Impact of mussel (*Mytilus galloprovincialis*) raft-culture on benthic macrofauna, in situ oxygen uptake, and nutrient fluxes in Saldanha Bay, South Africa

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**Abstract:** Culture of the mussel *Mytilus galloprovincialis* in a South African bay created organic enrichment and anoxia in sediments. Particulate organic matter (POM) was high under rafts versus the references, especially in the first 10 cm (C = 7.5 versus 0.4%, N = 0.7 versus 0.08%). Total reducible sulphides (TRS) increased threefold downcore (from 0.04 to 0.12%). High C:N ratios (12–15) indicated accumulation of refractory POM, derived mainly from faeces and decaying mussels and foulers. Although O₂ uptake by raft sediments was the lowest, rates could not conclusively be separated from the references. Ammonium dominated N efflux, the highest and most variable rates being under mussels ($825 \pm 500 \mu\text{mol NH}_4 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$). Phosphate efflux ($25–140 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) could not be ascribed to culture biodeposition, but there was an inconclusive trend for the molar N:P ratio to be highest in these sediments. Macrofauna biomass was reduced and trophic groups and taxa altered. Under rafts, macrofauna and organic debris were linked to O₂ uptake rates, whereas at the reference sites, macrofauna appeared to be the major O₂ consumer. It was concluded that POM and TRS in sediment as well as macrofauna biomass, and potentially molar N:P ratios, were more sensitive indicators of benthic impact from mussel culture than O₂ uptake rates or nutrient fluxes.

**Résumé :** La mytiliculture de la moule *Mytilus galloprovincialis* dans une baie d’Afrique du Sud cause un enrichissement organique et une désoxygénation des sédiments. La matière organique particulière (POM) est abondante sous les radeaux par comparaison aux zones témoins, particulièrement dans les 10 cm supérieurs (carbone = 7.5 contre 0.4%, azote = 0.7 contre 0.08%). Les sultures totaux réductibles (TRS) augmentent par un facteur de 3 en profondeur (de 0.04 à 0.12%) dans les carottes. Les rapports élevés de C:N (12–15) indiquent qu’il y a accumulation de POM réfractaire venant surtout des fèces, des moules en décomposition et des espèces qui contaminent la culture. Bien que la consommation d’O₂ soit plus faible dans les sédiments sous les radeaux, ces taux ne peuvent être clairement distingués de ceux des zones témoins. L’efflux d’azote est dominé par l’ammonium, les taux les plus élevés et les plus variables se retrouvant sous les moules ($825 \pm 500 \mu\text{mol NH}_4 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$). Les efflux de phosphate ($25–140 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) ne peuvent être attribués à la biosédimentation due à la culture, mais le rapport N:P molaire tend à plus élevé dans les zones de culture, mais de façon peu probante. Il y a une réduction de la biomasse de la macrofaune et des différences dans les groupes trophiques et les taxons. Sous les radeaux, il y a une relation entre la macrofaune et les débris organiques, d’une part, et les taux de consommation d’O₂, d’autre part, alors que dans les zones témoins, la macrofaune semble constituer le plus important consommateur d’O₂. En conclusion, la POM et les TRS, ainsi que la biomasse de la macrofaune dans les sédiments, et potentiellement les rapports N:P molaires, sont des indicateurs plus sensibles de l’impact de la mytiliculture sur la région benthique que ne le sont la consommation d’O₂ ou les flux des éléments nutritifs.

**Introduction**

The raft-culture of the mussel *Mytilus galloprovincialis* has taken place in South Africa for 15 years in Saldanha Bay (33°S, 18°E), north of Cape Town. This bay is the only natural sheltered embayment in the country and is thus seen as the major area for mariculture. In 1997, the bay was zoned to cater to mariculture expansion while defining areas for other uses such as angling, boat anchorage, marine reserves, recreation, conservation, a fishing harbour, ore loading, marina development, and net fishing (Fig. 1). At present, 80 ha is under mussel culture with an annual marketable yield of 2000–3000 t wet weight with shell. A further 1000 ha has been demarcated for mariculture, which increases the potential mussel harvest from Saldanha Bay to 30 000 t.

