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Seasonal changes in benthic fluxes of dissolved oxygen and ammonium associated with marine cultured Atlantic salmon

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ABSTRACT: Benthic fluxes of dissolved oxygen and ammonium were measured at bi-weekly to monthly intervals during 1990–91 proximate to and under an array of pens holding Atlantic salmon *Salmo salar* Linn. in L'Etang Inlet, a macrotidal embayment in the Bay of Fundy, Canada. Hierarchical clustering of data indicated that the 7 stations could be divided into 3 groups (3 stations under the pen array, 2 at the perimeter of the array and 2 away from pens). Average rates of oxygen uptake and ammonium release for the 3 stations under the pens were 4 and 27 times higher, respectively, than values at the 2 stations distant from the cages. Maximum average rates of ammonium release (38 mmol m^{-2} d^{-1}) in late July and oxygen uptake (99 mmol m^{-2} d^{-1}) in early September for stations under the pens coincided with maximum water temperatures and sediment sulfide accumulation, respectively. Negative redox (Eh) potentials (< 0 mV) and reduced numbers of benthic polychaetes *Capitella* spp. also occurred in sediments under pens between mid-July and September. Values of > 100 mM $S^=$ in sediment pore water during September could have been toxic to benthic fauna as well as to heterotrophic bacteria that produce substrates utilized by sulfate-reducing bacteria.

INTRODUCTION

There is a recognized need for assessment of environmental impacts of expanding marine shellfish and finfish aquaculture operations in coastal marine embayments (Hakanson et al. 1988, Wildish et al. 1990, Grenz et al. 1991, Holmer & Kristensen 1992). Environmental changes in the benthos are likely to be greatest in the case of caged finfish mariculture because of high stocking densities and high rates of food addition to a localized area. Settling of unconsumed food and fish feces under and adjacent to culture pens has been found to reduce species diversity and biomass of benthic macrofauna (Ritz et al. 1989, Weston 1990). This is due to enhanced aerobic and anaerobic microbial activity in organically rich sediments resulting in oxygen depletion, production of toxic substances such as H_2S, and low oxidation-reduction (Eh) potentials characteristic of anaerobic marine sedimentary environments (Blackburn et al. 1988, Holmer & Kristensen 1992).

Mass balance calculations for marine salmonid fish farms have shown the magnitude of local enrichment of sediment organic matter that results from increased particle sedimentation of waste food and feces under pens. From 13 to 23 % of the nitrogen and energy supplied as food to caged salmon and trout was estimated to sediment as food pellets and feces (Hakanson et al. 1988, Folke & Kautsky 1989, Hall et al. 1990) while from 30 to 70 % of organic carbon and approximately 55 % of the phosphorus offered as food settled to the bottom (Hall et al. 1990, Holby & Hall 1991, Holmer & Kristensen 1992). Since rates of benthic aerobic and anaerobic decomposition within sediments increase

with organic matter loading (Sampou & Oviatt 1991, Holmer & Kristensen 1992), increased dissolved oxygen and nutrient fluxes between sediments and overlying water should occur under culture pens. Such increases have been observed in marine fishponds (Blackburn et al. 1988) and at shellfish (Baudinet et al. 1990) and salmonid (Pamatmat et al. 1973, Hall et al. 1990, Holby & Hall 1991, Holmer & Kristensen 1992) aquaculture sites.

Our observations between 1990 and 1991 were carried out to determine the horizontal variability, areal extent and magnitude of seasonal changes in benthic fluxes of dissolved oxygen and ammonium due to organic loading from a fish farm. This work is part of a larger collaborative study to determine the environmental impacts of an expanding salmon mariculture industry on a macrotidal estuary (Wildish et al. 1993).

METHODS

Study site. Sediment samples were collected by divers from 3 stations under pens at a salmon aquaculture site, 2 stations at the edge of the pen array and 2 stations 5 and 50 m away from the edge of the pens in Bliss Harbour, L'Etang Inlet, Bay of Fundy (45 °2.25' N, 66 °50.40' W) (Fig. 1). This farm was the largest in eastern Canada, holding up to 120 000 salmon in thirty-six 100 m^2 pens within a 0.5 km^2 area, at the time of our study between May 1990 and February 1991. Fish were fed dry food pellets (up to a maximum of 80 kg pen^{-1} d^{-1} in August) through food addition several times a day during the spring and summer with less frequent feeding during other months.

Hydrographic characteristics of Bliss Harbour and the aquaculture area are described in detail in Wildish et al. (1990) and Wildish et al. (1993). Water depth at the site varied from 12 to 14 m at mean low water with a neap-spring tidal amplitude of 5 to 8 m. Maximum tidal currents of 16 cm s^{-1} were measured at 7 m depth outside of fish cages (Wildish et al. 1993). Small vertical gradients in physical chemical properties existed in the water column due to tidal exchange and wind/wave action. Salinity varied from 27 to 32 ‰, ammonium concentrations ranged from 3 to 10 µM in surface water and from 1 to 6 µM at 10 m during August 1990 (Wildish et al. 1993). Dissolved oxygen at depths to 1 m above bottom was never below 75 % of saturation values.

