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Prediction of benthic impact for salmon net-pens based on the balance of benthic oxygen supply and demand

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ABSTRACT: The ratio between oxygen supply and oxygen demand was examined as a predictor of benthic response to organic enrichment caused by salmon net-pen aquaculture. Oxygen supply to the benthos was calculated based on Fickian diffusion and near-bottom flow velocities. A strong linear correlation was found between measured carbon sedimentation rates and rates of benthic metabolism. This relationship allowed an estimation of oxygen demand based on sedimentation rates. Comparison of several production sites in Maine (USA) coastal waters showed that for sites where oxygen demand exceeded supply benthic impacts were high and for sites where oxygen supply exceeded demand benthic impacts were low. These findings were summarized in the form of a predictive model that should be useful in siting salmon production facilities.

KEY WORDS: Aquaculture · Benthic metabolism · Marine pollution

INTRODUCTION

As salmonid net-pen culture has become increasingly prevalent in marine near-shore environments so has concern for potential environmental damage. Numerous studies have demonstrated alterations of the benthos beneath and proximal to net-pens (Table 1). Effects are generally restricted to within 30 m of the pens and the magnitude of the effects has been categorized from 'no gross impact' (e.g. Frid & Mercer 1989) to 'highly eutrophicated' (e.g. Hall et al. 1990). Although effects have been documented, interpretation has been on a site by site basis due, in part, to the failure of linear models to relate benthic loading to benthic impacts, as well as the assumption that a single benthic assimilative capacity is applicable to all sea bottoms (e.g. Silvert 1992). It is clear that the first 7 effects documented in Table 1 are either direct or in-

direct consequences of increased benthic metabolism. Recent developments in our understanding of benthic-pelagic coupling suggest these responses can be directly linked to increases in carbon flux to the benthos (Nixon 1981, Hargrave 1984, Sampou & Oviatt 1991, Kemp & Boynton 1992, Hatcher et al. 1994).

The 2 main processes associated with organic matter degradation in shallow-water marine systems are the delivery of particulate organic matter from the water column to the benthos, and benthic decomposition and resulting solute fluxes. Recent developments in sediment trap technologies have greatly improved our ability to measure benthic carbon flux. Cylindrical traps should have the appropriate diameter to match the flow characteristics of the environment and aspect ratios >3.5 to minimize trap sampling bias (Butman 1986, Butman et al. 1986, Baker et al. 1988). In shallow-water systems resuspension followed by settling can confound measurements of deposition, but a comparison of the organic and inorganic content of sediments can be used to correct for the effect of resuspension on deposition rates (Kemp & Boynton 1992).

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Table 1 Effects of fish net-pen culture on benthos beneath and proximal to net-pens

Effect	Citation
Increased sediment carbon inventories	Brown et al. (1987), Rosenthal et al. (1988) and citations within, Hall et al. (1990), Weston (1990), Hansen et al. (1991), Ye et al. (1991), Hargrave et al. (1993)
Decreased sediment redox potential	Brown et al. (1987), Gowen & Bradbury (1987), Rosenthal et al. (1988) and citations within, Wildish et al. (1988), Lumb & Fowler (1989), O'Connor et al. (1989), Wildish et al. (1990), Hargrave et al. (1993)
Increased benthic metabolism measured as O ₂ or CO ₂ flux rates	Gowen & Bradbury (1987), Rosenthal et al. (1988) and citations within, Hall et al. (1990), Hansen et al. (1991), Holmer & Kristensen (1992), Hargrave et al. (1993), Findlay et al. (1995)
Increased H ₂ S and methane flux from the sediments	Brown et al. (1987), Gowen & Bradbury (1987), Rosenthal et al. (1988) and citations within, Lumb & Fowler (1989), Hall et al. (1990), Weston (1990), Hansen et al. (1991), Holmer & Kristensen (1992)
Increased nutrient flux from sediment	Gowen & Bradbury (1987), Rosenthal et al. (1988) and citations within, Hansen et al. (1991), Holby & Hall (1991), Hargrave et al. (1993)
Altered microbial community structure	Brown et al. (1987), Gowen & Bradbury (1987), Rosenthal et al. (1988) and citations within, Lumb & Fowler (1989), Findlay et al. (1995)
Altered macrofauna abundance and community structure	Brown et al. (1987), Gowen & Bradbury (1987), Rosenthal et al. (1988) and citations within, O'Connor et al. (1989), Weston (1990), Lim (1991), Ye et al. (1991), Findlay et al. (1995)
Increased carbon flux to the benthos	Hall et al. (1990), Ye et al. (1991), Findlay et al. (1995), Tsutsumi (1995)

In several manipulative experiments, marine sediments enriched with organic matter showed increases in total benthic metabolism measured as CO₂ flux from and O₂ flux to the benthos (Anderson & Hargrave 1984, Keplay & Andersen 1985, Schwinghamer & Keplay 1987, Sampou & Oviatt 1991, Schwinghamer et al. 1991). In most of these experiments water movement was restricted and enrichment was sufficient to generate an oxygen demand greater than the supply deliverable by diffusion. Decomposition was mediated by anaerobic processes and virtually all oxygen consumption could be related to the reoxidation of reduced alternative electron acceptors. Under these conditions natural sediments will be devoid of macrofauna and sulfide-oxidizing bacteria will form mats at the water-sediment interface.