Environmental impacts from anthropogenic activities in the bay have been an issue since the construction of the iron ore jetty in 1977. In this year, a baseline survey of macrobenthic community structure was undertaken (Christie and Moldan 1977), and this was followed by further benthic sur-
veys to assess the impact of effluents from fish factories (Moldan 1978; Jackson and McGibbon 1991). These studies indicated a shift from suspension to deposit feeders that was attributed to organic loading from fish factory effluent and the reduction in water circulation imposed by harbour construction. In response to mussel farming started in 1985, a 4-year project was initiated to assess the spatial and temporal changes in benthic macrofaunal communities under the rafts and outside the farm. Below rafts, the abundance and biomass of suspension feeders were further reduced, while those of carnivores increased (Stenton-Dozey et al. 1999). Moreover, within the farm, position rather than age of a raft correlated with the degree of community disturbance. From transect lines leading out from the farm, it was deduced that impact was localised.

Monitoring changes in macrobenthic communities has proven to be a successful signal of benthic impact from culture biodeposition (Mattsson and Lindén 1983; Gowen and Bradbury 1987; Ritz et al. 1989). However, this signal gives no indication of changes in benthic processes that could quantify the level of impact. Our focus in Saldanha Bay thus shifted toward investigating in situ net fluxes of O₂ and nutrients across the sediment–water interface in relation to the biomass of macroinfauna and sediment biogeochemistry.

The hypothesis posed in this paper is that biodeposition from mussel rafts has a significant effect on the benthic environment in Saldanha Bay leading to organic enrichment and anoxia in the sediments, altered O₂ uptake and nutrient flux rates, and impoverishment of the macrofauna. The extent of impact is assessed by comparing the raft site with three reference sites at a distance of 1–3 km from the mussel farm. Results are presented as the content of organic C, N, and S₂O₄ in sediments and in situ measures of the uptake and (or) release of O₂, ammonium (NH₄), and phosphate (PO₄). The role of benthic macrofauna in the uptake of O₂ and flux of nutrients is discussed in relation to faunal biomass and the key trophic groups, namely suspension feeders, detritivores, and carnivores.

Material and methods

Study area

The mussel farm (80 ha) is located within an area called Small Bay formed by an iron ore jetty and a causeway that shelters the rafts on the west side from the Atlantic Ocean (Fig. 1). The sediments are dominated (70%) by fine to medium sand (63–500 μm) (Stenton-Dozey et al. 1999). Currents are subject to wind and tidal forcing (Monteiro et al. 1998) as well as bay resonance at the bay scale and retardation by the rafts at the farm scale. Velocities are therefore highly variable, with an average of 7.5 cm·s⁻¹ between and 1.25 cm·s⁻¹ within the rafts (Boyd and Heasman 1998). The water column in Saldanha Bay varies from being strongly thermally stratified between 10 and 18°C during most of the upwelling
season of summer to being well mixed between 10 and 14°C in winter (Monteiro et al. 1998).

Mussels are grown on ropes by natural seeding to a depth of 6 m, with 320 ropes per raft yielding approximately 27 t wet weight with shell (Heasman 1996). This amounts to an annual marketable yield of between 2000 and 3000 t for a total of 74 rafts with two harvests per year on average (V. Pienaar, Sea Harvest, Saldanha Bay, South Africa, personal communication).

Two field trips were undertaken, one in winter (June 1997) and another in summer (February 1998). A 10-year-old raft (R28) was selected as a study site together with three reference sites (RC, B10, and NS) similar in depth (between 12 and 15 m) and sediment granulometry but at varying distances from the farm (Fig. 1). These reference sites refer to an initial raft control site (RC), a monitoring buoy (B10), which has served as a bay monitoring site since 1989, and a new 50-ha lease site (NS), which has not yet been farmed.

Sediment C, N, and total reduced sulphides (TRS)

To assess the extent of organic debris accumulated below rafts, sediment cores were extracted by divers from beneath R28 and a reference site (RC) and analysed for the content of particulate organic C (POC) and N (PON) and TRS. The depth of cores varied between 20 and 25 cm depending on penetrability, which was often limited at the raft site by mussel shell fragments.