Inorganic grain size measured in the upper 5 to 10 cm layer of sediment by Coulter Counter (Kranck & Milligan 1979) consisted of flocculated silt-clay particles with a modal size of 20 µm. Sediment layers between 10 and 30 cm at all stations had modal inorganic grain size similar to that at the surface. Sediments under the pens were colonized by the polychaete *Capitella* spp. which bound the fine brown-black silt-clay in an organically rich (7 to 25 % weight loss on ashing at 550 °C for 24 h) matrix of tubes. The upper 20 to 30 cm layer of sediments from under pens was brown-black in colour, in contrast to stations at the edge of the pens and proximate to the culture site where colour differences (light to medium brown and grey) were restricted to the upper 5 to 15 cm.

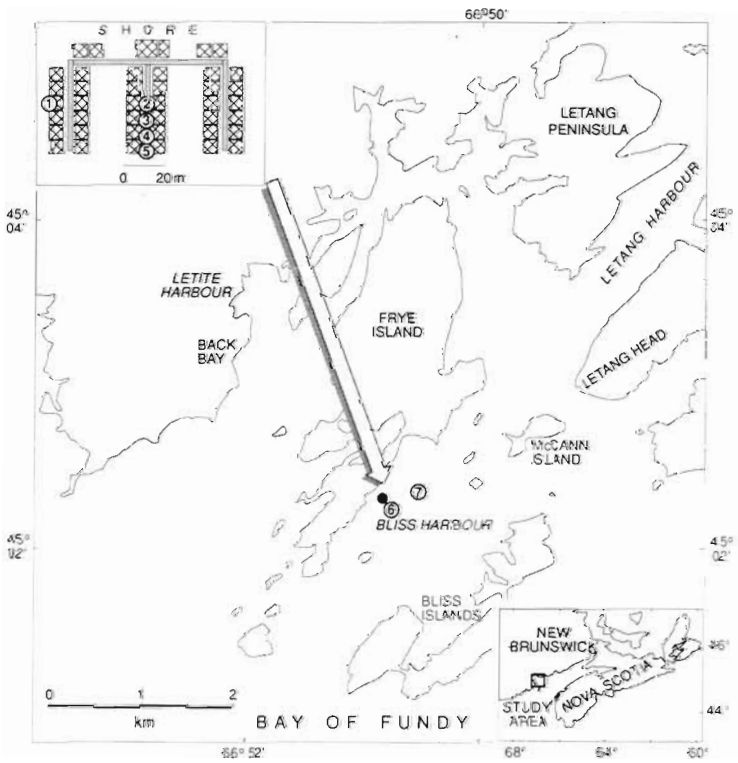

Fig. 1. Location of 7 sampling stations at the study site in Bliss Harbour, L'Etang Inlet, Bay of Fundy

Sample collection. Three replicate sediment cores (two 25 cm long, 5.6 cm diam. and one 50 cm long, 5 cm diam.) were collected from Stns 1 through 6 by diver at bi-weekly to monthly intervals between May and November 1990 and in February 1991. Sediment from Stn 7 was collected by an Ekman grab. The open-ended cores were inserted to at least 15 cm depth, capped to enclose 60 to 120 ml of seawater and sealed at the bottom with a rubber stopper. The flocculent sediment surface layer was undisturbed. Temperature of surface sediment was measured with a glass thermometer (± 0.1 °C precision). Sediment water content was measured as weight loss on drying at 60 °C for 24 h. The upper 10 cm of sediment in 50 cm long cores was examined for numbers of

Capitella spp. by sieving in a steel mesh sieve (0.5 mm mesh size).

Plastic syringes were used to take subcores (1 cm^3) of surface sediment from 25 cm long cores after the cores were incubated for measurements of oxygen and ammonium fluxes without the addition of $HgCl_2$ described below. Organic carbon and nitrogen in dry sediment were determined by elemental analysis using a Perkin Elmer 240 analyzer. Test sediment samples were fumed over 1N HCl and carbon concentrations did not change, thus measures of total carbon were assumed to be organic carbon in all subsequent samples. Values of porosity, organic carbon and nitrogen were combined to calculate concentrations of C and N as mol m^{-2} for surface sediment to 1 cm depth.

Redox measurements. Oxidation-reduction (Eh) potentials were measured in the 50 cm sediment cores immediately after collection as described by Wildish et al. (1990). A cleaned platinum electrode was inserted into the sediment (usually at 5 to 7 cm depth) through a tape-covered hole in the coring tube. Voltage output (mV) was expressed relative to the normal hydrogen electrode.