We reasoned that if the ability of the benthos to oxidize organic matter aerobically could be determined and compared to the organic flux originating from the net-pens, a prediction of benthic impact would result. As the State of Maine, USA (site of our study) has chosen the occurrence of azoic conditions or the development of *Beggiatoa* sp. mats as defining an unacceptable benthic impact (Sowles et al. 1994), we chose these criteria as the endpoints of our model and focused on the factors that control the balance between aerobic and anaerobic metabolism in marine sediments. We broke the problem of siting net-pens into 2 halves: (1) predicting the impact of a known benthic carbon flux and (2) predicting *a priori* the flux from a net-pen system. Both are very significant problems and we have chosen to deal with the first in this manu-

script. The purpose of this paper is to describe the theoretical basis of our model and the relationship between benthic organic matter loading and benthic metabolism as it relates to sediments proximal to several salmon net-pens in Maine coastal waters. We have developed our model of benthic impact associated with net-pen aquaculture using 2 parameters—oxygen supply to the sediments and sediment oxygen demand. We assumed that benthic metabolism, and therefore maximum sediment oxygen demand, would be limited by the maximum rate of oxygen delivery to the sediments. We calculated oxygen supply by assuming delivery by Fickian diffusion, using 3 key environmental variables: (1) flow velocity, (2) temperature, and (3) oxygen concentration of the bottom water. Sediment oxygen demand was predicted from measured carbon sedimentation rates as they related to benthic respiration. Our results, if coupled with a predictive model of carbon flux from a net-pen systems (for examples see Gowen & Bradbury 1987, Silvert 1992), will yield a tool that can potentially minimize the environmental impacts of salmonid net-pen culture through regulation during the siting process.

MATERIALS AND METHODS

Study sites. We studied 3 salmon net-pen facilities within Maine coastal waters (Fig. 1). The sites were: (1) 2 individual net-pens located on a single lease site in Toothacher Cove, Swans Island, (2) an erosional site in Eastport and (3) a depositional site in Eastport

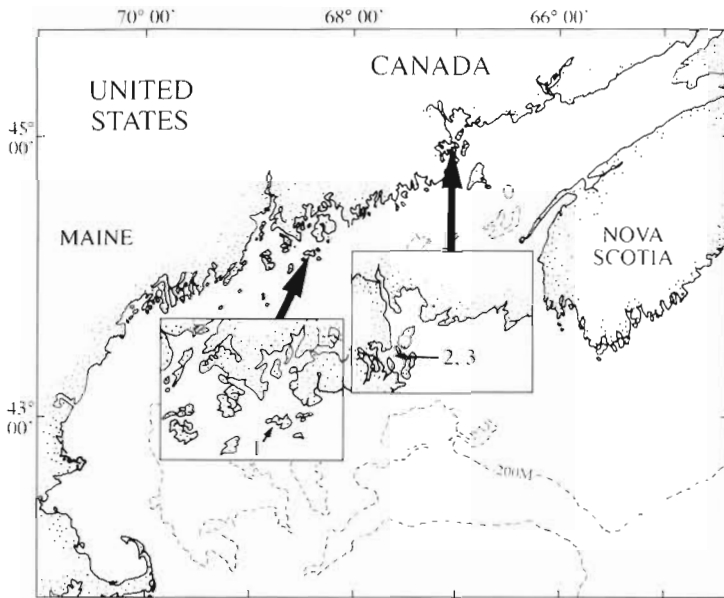


Fig. 1 Location of study sites

(Table 2). Exact biomass figures are not available, but we estimate that the Eastport depositional site contained approximately 250 000 kg of fish biomass, the Eastport erosional site 41 500 kg of fish biomass and the 2 net-pens at the Swans Island site 15 000 and 7 200 kg of fish, respectively. The Eastport sites were mature sites that had been in production for 7 to 10 yr while the Swans Island sites had been in production for less than 3 yr. All sites were free of visible waste accumulation.

Experimental design. Permanent stations were developed at each study site. Concrete mooring blocks were positioned on the sea bottom directly below the edge of the net-pen being studied and a 'rope

highway' constructed on the sea floor using braided nylon line that led to distal mooring blocks placed such that the ropes were parallel to the main current flows (currents at all sites were predominately bi-directional). Sampling stations were established at regular intervals along this transect. Sediment traps (2 each at the pen edges and at the ambient stations) were deployed at each sampling station and at the time of their recovery sediment cores for benthic metabolism (3 each) and microbial biomass (3 each) were taken. At selected intervals, cores for macrofaunal analysis were also taken. Samples reported in this study were taken directly beneath the down-current edge of a pen or pen complex (proximal sediments) and 100 m from the net-pen or pen complex (ambient or distal sediments). When possible, ambient stations were located perpendicular to the main current flow with respect to the net-pen or pen complex.