Of the four cores extracted per site per season, two cores were frozen and later sliced into a 1-cm section from the surface and every 2 cm thereafter, resulting in a possible maximum of 13 segments per core. Each segment was freeze-dried, ground, and analysed on a LECO CHN analyser for POC and PON after inorganic carbonates were acid leached with diluted HCl. A further two cores, segmented as above, were kept under nitrogen and frozen for later extraction into hot concentrated HCl in the presence of Chrome 11 (modified from Canfield et al. 1986). The H₂S that evolves in extraction into hot concentrated HCl in the presence of Chrome 11, which is resistant to oxidation by gentler means. H₂S was trapped filled reference electrode. Data were expressed as percentages by metrically using a silver/sulphide ion-selective electrode and a KCl-against 0.1 M lead acetate. The endpoint was determined electrically using a sulphide antioxidant buffer and titrated on a Dosimat system covered by the chambers (0.115 m²) was sampled for macrofauna and corrected for ambient changes in O₂ levels. The chambers were repeated on consecutive days, one of the two chambers being temperature were logged every minute. At each site, incubations were carried out with benthic currents. Creamy films of chemoautotrophic sulphur bacteria, not present at reference sites, cover the bottom in patches.

O₂ uptake and nutrient fluxes

A benthic data-logging respirometer with a light meter, temperature probe, and three Kent O₂ probes were deployed by divers. Two O₂ probes were inserted into benthic chambers (16 L, surface area 0.115 m²), and one probe hung free in the water column to monitor O₂ uptake and nutrient fluxes. The chambers were flushed by a pump attached to the respirometer and then isolated to follow the decline in O₂ levels over 2 h. Water was circulated within the chambers by current-driven impellers, and O₂ levels and temperature were logged every minute. At each site, incubations were repeated on consecutive days, one of the two chambers being darkened to take account of phytobenthic activity. The sediment covered by the chambers (0.115 m²) was sampled for macrofauna using a diver-operated suction sampler as described in Stenton-Dozey et al. (1999).

It is important to note that the sediment surface below rafts is littered with shell debris to a depth of 20 cm in some places, and above this is occasionally suspended an organic-rich nepheloid layer that varies between 10 and 30 cm in thickness, depending on benthic currents. Creamy films of chemosynthetic sulphur bacteria, not present at reference sites, cover the bottom in patches. These conditions created difficulties for divers when placing the chambers and the respirometer. A clear, relatively smooth area devoid of shells had to be selected, and great care was necessary when positioning the chambers so as not to disturb surface sediments. Chambers were gently flushed for 0.5 h before the 2-h incubation commenced to allow the sediment surface environment to normalise.

During the 2-h incubations, 50-mL seawater samples were extracted from the benthic chambers at 0.5-h intervals, commencing at time zero. The pressure in the chambers was kept constant by active volume compensation during sampling. These were immediately filtered through GF/F filters into darkened bottles and stored on ice to be analysed ashore for NH₄, nitrites (NO₂), nitrates (NO₃), and PO₄ according to the methods of Grasshoff et al. (1983). Fluxes were defined as the slope of the regression between concentration of nutrient and incubation time.

To quantify the impact of raft mussel culture on the benthos, significant differences between raft and reference sites were assessed using univariate and multivariate analyses of variance and Tukey’s honestly significant difference post hoc comparative test according to Zar (1984) using Microsoft Software Statistica 5.3.

Results

Sediment carbon, nitrogen, and sulphide profiles

Sediment profiles were analysed to assess the depth of impact from biodeposition rather than to identify a seasonal trend in POC, PON, and TRS. Thus, data for the two field trips (summer and winter) were pooled, resulting in four replicates for estimates of POC, PON, and TRS for each core segment (1-cm section from the surface and 2-cm segments thereafter) for each site. Intra- and intersite differences were analysed using one-way analysis of variance and Tukey’s test for post hoc comparisons. Data without four replicates per core segment, as at depths >19 cm under the raft, were omitted from analyses.

