longa</i>	20	20	0.14	0.2
	<i>Capitella capitata</i>	13	12	0.02	0.0
	<i>Abra alba</i>	7	12	0.07	0.1
		Total	233	295	0.95
18	<i>Pseudopolydora antennata</i>	60	69	0.05	0.1
	<i>Capitella capitata</i>	20	20	0.07	0.1
		Total	80	89	0.13
22	<i>Pseudopolydora antennata</i>	7	12	0.01	0.0
		Total	7	12	0.01
30	<i>Capitella capitata</i>	47	31	0.21	0.2
	<i>Pseudopolydora antennata</i>	47	42	0.11	0.1
		Total	93	72	0.32
40	<i>Capitella capitata</i>	13	12	0.07	0.1
	<i>Pseudopolydora antennata</i>	7	12	0.01	0.0
		Total	20	23	0.07

earlier. The white patch on the sediment surface appears to be a mat of sulphur bacteria, *Beggiatoa* spp.

The functional relationship between the mean RPD measured from cores and SPIs (aRPD) was analysed using linear regression (Figure 4). The mean RPD of 0.6 cm compared to the aRPD of 0.0 cm at station 40 contributes to an intercept of 0.21. This value should have been close to the origin if the RPD was zero.

The mean BHQ index was greatest at station 15 (7.8) and lowest at station 40 (1.2; Table 2). Low indices are indicative of environmental disturbance. Values ≤ 4 are suggested to indicate a disturbed fauna with presence of the pioneering benthic successional stage I, i.e. stations 22, 30 and 40. The BHQ indices on the other stations were between 5.2 and 7.8 and were assigned to successional stage II, a transitory stage between a pioneering community and an 'equilibrium' stage community (III) (Nilsson & Rosenberg, 2000).

The content of total C and N in the surficial sediment was highest at stations 15 to 30 and lowest at stations 10 and 40 (Table 2).

Discussion

Redox conditions in the sediment

Animals are dependent on dissolved oxygen for their respiration. Most of the macrofauna on soft bottoms are buried in the sediment and pump oxygenated water down into their burrows and tubes. As dissolved oxygen penetrates only a few millimetres into the sediment by molecular diffusion (Revsbech *et al.*, 1980), animal irrigation is the main process where dissolved oxygen is transported deep into the sediment. Bioturbation, irrigation and building of structures of the infauna are important activities for the presence of oxidized conditions deep down in the