Sampling. We attempted to sample monthly throughout the year, but rarely were able to complete sampling during the winter months. All sediment traps and sediment cores were taken by SCUBA assisted divers. Cores used for benthic metabolism and microbial biomass were made from clear, 6.5 cm ID polycarbonate tubing. Cores were carefully inserted into the sediments to a depth of approximately 10 cm and the top capped with a rubber stopper. The diver then dug a small hole along the outside of the core and slipped a similar stopper under the core. The top stopper was loosened slightly (to allow pressure relief) and the bottom stopper firmly inserted into the core. The top stopper was then also firmly inserted. Cores were

Table 2. Summary of ambient physical and chemical characteristics of net-pen study site

Measure	Eastport depositional	Eastport erosional	Swans Island ^d
Depth (MLW, m)	11.9	11.4	14.3
Sediment type	Muddy sand	Poorly sorted gravel	Muddy sand
Current velocities ^b :			
Maximum (cm s ⁻¹)	35.8	52.3	17.6
Average (cm s ⁻¹)	12.6	21.5	2.1
Minimum 2 h velocity (cm s ⁻¹)	3.1	9.0	0.0
>25 cm s ⁻¹ (% time)	8.7	61.7	0.0
Mass accumulation rate (g m ⁻² d ⁻¹)	7.29 ± 1.29	14.45 ± 1.70	3.87 ± 0.59
Maximum carbon flux to the benthos (mmol m ⁻² d ⁻¹)	1075.0	253.0	555.0/671.0
Benthic Index score ^c	3	1	4/4

^dTwo individual circular pens were studied at this site

^bMeasured 1 m above the sea floor

^cAs determined by the presence of *Beggiatoa*-type mats, azoic conditions or other alterations of the benthic environment. '4' represents *Beggiatoa*-type mats and/or azoic conditions, '3' modification of benthos and '1' little measurable impact (after Sowles et al. 1994)

placed in a rack designed to maintain vertical orientation during recovery and were recovered by the dive tender by means of a marker buoy and recovery line. Only cores that showed no signs of sediment resuspension were accepted for analysis.

Physical and production data. Recording current meters (Endeco Model 105) were moored 1 m from the bottom at all sites and refreshed monthly. These meters provided an average current velocity and direction every 30 min. The minimum current velocity detected by these meters was typically 0.15 to 0.30 cm s⁻¹. Meters were calibrated before each use. Water depths, sediment granulometry, temperature data, the number and weight of fish per pen, the number, size, configuration and orientation of the pens in use, and the size and type of food being fed were (when possible) obtained from the firms involved and corroborated, when possible, by diver observations.

Organic matter deposition. Carbon deposition was measured using sediment traps. Trap construction incorporated the latest technological suggestions (Butman 1986, Butman et al. 1986, Baker et al. 1988) and were designed to minimize sampling bias. Butman has clearly shown that the critical parameter is the relationship of trap diameter to current velocity. As such, we constructed traps from clear polycarbonate tubing, and matched trap diameter to the current velocity at each study site. Traps were either 37.5 cm in height and 10 cm in diameter (aspect ratio 3.75) and, at low-flow study sites, produced an appropriate Reynolds' number ($Rt \approx 1 \times 10^4$) or were 37.5 cm in height and 6.5 cm in diameter (aspect ratio 5.77) and, at high-flow study sites, produced a similar Reynolds' number. Traps were placed in swivel-mounted holders with the trap mouth 1 m above the sediment-water interface. Due to the long trap deployment times (~ 30 d), material collected in the traps was preserved with salt (TX-10, Akzo Salt, Inc.). The trapped material was sieved (500 μ m) to remove animals (e.g. copepods) that swam into the traps and were killed. Sieving also removed detritus >500 μ m. The removal of the >500 μ m fraction decreased measured ambient and pen carbon flux rates by 10 to 100% (depending on time of year), but the vast majority of this fraction was dead zooplankton. No significant differences in the carbon and nitrogen content of the >500 μ m fraction from pen and ambient traps were detected. The amount of material collected in the traps was determined gravimetrically, corrected for any remaining salts, and total organic carbon and nitrogen content determined using a Carlo Erba elemental analyzer. Sediment samples were first treated with fumes of hydrochloric acid to remove any inorganic carbon (usually present as calcium carbonate). Carbon deposition rates were corrected for sediment resuspension by

assuming that all ash present within the trap originated from seabed sediment. The amount of carbon entering the trap due to resuspension of sediment was then estimated as: $\text{Carbon}_{\text{resuspension}} = (\text{Trap ash content} \times \text{Seabed sediment carbon content}) \times (\text{Seabed sediment ash content})^{-1}$. The component of variation for duplicate traps was typically less than 10%.

Benthic metabolism. Benthic metabolism was measured as the rate of oxygen consumption and benthic ΣCO_2 flux. The rate of oxygen consumption was estimated by measuring the loss of oxygen from the overlying water and benthic ΣCO_2 flux was estimated by measuring accumulation of ΣCO_2 in the overlying water over time. Undisturbed sediment cores were collected, immediately transported to shore-side facilities, the overlying water removed and replaced with ambient sea water and the cores sealed with an air-tight cap such that approximately 400 ml of ambient sea water overlay the sediment. The underside of the sealing cap was fitted with a small, caged magnetic stir bar and the overlying water was stirred at approximately 5.0 cm s⁻¹. Cores were incubated at ambient temperature for 1 to 4 h (depending on temperature) in the dark. Oxygen concentrations declined 20 to 50% during the incubation period. At the end of the incubation period the cores were unsealed and samples removed for oxygen and ΣCO_2 determinations and the volume of the remaining water measured. Oxygen concentration was determined by microWinkler titration performed on site and ΣCO_2 concentration was determined using the potentiometric Gran titration and the method of Edmond (1970) as modified (where appropriate) by Bradshaw et al. (1981). Water samples used for ΣCO_2 determinations were fixed with HgCl₂ and titrations were performed in the laboratory within 2 wk of collection. The component of variation for triplicate determinations of oxygen uptake rates was typically less than 20% and for triplicate ΣCO_2 determinations was typically less than 25%.