POC was significantly greater under the raft than at reference site RC (F(18,56) = 3.53, p < 0.0001), with surface POC an order of magnitude higher (7.5 versus 0.4%) (Fig. 2a). Downcore ≥9 cm, raft POC declined (5.8%) (F(9,30) = 7.29, p < 0.05), whereas at RC, there was an increase from 0.4% subsurface to 0.9% at 19 cm (F(9,30) = 3.15, p < 0.05). POC showed trends similar to those of POC (Fig. 2b); below mussels, the greater PON (F(20,64) = 3.28, p < 0.0002) was most obvious at the surface (0.7 versus 0.08% at RC) but declined downcore ≥11 cm (F(10,33) = 5.87, p < 0.05) while increasing ≥17 cm at the reference site (F(10,33) = 3.73, p < 0.05). Figure 2c shows that organic C:N ratios were higher at R28, between 12 and 15 compared with a range of 5–7 at RC (F(17,64) = 29.76, p < 0.05). Further, the ratios did not significantly vary down the sediment cores at either site (R28: F(8,27) = 1.87, p < 0.05; RC: F(8,27) = 0.73, p < 0.05).

Sediment below mussels was anoxic and significantly different from the reference, even at the surface (TRS = 0.04 versus 0.014% at RC) (F(20,64) = 16.94, p < 0.05) (Fig. 2d). TRS increased threefold down to 20 cm where black colouration confirmed the reduced state of deeper raft sediments (F(10,33) = 80.60, p < 0.05); this increase was the reciprocal of the downcore decline in POC (Fig. 2a) and PON (Fig 2b). At RC, TRS remained fairly constant with depth between 0.01 and 0.02% (F(10,33) = 1.04, p > 0.05).

O₂ uptake and nutrient fluxes

There was little variation in measures of O₂ uptake or nutrient fluxes between light and dark chambers, so these data were combined to provide four replicates for each site. Theo-
Theoretically, darkening chambers should eliminate photosynthetic production of $O_2$, thereby reflecting net uptake by sediments at depths of 12–15 m. These expected results were not obtained, which questions the validity of using darkened chambers during the day. Future surveys are planned to overcome this problem by incubating at night and quantifying chlorophyll production in surficial sediments.

Two-way analysis of variance (type II SS), followed by Tukey’s test, showed that $O_2$ uptake by sediments was lowest under the raft ($F_{(3,24)} = 6.46$, $p < 0.002$), the principal difference being between sites ($F_{(3,24)} = 5.34$, $p < 0.006$) rather than season ($F_{(1,30)} = 1.9$, $0.05 < p < 0.178$) (Fig. 3). However, these data are misleading in that intersite differences were not attributable to the low $O_2$ uptake rate by raft sediments.

Fig. 2. Sediment core profiles (25 cm deep) at raft site R28 (squares) and reference site RC (triangles) showing the percentage by weight of (a) POC and (b) PON, (c) C:N ratios, and (d) TRS. Each data point is a mean ($n = 4$) ± 1 SE.
ments (1100 µmol·m⁻²·h⁻¹) but rather to a significantly high rate (2463 µmol·m⁻²·h⁻¹) at one of the reference sites (B10). This site proved to be an anomalous control because of dense patches of the burrowing prawn U. capensis. Thus, changes in the rate of O₂ uptake by sediments could not be linked to heavy biodeposition from mussel culture.

NH₄ was the main N-containing mineral component released from the sediments. Since NO₂ and NO₃ releases were consistently negligible by comparison, being two to three orders of magnitude lower (<5 µmol·m⁻²·h⁻¹), these data were excluded from analyses. There was no indication of negative NH₄ fluxes, the lowest rate (40 µmol·m⁻²·h⁻¹) being measured in summer at NS.

While NH₄ flux from sediments was highest under the raft (825 µmol NH₄·m⁻²·h⁻¹ in winter), the standard error around the mean was also the highest (±500 µmol NH₄·m⁻²·h⁻¹) (Fig. 4). This is indicative of within-sample variance, which negated identifying intersite differences other than between R28 and NS ($F_{(3,24)} = 3.59, p < 0.028$). Although not significant, reference fluxes were lower and less variable than at R28. The interaction effect of site and season was not significant ($F_{(3,24)} = 0.57, 0.05 < p < 0.64$) and neither was season alone ($F_{(3,24)} = 0.57, 0.05 < p < 0.83$).