Total soluble sulfide. Total soluble sulfide (H_2S, HS^- and $S^=$) in sediment pore water from Stns 1 through 6 was measured on subsamples collected from vertically separated holes in the 50 cm core tube immediately following Eh measurements using 1 ml cut-off syringes as described by Orion Research Corp. (1969). The method determines total $S^=$ (precision ± 3 µM) by fixing samples in an alkaline solution with a sulfide anti-oxidant buffer containing ascorbic acid. Samples were extruded without exposure to air into plastic vials filled with 5 ml of anti-oxidant buffer. Vials were closed with air-tight caps and mixed on a Vortex mixer. Vials were refrigerated before analysis within 72 h.

An Orion model 94-16 silver/silver electrode and an Orion model 90-02 double junction reference electrode were used for potentiometric (mV) $S^=$ measurements. A standard solution of known sulfide concentration (1 g l^{-1} $Na_2S{\cdot}9H_2O$) was prepared daily for calibration of the electrode using 0.1 M $Pb(ClO_4)_2$ to titrate the standard. The clear supernatant over samples was carefully removed to avoid resuspending sediment and placed in a beaker with a magnetic stirrer for potentiometric measurements with the ion-specific electrode. Concentrations were expressed as mM $S^=$ correcting for dilution of samples by the buffer solution.

Benthic fluxes. The 15 cm cores were transported to the laboratory within 2 h of collection for measurements of benthic flux. Supernatant water in 1 replicate core was replaced with aerated filtered (Whatman No. 2) seawater, and the other replicate by 0.1 % (w/v) $HgCl_2$ in filtered seawater with care to avoid disturbance of the surface sediment layer. Cores containing only seawater (± $HgCl_2$) served as blanks. Cores were held at ambient sediment temperature for up to 1 h.

Samples of supernatant water were taken before and after incubation for dissolved oxygen (Radiometer Blood Gas Analyzer, precision ± 2 µM) and ammonium (Solorzano 1969) (precision ± 0.05 µM) determinations. Cores were kept dark during incubations (30 to 60 min) at original sediment temperatures (± 1 °C) and supernatant water was continuously mixed by magnetic stirring bars mounted in lids used to cap cores and rotated by induction. The stirring rate (20 to 30 rpm) avoided resuspension of surface sediment and supernatant water remained clear during incubations.

Fluxes of oxygen and ammonium as mmol m^{-2} d^{-1} were calculated from initial and final concentrations (corrected for changes in controls), supernatant water volume, incubation time and sediment area. Sequential samples over 4 h showed linear rates of ammonium release. Oxygen uptake was also not time-dependent as long as concentrations remained above 50 % of initial values. Oxygen levels were reduced by 20 to 50 % during incubations of < 1 h.

RESULTS

Spatial variations in oxygen and ammonium fluxes

Measurements of oxygen uptake and ammonium release along the transect showed large variations that were not consistently related to linear distance from the edge of the pen. Coefficients of variation (σ/mean) (0.3 to 0.9) were as large for stations under net pens (Group 1; Stns 2, 3, 4) as they were near the perimeter (Group 2; Stns 1, 5). Linear regression analyses to test for gradients over distance under the cages ($n = 5$, Groups 1 and 2 stations) were non-significant ($p < 0.05$). However, rates measured on the same date outside the pens (Group 3; Stns 6, 7) were significantly lower (Mann-Whitney *U*-test $p < 0.05$) than values measured under the pens for 10 of 11 sampling dates.

A clustering algorithm (Wilkinson 1990) was used to compare benthic fluxes measured throughout the study to identify similarities between stations (Fig. 2). Dendrograms of Euclidean distances joined Stns 6 & 7, 1 & 5 and 2 & 3 with similar patterns for both oxygen and ammonium fluxes. Stn 4 was clustered with Stns 2 & 3 on the basis of oxygen uptake but it was separated from other clusters on the basis of ammonium release.

Seasonal changes in oxygen and ammonium fluxes

On the basis of the cluster analysis, measurements of benthic fluxes under the cage array (Group 1 stations),

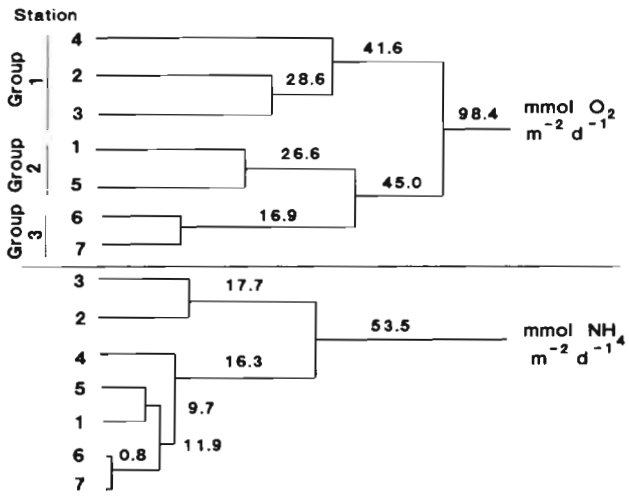

Fig. 2. Dendrograms from hierarchical clustering of data for oxygen and ammonium fluxes measured at 7 stations in Bliss Harbour. A single linkage method was used to calculate the normalized (root mean squared) Euclidean distances as described in Wilkinson (1990). Station numbers refer to locations shown in Fig. 1. Numbers on the dendrogram indicate the amalgamation distances between clusters with stations ordered to place those most similar closest to each other