Data presentation and analysis. Oxygen uptake, ΣCO_2 production and carbon deposition rates are reported in the literature using a variety of units. To facilitate comparison between the various rates we have reported all rate measurements in units of mmol m⁻² d⁻¹. The relationships between O₂ uptake, ΣCO_2 production and carbon deposition were determined by linear regression analysis. As O₂ consumption and ΣCO_2 production were both measured during the determination of benthic metabolism, data from individual cores were compared. The relationship between carbon flux to the sediments and benthic metabolism was also determined by linear regression, but using mean values. The carbon flux to the sediment was determined using sediment traps (mean of 2 traps) deployed for 10 to 30 d prior to the determination

of benthic metabolism. This value was compared to the mean (3 replicate analyses) O_2 consumption or ΣCO_2 production rates for that station at the date of the recovery of the sediment traps. Only 6 data points out of a possible 11 (4 were lost and 1 excluded) were used for the comparison of carbon sedimentation rate to ΣCO_2 production due to losses of ΣCO_2 production samples and exclusion of stations when *Beggiatoa*-type mats were present (chemosynthetic activity strongly skewed ΣCO_2 fluxes).

Oxygen supply to the benthos. We predicted maximum rates of benthic oxygen supply using Fick's first law:

$$J = D(C_{\infty} - C_0) / Z_0 \quad (1)$$

where D is the molecular diffusion coefficient of the solute at the ambient temperature (in $m^2 h^{-1}$); C_{∞} and C_0 are the solute concentrations in the bulk water and at the interface, respectively (in $mmol m^{-3}$); and Z_0 is the thickness of the diffusion boundary layer (in m). The average thickness of the diffusive boundary layer (Z_0) for current velocities between 0.3 and 7 $cm s^{-1}$ and the O_2 molecular diffusion constant at 15°C (D) were obtained from the literature (Jørgensen 1989, Broecker & Peng 1974, respectively). Oxygen concentrations at 15°C at saturation and zero were used for C_{∞} and C_0 , respectively.

RESULTS

Oxygen supply to the benthos

Field measurements supported the assumption of O_2 saturation for the bulk water. The relationship between flow velocity and the predicted maximum rates of benthic oxygen supply by molecular diffusion was non-linear with greatest increases in flux occurring at the lowest current velocities (Fig. 2). We consider this prediction accurate within a narrow range of key environmental parameters but an underestimation for most sediments. We consider it valuable because many sediments proximal to net-pens are constrained such that the prediction is accurate, at least during key periods of the tidal cycle.

Benthic carbon deposition rates and benthic metabolism

Carbon sedimentation rates at ambient sites ranged from 73.4 to 195.8 $mmol m^{-2} d^{-1}$. Carbon sedimentation rates at sites proximal to net-pens ranged from 108.0 to 1075.0 $mmol m^{-2} d^{-1}$. Losses during sampling and processing decreased the range of carbon sedimentation

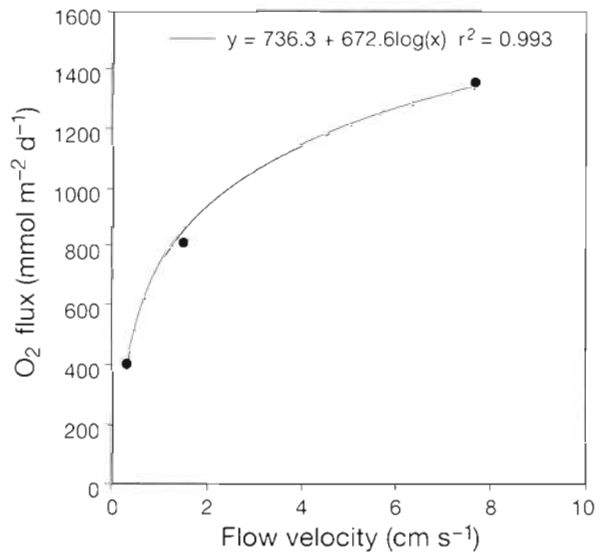


Fig. 2. Maximum Fickian diffusion of oxygen as a function of flow velocity, calculated using depths of diffusive boundary layer given in Jørgensen (1989) after Jørgensen & Des Marais (1990). Rate was calculated for 15°C and the average O_2 concentration at 15°C in the bottom water (9.6 $mg l^{-1}$) during the 2 yr of the study

rates for which measurements of benthic metabolism were made to between 73.4 and 554.9 $mmol m^{-2} d^{-1}$. Benthic metabolism was measured in 2 ways in this study; O_2 flux rates and ΣCO_2 production rates. Measured oxygen uptake rates ranged from 29.0 to 100.0 $mmol m^{-2} d^{-1}$ in ambient sediments and 107.9 to 581.8 $mmol m^{-2} d^{-1}$ in sediments proximal to net-pens. Carbon flux rates from sediments distal to the pens ranged from 42 to 167 $mmol C m^{-2} d^{-1}$ while flux rates from sediments proximal to salmon net-pens ranged from 152 to 384 $mmol C m^{-2} d^{-1}$. There was a strong linear relationship ($r^2 = 0.965$) between organic carbon flux to sediment and benthic oxygen consumption (Fig. 3). The molar ratio of carbon flux to the benthos to O_2 flux was near unity and this relationship was dominated by net-pen sediments. There was a strong 1:1 molar ratio (slope = 1.084, $r^2 = 0.936$) between the average daily carbon flux to the sediments and the benthic metabolism as estimated by ΣCO_2 production if sediments covered with *Beggiatoa*-type mats were not included in the analysis (Fig. 4).