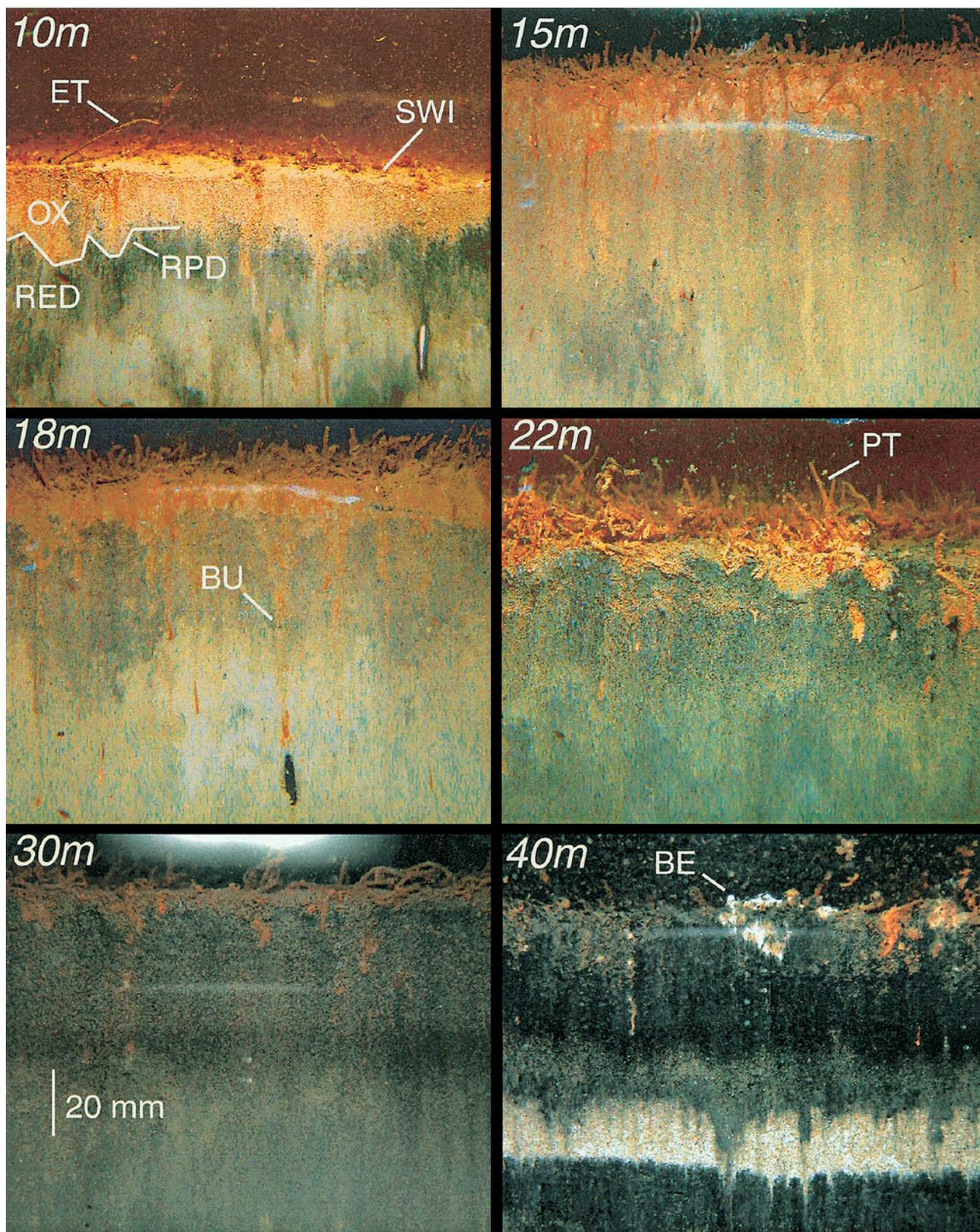


FIGURE 3. Sediment profile images from the six sampling depths. Contrasts are enhanced digitally. SWI = sediment water interface, RPD = redox potential discontinuity, OX = oxidized sediment, RED = reduced sediment, BU = burrow, ET = tube of *Euchone papillosa*, PT = tubes of *Pseudopolydora antennata*, BE = sulphur bacteria *Beggiatoa* spp.

TABLE 2. Sediment characteristics at various depths in the Koljöfjord: depth of RPD measured from cores and apparent RPD (aRPD) measured from the SPIs are presented as means (cm), maximum and minimum aRPD are from individual images; mean Benthic Habitat Quality (BHQ) indices are from all images, and mean total carbon (C) and nitrogen (N) are from the top 0–1 cm sediment layer

Depth (m)	Mean RPD	Mean aRPD	Max. aRPD	Min. aRPD	BHQ	C (%)	N
10	1.8	1.9	3.6	0.6	0.2	2.9	0.3
15	2.6	2.9	7.2	0.9	7.8	5.4	0.6
18	1.0	1.5	2.7	0.4	6.0	6.0	0.6
22	0.7	0.9	2.8	0.0	3.7	6.6	0.7
30	0.5	0.6	1.3	0.3	4.0	6.1	0.7
40	0.6	0.0	0.0	0.0	1.2	3.1	0.3

sediment. A diverse benthic fauna with many functional groups (Pearson & Rosenberg, 1987) has been shown to correlate with a deep aRPD (Nilsson & Rosenberg, 2000). In the sub-oxic zone, $\text{NO}^{-\text{III}}$, $\text{Mn}^{+\text{IV}}$ and $\text{Fe}^{+\text{III}}$ act as oxidising agents (Aller, 1988), and may react continuously with each other in bioturbated layers with high organic content (Santschi *et al.*, 1990). In aquatic sediments, the concentration of $\text{Fe}^{+\text{3}}$ frequently exceeds that of other electron acceptors, and sulphur reduction only takes place when the other electron acceptors are exhausted (Santschi *et al.*, 1990).