those at the perimeter of the array (Group 2) and those proximate to the culture site (Group 3) were combined to examine seasonal changes. Mean values (with ranges) for each sampling time for oxygen uptake (Fig. 3A) and ammonium release (Fig. 3B) at the Group 1 stations exceeded rates at the other 2 groups of stations on all sampling dates except in early June. The average fluxes for Group 1 stations throughout the study (71 mmol O_2 m^{-2} d^{-1}, 19 mmol NH_4 m^{-2} d^{-1}) were 4 and 27 times greater for oxygen and ammonium fluxes, respectively, than those measured at Group 3 stations (18 mmol O_2 m^{-2} d^{-1}, 0.7 mmol NH_4 m^{-2} d^{-1}).

Maximum rates of oxygen uptake (149 mmol O_2 m^{-2} d^{-1}) and ammonium release (62 mmol NH_4 m^{-2} d^{-1}) occurred within Group 1 stations in late July and August (Fig. 3A, B). Throughout the study, rates of fluxes at Group 2 stations were less than 50 % of values at Group 1 stations during early June when averages and ranges of flux rates were equivalent. Benthic oxygen and ammonium fluxes at Group 3 stations were relatively constant or increased slightly throughout the study. Ammonium fluxes were not significantly different from zero nor did they show an uptake between May and early August at these stations.

Ratios of oxygen and ammonium fluxes

When data from all stations were combined there was a weak positive linear relationship between oxygen uptake (x) and ammonium flux (y) (y = -5.65 +

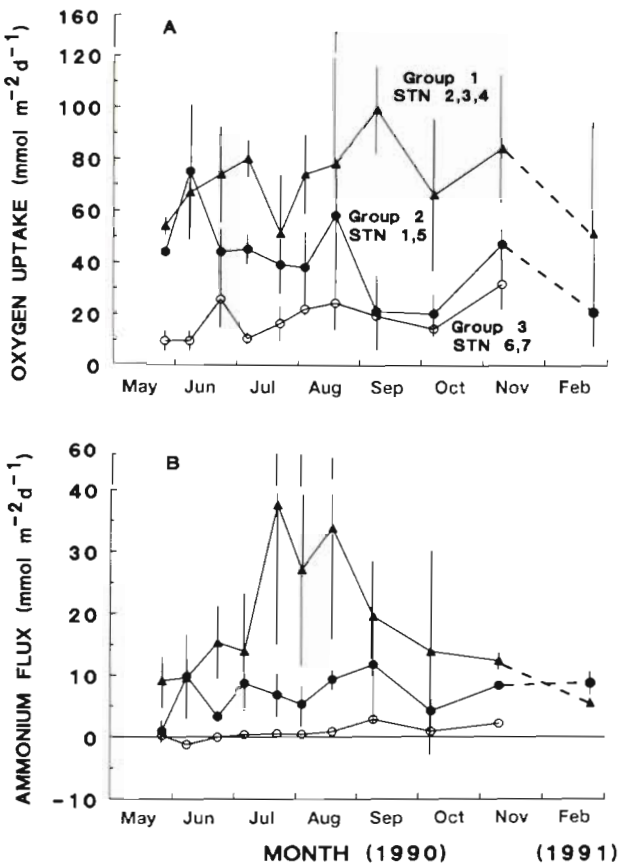

Fig. 3. Benthic oxygen (A) and ammonium (B) fluxes for 3 groups of stations identified in Fig. 2. Points indicate means with ranges as vertical lines for single cores incubated without addition of $HgCl_2$ to supernatant water from Group 1 (n = 3), Group 2 (n = 2) and Group 3 (n = 2) stations described in Fig. 2

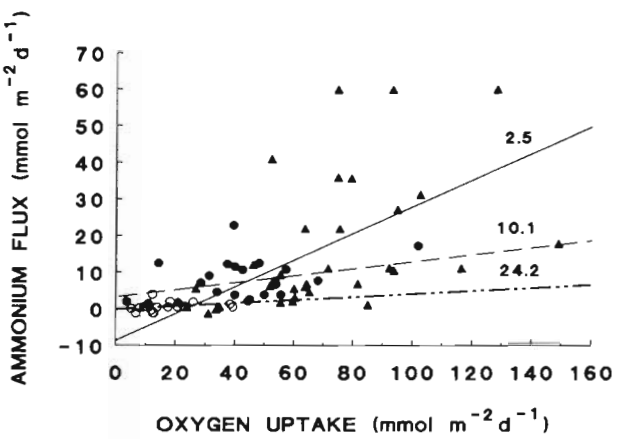

Fig. 4. Linear regressions between benthic oxygen and ammonium fluxes for 3 groups of stations from data summarized in Fig. 3. Group 1 (▲, —, y = -6.69 + 0.40x, r^2 = 0.22, n = 33), Group 2 (●, – –, y = 2.38 + 0.10x, r^2 = 0.09, n = 22), Group 3 (○, —·—, y = -0.13 + 0.04x, r^2 = 0.14, n = 20). Numbers associated with each line are the reciprocal of the slopes in each regression (O:N ratio)