Measurements of oxygen uptake and ΣCO_2 production showed the most complex relationship. If sediments both proximal and distal to net-pens with O_2 fluxes of $\leq 150 mmol O_2 m^{-2} d^{-1}$ were considered, then a strong linear relationship ($r^2 = 0.697$) between these 2 parameters was observed (Fig. 5a). The average respiratory quotient for these stations was 1.41. If all sediments proximal to the net-pens except those covered with *Beggiatoa*-type mats were included in

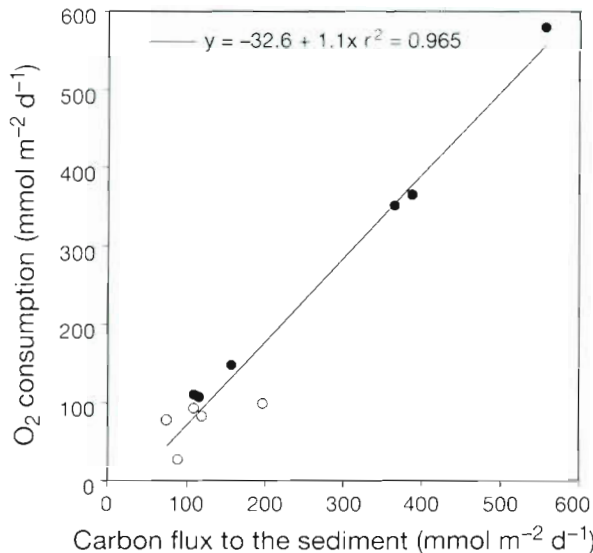


Fig. 3. Relationship between carbon flux to the sediment and benthic metabolism as measured by O₂ consumption. (○) Sediments distal to salmon net-pens; (●) sediments proximal to salmon net-pens

the analysis, a linear relationship was again observed ($r^2 = 0.883$) but the respiratory quotient dropped to 0.98 (Fig. 5). Sediments covered with *Beggiatoa*-type mats showed respiratory quotients ranging from 0.12 to 0.38 and ΣCO_2 flux from the sediments decreased with increasing O₂ uptake rates.

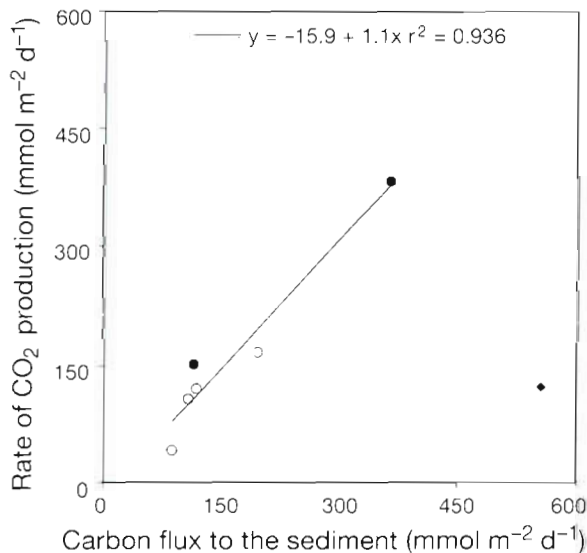


Fig. 4. Relationship between carbon flux to the sediment and benthic metabolism as measured by CO₂ production. (○) Sediments distal to salmon net-pens, (●) sediments proximal to salmon net-pens. (◆) Sediments with visible *Beggiatoa*-type mats, not included in the regression analysis

Benthic impact as a function of flow velocity and carbon flux to the benthos

The 4 net-pen locations were compared on the basis of their maximum carbon sedimentation rates and minimum 2 h flow velocities (Fig. 6). The 1:1 molar ratios between carbon deposition and O₂ and ΣCO_2 flux (Figs. 3 & 4) observed suggest that waste salmon food and feces are readily degradable and that sedimentation rates are a good predictor of the ultimate oxygen demand generated by the sediments. Minimum 2 h flow velocities were chosen as the key parameter to describe oxygen supply to the benthos because current velocities varied with tidal stage, and 2 h exposures to reduced oxygen and elevated hydrogen sulfide concentrations causes permanent damage to the gill tissues of sensitive infauna (Theede et al. 1969). The loss of macrofauna will shift apparent sediment oxygen diffusion coefficients toward the molecular coefficient — under these conditions Fickian diffusion constrains the maximal rate of oxygen delivery.

The circular net-pens located within Toothacher Cove had minimum 2 h flow velocities of 0.0 cm s⁻¹ and moderate maximum carbon sedimentation rates. Their level of impact, however, was quite high with *Beggiatoa*-type mats forming beneath both pens (Findlay et al. 1995, authors' unpubl. obs.). In contrast, the Eastport depositional site had a much higher maximum carbon sedimentation rate; yet the benthos maintained