In most studies, redox potentials in sediments are measured by inserting electrodes into the sediment at different depths (e.g. Fenchel, 1969). The recordings will thus be influenced by the activity and construction of the animals. If an electrode is pushed down vertically and gradually from the sediment surface, the sediment structure and pore water content may be affected and have an impact on the redox measure-

ments. In the present study pre-drilled holes in the cores were used and the electrodes inserted horizontally. This allows independent measurements with several different electrodes, but a drawback is that it is not possible to make measurements at the same distance from the sediment surface in different cores unless the sediment in the core is pushed upwards. In this study, the vertical resolution was only 1 cm. To move the sediment may, however, distort the redox conditions. Moreover, when sediment cores are collected, the sediment will be compacted, especially if the core diameter is small.

In the present study, the linear regression analysis showed a good agreement between measurements of RPD and aRPD (Figure 4). Thus, the mean aRPD measured as the border between rust-brown sediment and green-grey or black sediment in the images correlated to the mean RPD in the cores (corrected with +240 mV). Others (Mortimer, 1941–42; Fenchel, 1969) have also recorded a colour shift at this voltage. The greatest RPD values were recorded at station 15, where the animal activity penetrated deepest into the sediment. The surficial sediment at station 40 smelled of H_2S , which is indicative of ferrous ions being exhausted (Mortimer, 1941–42). The patch of *Beggiatoa* spp. in one image at this station is indicative of the zone between reduced sediment with H_2S and overlying water containing at least some oxygen (Jørgensen & Revsbech, 1983; Rosenberg & Diaz, 1993).

Organic enrichment of the sediment surface will lead to increased oxygen consumption and reduce the depth distribution of the RPD. The high carbon content of the surficial sediment is indicative of a high oxygen demand. A high sedimentation may also lead to increased oxygen demand in the near-bottom water, and this may be higher than in the surficial sediments (Rydberg *et al.*, 1990). Temporal changes in oxygen concentrations have been shown to correlate to changes in depth distribution of the RPD (Rosenberg, 1977).

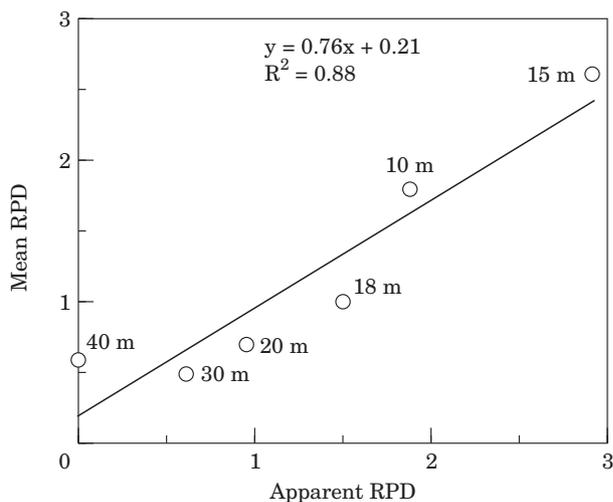


FIGURE 4. Linear regression of mean RPD measured by electrodes from cores and mean apparent RPD measured from sediment profile images.

Use of the SPI technique for assessing thickness of the RPD has many advantages. SPI allows an *in situ* observation of the sediment. The width examined in the present study was 15 cm and the height of the sediment is dependent on penetration depth of the prism (maximum 30 cm). As seen in the images (Figure 3), aRPD is not level but undulates in relation to animal structures, such as burrows and tubes. The minimum and maximum aRPD can vary between several centimetres in one image at these oxygen stressed stations (Table 2). A digital measurement of the area of the RPD is likely to give an accurate assessment of the mean depth distribution of the aRPD in a particular image. The possibility to digitally enhance the contrast in the images is an advantage for an accurate assessment of the aRPD. Smearing on the front plate of the prism can for some sticky sediments cause problems for the interpretation of part of an image. Where this is the case, this part of the image should be left out of the analysis.