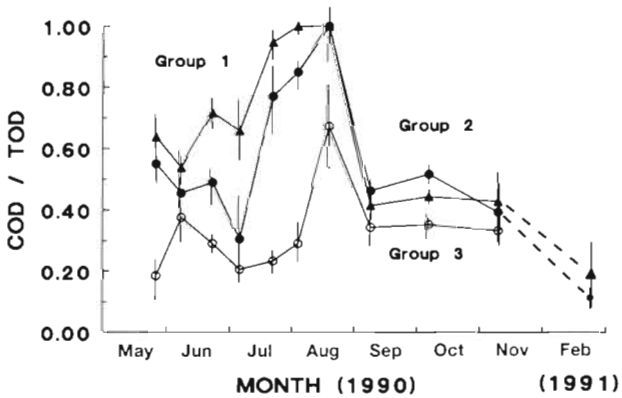

Fig. 5. Chemical oxygen demand as a ratio of benthic oxygen uptake without treatment with $HgCl_2$ to the rate after treatment with $HgCl_2$ to remove biological oxygen consumption. Points with lines represent averages and ranges for 3 groups of stations identified in Fig. 2

0.36x, $r^2 = 0.36$, n = 75) (Fig. 4). The reciprocal of the regression line slope corresponds to an O:N ratio of 2.8, much lower than the theoretical Redfield ratio (13.25) expected for complete oxidation of organic matter derived from phytoplankton production. Separate regressions for data from the 3 groups of stations showed that the O:N ratio for benthic fluxes at Group 2 and 3 stations (10.1 and 24.2, respectively) bracketed the theoretical ratio, but variance in the data was large. Even greater variation and lower O:N ratios occurred for Group 1 stations (mean O:N of 2.5, range 1.9 to 7.8).

Chemical oxygen demand

There was a clear seasonal pattern to changes in the proportion of benthic oxygen uptake sensitive to poisoning with $HgCl_2$ (Fig. 5). The highest ratios of chemical oxygen demand to total oxygen demand (COD:TOD) occurred at all stations in late July and August. The maximum value for the ratio (1.00) (i.e. all oxygen demand due to COD) occurred at stations under and at the perimeter of the pens during August while a lower ratio (0.65) occurred at Stns 6 & 7 Earlier and later in the year, lower proportions of oxygen uptake were due to chemical demand with the lowest ratios in May at Group 3 stations and in February at all other stations.

Variables affecting benthic fluxes

Temperature and sediment sulfide concentrations

Benthic oxygen and ammonium fluxes for Group 1 stations were significantly ($p > 0.05$) linearly correlated ($r^2 = 0.40$) with temperature but correlations for Group 2 and 3 stations were non-significant ($p < 0.05$). Peaks in fluxes at stations under the pens during late July and August (Fig. 3A, B) corresponded to the seasonal maximum temperatures (13 to 14 °C). Fluxes in February 1991 at these stations were among the lowest meas-