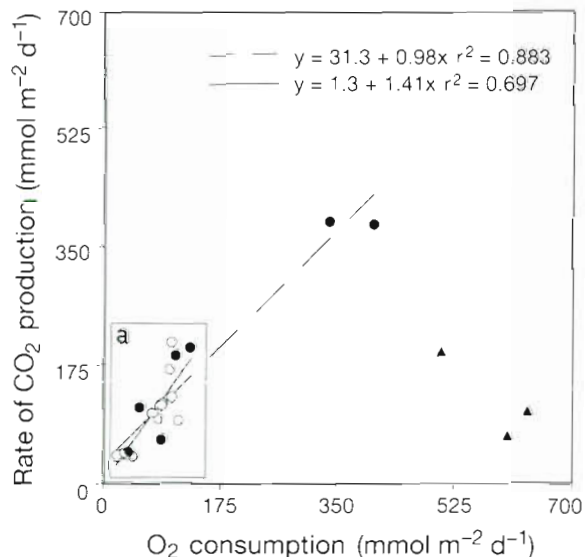


Fig. 5. Relationship between O₂ consumption and CO₂ production rates in sediments. Sediments with carbon sedimentation rates $\leq 150 \text{ mmol m}^{-2} \text{ d}^{-1}$ are detailed in the box (a) and are represented by the solid regression line. The relationship found for sediments proximal to salmon net-pens (excluding those with visible *Beggiatoa*-type mats) is given by the dashed regression line. Symbols as in Fig. 4

Table 3. Comparison of carbon deposition and sediment metabolic rates measured in this study to those reported for other salmonid production sites. All values reported as $\text{mmol m}^{-2} \text{d}^{-1}$

Parameter	This study	Literature range	Citations
Carbon deposition	108–1075	106–6483	Hall et al. (1990), Hansen et al. (1991) ^a , Ye et al. (1991), Hargrave (1995), Tsutsumi (1995)
Sediment O ₂ uptake	108–582	20–443	Hall et al. (1990), Hansen et al. (1991), Hargrave et al. (1993), Wu et al. (1994)
ΣCO ₂ production	152–384	32–619	Hall et al. (1990), Holmer & Kristensen (1992)

^aCalculated assuming a 50% carbon content for particulate organic matter caught in sediment traps

a modified but aerobic community. Minimum 2 h flow velocities were 3.1 cm s^{-1} . The benthic macrofaunal community beneath this pen system was abundant and diverse (Watling unpubl. data). The Eastport erosional site showed the highest flows (including minimum 2 h flow velocities) and the lowest carbon sedimentation rate. Using a suite of geochemical and biological indices, no benthic impact was detected at this pen system (authors' unpubl. data).

Two sites, Eastport depositional and Eastport erosional, showed carbon deposition rates (in $\text{mmol m}^{-2} \text{d}^{-1}$) approximately equal to or less than the predicted oxygen supply rate (Fig. 6). These sites showed minimal impacts compared to other Maine sites (Table 2) and most sites from around the world (e.g. Hall et al.

1990, Holmer & Kristensen 1992, Hargrave et al. 1993). The 2 net-pens located in Toothacher Cove showed higher levels of impact than the Eastport sites even though their carbon deposition rates were approximately one-half to two-thirds the rate measured at the Eastport depositional site. We believe that the higher level of impact is due to the fact that oxygen demand exceeded supply. Oxygen supply at the Toothacher Cove locations was constrained by no-flow conditions not present at the Eastport sites.

DISCUSSION

Oxygen is delivered to sediments in shallow-water marine environments by a variety of mechanisms—molecular diffusion, bioturbation, and flow and wave advection. We have based our model on the delivery of oxygen by molecular, or Fickian, diffusion alone. We do so based upon the conditions encountered at many salmonid production sites that experience the azoic sediments/*Beggiatoa*-mat endpoint. Most, if not all, of the sites have minimum flow velocities of $<3.0 \text{ cm s}^{-1}$ (for many minimum flow is 0.0 cm s^{-1}). At these velocities pressure gradients are insufficient to generate advection (Huttel & Gust 1992, Huttel et al. 1996). Wave advection, while possible in 10 to 15 m water depth, is a highly variable phenomenon in the sheltered coves and bays typical of net-pen aquaculture. Bioturbation will decrease in importance as the macrofaunal community experiences organic enrichment (moving from 'reference' through 'peak of opportunists' to 'azoic' sensu Pearson & Rosenberg 1978), and, by definition, will not be a significant factor in azoic sediments. Bioroughness, a factor in both molecular diffusion and advection, will also be quite low at the azoic sediments/*Beggiatoa*-mat endpoint. Detailed drawings of *Beggiatoa* mats (Møller et al. 1985) indicate bioroughness on the order of 0.1 mm. This is significantly less than the observed roughness of $\sim 3.0 \text{ mm}$ for a photosynthetic microbial mat studied by Jørgensen & Des Marais (1990) in which surface relief was found to

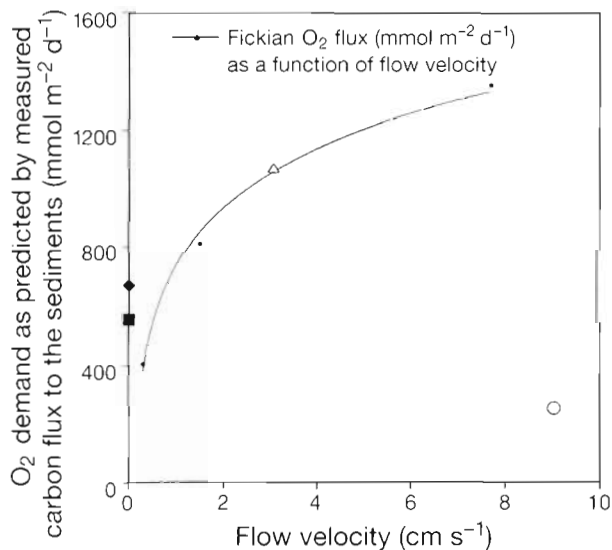


Fig. 6. Comparison of oxygen supply, as predicted from minimum flow velocity at each site and Fickian diffusion, to oxygen demand predicted from maximum carbon sedimentation rates. (◆, ■) The 2 individual net-pens in Toothacher Cove (high benthic impact); (△) Eastport depositional site (moderate benthic impact); (○) Eastport erosional site (no detectable benthic impact). Physical and chemical characteristics of sites are given in Table 2