Faunal response to hypoxia

The critical oxygen concentration for the survival of coastal benthic fauna is around 0.7 ml l^{-1} (Nilsson & Rosenberg, 2000). Based on the oxygen recordings in the Koljöfjord it seems that little to no fauna could have been present in September 1999 at $\leq 15 \text{ m}$ water depth. At 15 m, the oxygen concentration was 0.78 ml l^{-1} , and then only few if any species could have survived. After this date, colonization might have occurred with peaks in spring 2000, when higher oxygen concentrations prevailed. By July, oxygen levels were again low at 30 and 40 m, $\leq 0.6 \text{ ml l}^{-1}$. Few species can persist through such great changes in oxygen concentrations.

The vertical distribution of the fauna was restricted to the upper few centimetres of the sediment. Such a narrow distribution has been found in other oxygen stressed fjords (Rosenberg 1977), with the fauna pushed upwards as the RPD layer depth shallows (Ankar & Jansson, 1973). The only sub-surface feeders in the Koljöfjord were the polychaetes *Capitella capitata* and *Scalibregma inflatum*. The biomasses were very low and only exceeded 1 g m^{-2} at the shallowest station. Sandnes *et al.* (2000) demonstrated that biomass correlated strongly with sediment mixing rates. Thus, the impact on physical and chemical processes in the sediment may be significantly reduced when the benthic fauna is continuously stressed by hypoxic/anoxic events. Organisms recruited during periods of normoxia ($>2 \text{ ml l}^{-1}$) to areas that experi-

ence hypoxia/anoxia tend to be smaller opportunistic species that have life histories which can be completed during the periods of normoxia. Larger bodied and long-lived species, which also tend to be dominant bioturbators such as sea urchins, are likely to be eliminated by hypoxia after settlement. Polychaetes with opportunistic features were the dominants in the Koljöfjord, which has also been recorded for other oxygen-stressed areas (Pearson & Rosenberg, 1978). Similarly, in Chesapeake Bay on the US east coast, oxygen stressed benthic communities were dominated by polychaetes, particularly opportunistic spionides (Llansó, 1992).

Pearson and Rosenberg (1978) stated that several *Polydora* species and *Capitella capitata* are rapid colonisers of defaunated areas. In the Koljöfjord, *Pseudopolydora antennata* was the most common species occurring at all stations $\leq 15 \text{ m}$. *Capitella* sp. and specimens of the genera *Pseudopolydora* have been found to be fast colonizers of defaunated sediments after hypoxic events in Japan (Tsutsumi, 1987). Tubes of *P. antennata* are clearly seen in the images, and at low oxygen concentrations it is likely to be an advantage to have tubes stretching up into the water that reach higher into the microgradients of oxygen. Such behaviour has been shown for several tube-building polychaetes in Swedish fjords, e.g. *Pectinaria koreni* (Nilsson & Rosenberg, 1994), *Euchone papillosa* (Nilsson & Rosenberg, 1997) and *Melinna cristata* (Nilsson & Rosenberg, 2000). The bivalve *Abra alba* and the polychaete *Pectinaria koreni* that occurred in the shallow areas of the Koljöfjord are rapid colonisers following hypoxic events (Arntz, 1981; Rosenberg & Loo, 1988). The tolerance limit of *A. alba* to low oxygen concentrations is around 0.8 ml l^{-1} (Rosenberg *et al.*, 1991).

The benthic species found in the Koljöfjord are probably not particularly tolerant to hypoxia, and only *Malacoceros fuliginosus* is listed as a tolerant species in the review by Diaz and Rosenberg (1995). Rather, the species have life history traits that facilitate rapid colonization of oxygen stressed areas when conditions improve (Gray, 1979). In several areas along the Swedish and the Norwegian Skagerrak coast, a temporal decline in oxygen concentrations at the bottom has been demonstrated during periods of the 2000 century (Rosenberg, 1990; Johannessen & Dahl, 1996; Aure *et al.*, 1996). The main reason for this decline was suggested by the authors to be eutrophication. In enclosed and stratified areas, as exemplified by the Koljöfjord, this will lead to an impoverished benthic fauna and unpredictable food conditions for demersal fish.

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