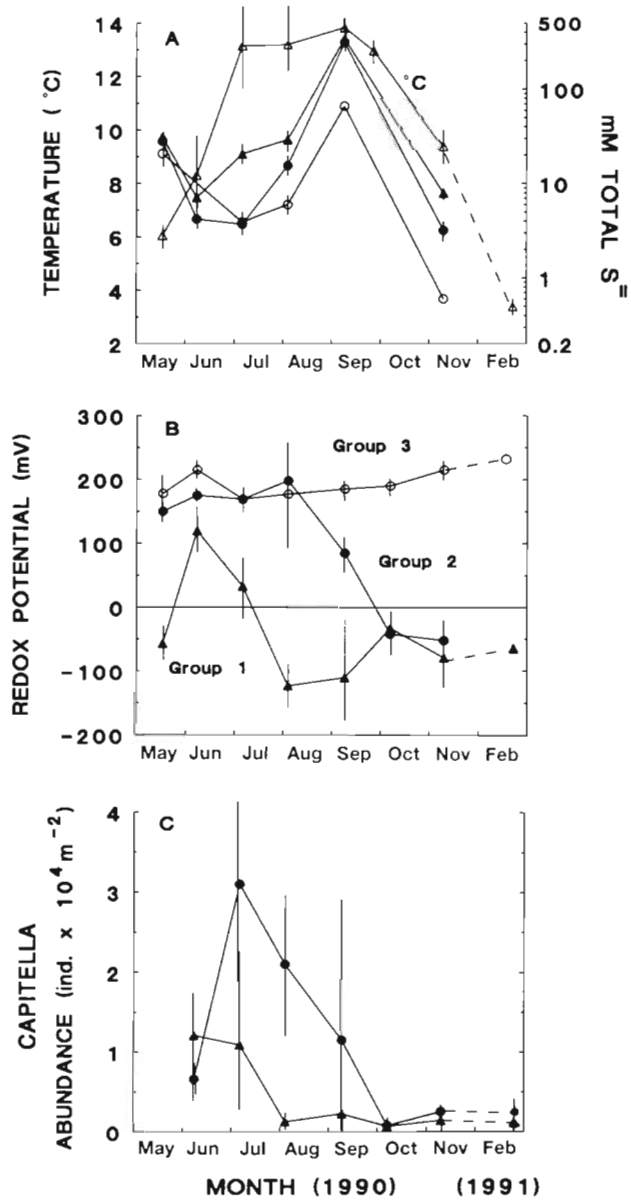

Fig. 6. Seasonal changes in variables measured under and adjacent to salmon culture pens throughout the study. (A) Sediment temperature (pooled data from all stations) (△) and total water-soluble $S^=$ at Group 1 (▲), Group 2 (●) and Group 3 (○) stations described in Fig 2. $S^=$ was not measured at Stn 7 in September and November and values represent single determinations for Stn 6. (B) Oxidation reduction (Eh) potentials for each group of stations. (C) Numbers of *Capitella* spp. present in cores from Group 1 and 2 stations. All points with lines represent averages and ranges

ured at the time of the lowest seasonal temperature (Fig. 6A).

Concentrations of total soluble $S^=$ in sediments under the cage array increased by an order of magnitude between August and September to maximum levels of 300 to 500 mM $S^=$ (Fig. 6A). Values decreased equally rapidly at all Group 1 stations between September and November. Levels of total soluble $S^=$ at Stn 6 were of a similar magnitude (5 to 10 mM) to values at Group 1 stations between May and early July. Although an order of magnitude increase in concentrations also occurred at this station in early September, the maximum value (70 mM) was 5 to 7 times lower than concentrations in sediments under pens.

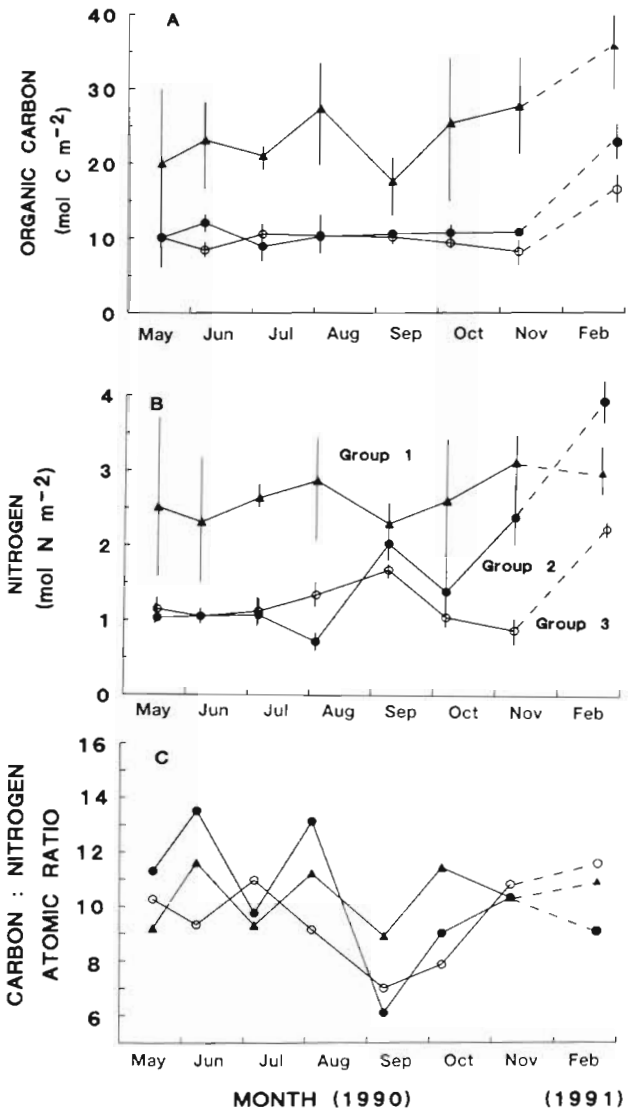

Fig. 7. Sediment organic carbon (A), nitrogen (B) and their atomic ratio (C) for 3 groups of stations described in Fig. 2. Points with lines represent averages and ranges for each group of stations determined for surface (upper 1 cm) sediment from single cores after incubations to measure benthic oxygen and ammonium fluxes (Fig. 3)

Redox potentials

Average Eh potentials for sediments under the cage array were < +150 mV throughout the study (Fig. 6B). Positive potentials (+150 to +250 mV) were measured at all other stations prior to early August, but after this potentials at Group 2 stations decreased to negative values in early October that were similar to those measured under cages. Average potentials under and at the edge of the pens remained low (< −50 mV) between November and February while values at Group 3 stations increased to > +200 mV

The largest variations in Eh potentials at Group 1 (−40 to −175 mV) and Group 2 (+90 to +260 mV) stations occurred between early August and September when patches of white sulfur bacteria (similar to *Beggiatoa* spp.) were observed by divers and appeared as irregular mats on the surface of sediment cores (Fig. 6B) Bacterial mats persisted at these stations between October and February. No mats were observed at Group 3 stations throughout the study.