increase diffusive flux by 49%. Studies in shallow or intertidal sediments where apparent sediment diffusion coefficients for oxygen are compared to the molecular coefficients typically note apparent diffusion coefficients 2 to 3 times higher than the molecular coefficient (e.g. Andersen & Helder 1987, Hofman et al. 1991). But these studies were also typically conducted using sediments with healthy macrofauna populations. Deep sea sediments are constrained in a fashion similar to salmonid production sites that experience the azoic sediment/*Beggiatoa*-mat endpoint (low to no flow, little bioturbation, low roughness); in these cases comparisons of apparent and molecular diffusion coefficients were in good agreement (Reimers et al. 1984, Reimers & Smith 1986).

For our model to be applicable to salmonid production sites around the world, the rates measured in this study should be comparable to those at other sites or, if they are not, then critical biogeochemical processes should operate similarly over the range of rates reported for all sites. Carbon deposition rates measured in this study were within the range reported in the literature but maximum values were 6-fold lower than the maximum value reported by Hall et al. (1990). In spite of this difference in benthic carbon flux, both sediment O₂ uptake and ΣCO₂ production rates measured in this study were comparable to those reported for other salmonid production sites (Table 3). As previously noted, none of the sites used in this study showed an accumulation of wastes beneath the net-pens, while this is commonly observed at sites with higher carbon flux rates (e.g. Hall et al. 1990, Hansen et al. 1991, Hargrave et al. 1993).

The observed correlation in the present study between O₂ flux and sedimentation does not imply that aerobic decomposition is directly responsible for degradation of organic matter at these sites. Aerobic oxidation of organic carbon with a similar redox state as carbohydrate (e.g. CH₂O) will produce 1 mole of CO₂ for every mole of O₂ consumed and a respiratory quotient (moles CO₂ produced/O₂ consumed) of 1.0. Respiratory quotients varied between sites and within sites depending on the rate of carbon flux to the benthos. For sediments, both proximal and distal, receiving organic carbon fluxes of ≤150 mmol m⁻² d⁻¹, the respiratory quotient averaged 1.4 (Fig. 5a). These values are within the range of respiratory quotients reported for sediments with active benthic fauna from around the world (Hargrave & Phillips 1981, Mackin & Swider 1989, Kristensen et al. 1991, Boucher et al. 1994). In marine sediments, respiratory quotients >1 have been interpreted to indicate active sulfate reduction with reduced sulfur retained at depth within the sediments (as S⁰ or FeS₂, often temporally, if considered on an annual basis). Under this interpretation

aerobic respiration plays a direct role in decomposition of organic matter (Jørgensen 1977, Sørensen et al. 1979, Jørgensen & Sørensen 1985). Recent work suggests that this may not be the case (e.g. Mackin & Swider 1989, Ditoro et al. 1990) and that chemical oxidation of reduced metabolic endproducts produced by anaerobic decomposition of organic matter (frequently referred to as chemical oxygen demand) may account for the majority (>90%) of benthic O₂ fluxes. Holmer & Kristensen (1992) and Hargrave et al. (1993) reported conditions beneath net-pen facilities exhibiting the azoic sediments/*Beggiatoa*-mat endpoint where chemical oxygen demand was sufficient to account for benthic O₂ flux rates. Oxidation of H₂S, produced during the anaerobic decomposition of organic matter by sulfate-reducing bacteria, is thought to be the major source of the chemical oxygen demand in marine sediments.

Regardless of the pathway of organic matter decomposition, if the supply of oxygen is sufficient then hydrogen sulfide will not accumulate within surface sediments. This lack of accumulation may be the key to maintaining an active macrofaunal community and ultimately maintaining the assimilative capacity of the benthos. Conversely, the azoic sediments/*Beggiatoa*-mat endpoint is an indication that H₂S is present at the sediment surface (Jørgensen & Revsbech 1983). As sulfide accumulates, a variety of metabolic processes may become inhibited and carbon preservation within the sediments enhanced (Hargrave et al. 1993). Measurements of CO₂ production suggest that sediment metabolism is constrained in sediment impacted by wastes from salmonid production facilities. Maximum rates reported were 387 mmol m⁻² d⁻¹ (this study), 619 mmol m⁻² d⁻¹ (Holmer & Kristensen 1992) and 553 mmol m⁻² d⁻¹ (Hall et al. 1990). These rates were all measured in sediments from environments with periods of zero flow but which differed by an order of magnitude in their rates of carbon sedimentation. If sulfate reduction rates are limited by the toxicity of H₂S to the anaerobic, fermentative bacteria that produce the substrates utilized by sulfate-reducing bacteria, then accumulation of organic matter under net-pen facilities would also be governed by oxygen supply and demand. Measurements of maximum CO₂ production rates suggest that benthic accumulation of carbon would occur at sites with periods of no flow at benthic carbon flux rates of approximately 600 mmol m⁻² d⁻¹.