Capitella abundance

Maximum numbers of *Capitella* spp. occurred at Group 2 stations at the perimeter of the cage array during early July when average abundance was 3×10^4 ind. m^{-2} (Fig. 6C). Numbers at stations under the pens were about 30 % lower. Either *Capitella* spp. did not occur at Group 3 stations or numbers were so low that no accurate assessment of abundance was possible. Average numbers decreased to < 2000 ind. m^{-2} at stations under the pens by August. Similar levels of abundance did not occur at Group 2 stations until October. Numbers in November and February at all stations remained below 2000 ind. m^{-2}

Sediment water content, organic carbon and nitrogen

There was no consistent pattern in seasonal changes of sediment water content for any group of stations but highest values (> 70 %) occurred during July and early August at stations under the cage array. Water content in sediment varied from 66 to 74 % at Group 2 and 51 to 65 % at Group 3 stations.

Organic carbon in the surface sediments at stations under the pens was highly variable ranging from 17 to 35 mol C m^{-2}, while nitrogen showed less variation (2.3 to 3 mol N m^{-2}) (Fig. 7A, B). There were no sea-

sonal trends in sediment organic carbon content for any group of stations except for increases between November and February. Increases to 15 and 20 mol C m^{-2} between November and February at Group 2 and 3 stations paralleled increases at stations under the pens during winter months. Nitrogen increased to maximum values at Group 2 and 3 stations in early September (Fig 7B) and as with organic carbon, concentrations increased throughout the winter at all stations. Unconsumed fish food pellets and fecal matter were often visible on the sediment surface of cores collected under the pens. Samples of dry food pellets fed to salmon in August 1990 contained 50.4 % C and 8.5 % N by weight (C:N atomic ratio of 6.92).

Atomic ratios for organic carbon:nitrogen varied from 6.1 to 13.4 during the study with no consistent temporal patterns (Fig. 7C). Minimum ratios between 6 and 7 occurred simultaneously at Group 2 and 3 stations in early September due to increased nitrogen content with no corresponding change in levels of organic carbon. C:N ratios under pens between October and February were close to seasonal averages despite increases in absolute amounts of organic carbon and nitrogen during this time.

DISCUSSION

Benthic oxygen fluxes previously measured directly under a marine mussel farm (48 mmol O_2 m^{-2} d^{-1}) (Baudinet et al. 1990) and salmon culture pens (134 mmol O_2 m^{-2} d^{-1}) (Pamatmat et al. 1973) span the range observed under salmon pens in our study (Fig 3A). Slightly higher values (220 to 240 mmol O^2 m^{-2} d^{-1}) have been reported for estuarine sediments enriched with pulp mill effluent and simulated sludge (Poole et al. 1978). Values measured at the control site in Bliss Harbour (7 to 24 mmol O_2 m^{-2} d^{-1}) are within ranges reported for intertidal sediments in the upper regions of the Bay of Fundy (Hargrave et al. 1983), in the Baltic Sea (Koop et al. 1990) and in estuarine sediments (Vidal et al. 1992).

Maximum rates of ammonium efflux of 62 mmol NH_4 m^{-2} d^{-1} observed between July and September under salmon pens in our study (Fig. 3B) exceed, by an order of magnitude, rates of benthic ammonium release observed in other studies with marine deposits at aquaculture sites. Ammonium efflux rates of 1 to 14 mmol m^{-2} d^{-1} reported for sediments in marine earthen fishponds (Blackburn et al. 1988) and at a mussel culture site (Baudinet et al. 1990) are similar to the range of values at Group 2 and 3 stations in our study (Fig. 3B). A similar magnitude of ammonium fluxes has been measured in other marine coastal and estuarine sediments (1.2 to 12 mmol m^{-2} d^{-1}) (Nixon et al. 1976, Zeitzschel 1980, Baudinet et al. 1990, Kemp et al. 1990, Koop et al. 1990, Vidal et al. 1992).