Most salmonid aquaculture sites around the world report current ranges of 0 to 10 cm s⁻¹. This suggests that these sites would experience significant periods of time with little or no flow and that they would be constrained by oxygen supply as were the Toothacher Cove sites. As such, a sedimentation rate in excess of 200 to 400 mmol C m⁻² d⁻¹ (extrapolated rate at 0.0 cm

s^{-1} and the rate at 0.3 cm s^{-1}) is predicted as the threshold value at which the azoic sediments/*Beggiatoa*-mat endpoint would be observed. In 2 cases where sedimentation rates exceeded $400 \text{ mmol C m}^{-2} \text{ d}^{-1}$ and no-flow conditions were reported (Hall et al. 1990, Hansen et al. 1991), this endpoint was observed. Hargrave (1995) reported sedimentation rates of 100 to $117 \text{ mmol m}^{-2} \text{ d}^{-1}$ at the pen edge and $650 \text{ mmol m}^{-2} \text{ d}^{-1}$ beneath the pens at the L'Etang Inlet site (New Brunswick, Canada). Impacts beneath the pens were consistent with the azoic sediments/*Beggiatoa*-mat endpoint but at the pen edge they were less severe (Hargrave et al. 1993). Ye et al. (1991) reported carbon sedimentation rates in excess of $400 \text{ mmol m}^{-2} \text{ d}^{-1}$ but only documented low to moderate benthic impacts at their site. No-flow conditions were not reported and average current velocities would have maintained oxygen supply in excess of oxygen demand as predicted from sedimentation rates.

Model summary

We have developed our model of benthic impact associated with net-pen aquaculture using 2 parameters: oxygen supply to the sediments and sediment oxygen demand (both expressed as $\text{mmol m}^{-2} \text{ d}^{-1}$). The relationship between these 2 parameters can be examined in 2 ways, either graphically as in Fig. 6 or by the calculation of an index of impact (I) given as:

$$I = O_2 \text{ supply} / O_2 \text{ demand} \quad (2)$$

We calculate oxygen supply by assuming delivery by Fickian diffusion, using Eq. (1) and 3 key environmental variables: (1) flow velocity as the determinate of diffusive boundary layer thickness, (2) temperature, and (3) oxygen concentration of the bottom water. For 15°C and saturated bottom water we estimate:

$$O_2 \text{ supply} (\text{mmol m}^{-2} \text{ d}^{-1}) = 736.3 + 672.5 \log(v) \quad (3)$$

where v is flow velocity in cm s^{-1} (Fig. 2).

Sediment oxygen demand is predicted from measured carbon sedimentation rates. Linear regression analysis of data from Maine production facilities yielded the equation used to convert carbon sedimentation rates to sediment oxygen demand, that is:

$$O_2 \text{ demand} (\text{mmol m}^{-2} \text{ d}^{-1}) = 1.07x - 32.6 \quad (4)$$

where x is carbon flux to the benthos in $\text{mmol m}^{-2} \text{ d}^{-1}$ (Fig. 3).

It is this balance between supply and demand that produces the prediction of impact. If the supply of oxygen is in excess of demand, then $I > 1.0$, and impacts are minimal. If supply and demand are near unity, then $I \approx 1.0$, and impacts are moderate. If de-

mand is in excess of supply, then $I < 1.0$, and the sediments exhibit the azoic sediment/*Beggiatoa*-mat endpoint. We suspect, but were unable to investigate since Maine does not have sites with accumulated organic matter, that I will be much less than 1.0 at sites where wastes form distinct deposits beneath the pens.

Conclusions

Flow velocities have long been recognized as important in predicting benthic impact associated with net-pen aquaculture, but only as a mechanism by which waste feed and feces are distributed within the environment. Our study clearly demonstrates the pivotal role of flow in reducing the benthic impact of net-pens. Increased flow velocity not only reduces carbon sedimentation rates, but also results in increased sediment oxygen delivery, in turn allowing greater benthic degradation of the waste stream. We hypothesize that the non-linear increase in oxygen delivery with increasing flow was the major cause of the inability to predict impacts across a variety of sites.

As O_2 supply is derived from an assumption that impacted sediments are constrained to oxygen delivery by Fickian diffusion and that this rate is under the control of a few key environmental variables, it is likely that the calculation of O_2 supply will be robust across a variety of geographical or hydrological regions. This may or may not be the case for O_2 demand. The calculation of O_2 demand is based on an empirical relationship developed for a series of sites from coastal Maine and none of the sites used showed significant accumulation of organic wastes beneath the pens. Data from Hansen et al. (1991) suggests that a different ($\sim 0.5:1$) molar oxygen demand may be needed for long-established facilities with visible waste accumulation. Regardless, if an accurate *a priori* prediction of benthic carbon flux can be made for proposed net-pen sites, then this model will be a useful tool for predicting levels of benthic impact. Studies of ΣCO_2 flux rates suggest that oxygen supply to the sediments and its role in regulating sediment sulfide concentrations might be useful in predicting carbon sedimentation rates at which accumulation of waste deposits would occur. This model may have general applicability to other types of organic enrichment if correlative studies linking carbon sedimentation rates to benthic O_2 flux rates can be performed (as was done in this study) or if organic matter decay rate constants are known or can be determined for the introduced organic material.

This model synthesizes the understanding that sediment oxygen delivery and sediment oxygen consumption both play a role in determining benthic commu-

nity structure and, if these 2 parameters are measured and compared, then the level of impact can be predicted for net-pen aquaculture. Key parameters become benthic carbon flux and oxygen delivery rates; comparison of these rates reveal whether the available carbon will be consumed aerobically with minimal environmental impact or anaerobically inducing environmental impact.

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