High ammonium fluxes during summer months would be expected as a result of high rates of food addition to pens during these months, but differences in the ratio of O:N fluxes from the Redfield ratio of 13.25 for decomposition of naturally produced organic matter (Fig 4) indicates that decomposition is incomplete. The organic carbon and nitrogen content of food pellets fed to salmon at the study site (atomic ratio 6.92) would result in an O:N ratio of 13.84 on complete oxidation. The low values for O:N ratios at stations under the salmon pens (mean of 2.5, Fig 4) indicate that ammonium release was high relative to oxygen consumption. Although a variety of factors affect the accumulation of sedimentary organic matter, more rapid decomposition of nitrogen than organic carbon might offer a partial explanation for the relatively low variability in nitrogen in surface sediments under the pens in contrast to more variable organic carbon content throughout the study (Fig. 7A, B).

Both absolute and relative benthic oxygen and ammonium fluxes under salmon pens showed more temporal and spatial variation than measurements at stations at the perimeter or proximate to the cage array (Fig. 3 A, B). Similar variability, also apparent in previous studies (Baudinet et al. 1990), could arise from non-homogeneous sedimentation of particulate organic matter Between-station variation in benthic fluxes, sediment Eh, numbers of *Capitella* spp. and organic carbon and nitrogen under fish pens could be caused by patchiness in deposition of food pellets and fecal matter. This would also explain the abundant but aggregated distribution of bacterial mats on the sediment surface under the pens.

Seasonal variations in oxygen and ammonium flux under salmon pens in Bliss Harbour generally followed seasonal temperature changes, with highest rates during summer months of maximum temperature, but the variables were not significantly correlated. Previous studies have found strong positive exponential and logarithmic correlations between temperature and these variables (Hargrave 1969, Nixon et al. 1976, Kemp et al. 1990). The high chemical oxygen demand under and adjacent to the salmon pens in our study, that accounted for >80 % of total oxygen uptake during summer (Fig 5), was non-significantly correlated with temperature (r^2 = 0.04, $p < 0.05$). Concentrations of sulfides in sediments under pens which increased sharply between June and August (Fig. 6) are probably the cause of high rates of chemical oxygen demand. Thus the lack of a significant correlation between temperature and benthic oxygen and ammonium fluxes in our study may be explained by the seasonal accumulation of sulfides

which lagged 1 to 2 mo behind the increase in temperature.

The observation that sediment sulfide concentrations increased between July and September while numbers of *Capitella* spp. peaked and then decreased at stations under and on the perimeter of the pens (Fig. 6A, C) indicates that this polychaete cannot tolerate soluble sulfides in sediment pore waters at concentrations greater than 5 mM $S^=$. Cuomo (1985) demonstrated that a sulfide concentration of between 0.1 and 1 mM elicited optimal settlement, metamorphosis and survival of *Capitella* spp. Sensitivity of this species to sulfide was determined in laboratory LT_{50} experiments by Theede et al. (1969) and Pfeiffer (1991) to be between 7 and 8 d at a concentration of 1 mM $S^=$. Numbers of *Capitella* spp. in sediment under the pens declined rapidly after early July as $S^=$ concentrations increased to above 10 mM (Fig. 6A). A positive feedback could occur when reduced numbers of polychaetes result in lower rates of bioturbation which, due to reduced pore water exchange, would allow $S^=$ to accumulate to high concentrations. Maximum concentrations of water-soluble $S^=$ that we observed at Group 1 stations under the cage array are about 10-fold higher than typical values in shallow coastal marine sediments (Jørgensen et al. 1990, Roden & Tuttle 1992).

Previous studies in temperate estuarine sediments enriched with pulp mill fibers (Poole et al. 1977) have shown seasonal changes in composition of a benthic microbial community that was thought to reflect sulfide toxicity. H_2S produced by sulfate-reducing bacteria, through anaerobic respiration stimulated by available substrate and increasing temperature during early summer, accumulated within sediments to levels that were toxic to benthic macrofauna and heterotrophic microflora. Poole et al. (1977) suggested that at high H_2S concentrations, metabolic activities of cellulolytic anaerobic and other non-heterotrophic bacteria that produce substrates (for example, lactate, pyruvate, malate) could be impaired. Since sulfate-reducing bacteria utilize these organic compounds as carbon and energy sources, inhibition of substrate production would limit sulfate reduction.

Methane and H_2S in gas released from sediment at Group 1 stations under the pens at our study site increased to maximum amounts between July and August and were absent by early September (D. Wildish unpubl. data). This is consistent with the suggestion that anaerobic bacteria are killed when sedimentary $S^=$ concentrations increase to high levels. Alternatively, antibiotics in food pellets fed to salmon could suppress bacterial activity in sediments where unconsumed food and feces accumulate. Hansen et al. (1993) found that numbers of bacteria and rates of sulfate reduction in sediments with added organic waste from a marine fish farm were reduced for 1 to 2 mo after treatment with antibiotics frequently used in finfish aquaculture. Simultaneous measurements of levels of antibiotics in sediments, sulfate reduction rates, sediment column profiles of H_2S concentrations and microbial metabolic byproducts are needed to fully understand the relative importance of various processes that lead to high levels of $S^=$ accumulation in sediments impacted by organic enrichment from marine aquaculture.

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