PO₄ fluxes presented no conclusive result; two reference sites (B10 and RC) were atypical in having the highest rates with wide variation (Fig. 5). Rates ranged between 25 and 140 µmol·m⁻²·h⁻¹ with no significant differences in a site–season interaction ($F_{(3,24)} = 0.636, 0.05 < p < 0.56$), between sites ($F_{(3,24)} = 0.248, 0.05 < p < 0.09$), or between seasons ($F_{(3,24)} = 3.57, 0.05 < p < 0.07$). A ratio of mean flux rates of NH₄ and PO₄ provided a clearer signal of the complex interactions during decomposition, denitrification, and remineralisation in sediments (Fig. 6). With inclusion of data from the winter 1998 survey, a pattern emerged wherein...
NH₄:PO₄ was always highest at R28 (10:1 to 27:1), with the ratio being maximal in winter. Since neither NH₄ nor PO₄ fluxes were significantly different between reference sites, these data were combined in a multiple regression that showed a significant positive correlation between the two fluxes ($r = 0.72$, $p < 0.0001$) with a geometric mean estimate for the N:P ratio of 2.89 ± 1.8 ($n = 24$). This mean is within the range shown for reference sites in Fig. 6 (2:1 to 8:1). No such positive correlation was shown between the fluxes at R28 ($r = 0.39$, $0.05 < p < 0.07$), possibly because of the high standard errors for NH₄ flux rates (Fig. 4) and a small sample size ($n = 8$). Based on the trend in Fig. 6, however, it is likely that with more data, a significantly higher N:P ratio would be identified in relation to heavy biodeposition.

**Benthic macrofauna**

Macrofauna biomass (grams dry weight per square metre) was significantly different between sites ($F_{(3,24)} = 27.44$, $p < 0.0001$), seasons ($F_{(3,24)} = 11.66$, $p < 0.0023$), and in an interaction of both of these variables ($F_{(3,24)} = 10.38$, $p < 0.0001$) (Fig. 7). Biomass at R28 was diminished compared with reference sites except that for summer at RC (Tukey’s test). At this reference site, low biomass could be attributed to the absence of the large burrowing prawn *U. capensis* rather than to season. This species is unevenly distributed at RC and B10 and, when present in samples (e.g., winter RC), can account for up to 80% of the biomass.

When distinguishing between trophic groups, data from all seasons were used to estimate the mean percentage domi-
nance by weight for each site \( (n = 8) \). At R28 detritivores (80%) and carnivores (19%) dominated and suspension feeders made up less than 1% of total biomass (Fig. 8). At B10 and RC, suspension feeders dominated (70% and 90% respectively), and at NS this group was second (25%) to detritivores (55%). The burrowing prawns \( U. \) \textit{capensis} and \( U. \) \textit{africana} accounted for most of the suspension feeding biomass at B10 and RC, and their dominance is reflected in Fig. 9 within the taxon Anomura. The echiuroidean \( Ochaetostoma \) \textit{capense}, a large species like the prawns, also frequented reference sites. Under the raft, different taxa were dominant: deposit-feeding Bivalvia (\textit{Nocula nucleous}, \textit{Macoma crawfordi}, and \textit{Tellina} spp.), detritivorous Polychaeta (\textit{Polydora} spp. and \textit{Prionospio sexuculata}), and carnivorous Gastropoda (\textit{Nassarius speciosa} and \textit{N. vinctus}).

**Fig. 7.** Organic biomass of benthic macrofauna in summer (open bars) and winter (shaded bars) at raft site R28 and the three reference sites (RC, B10, NS). Each data point is a mean \( (n = 4) \) \( \pm 1 \) SE.

**Fig. 8.** Percentage of macrofauna biomass as suspension feeders (open bars), detritivores (light speckled bars), and carnivores (dark speckled bars) at raft site R28 and the three reference sites (NS, B10, RC). Summer and winter data were combined. Each data point is a mean \( (n = 8) \) \( \pm 1 \) SE.

\( \text{O}_2 \) and nutrient fluxes in relation to macrofauna biomass

\( \text{O}_2 \) and nutrient exchange rates across a sediment–water interface were related to the macrofauna biomass in the sediment by standardisation to micromoles per hour per gram dry weight for each site and season \( (n = 4) \) (Fig. 10). These ratios were significantly greater at the raft relative to the reference sites \( \text{O}_2: F_{(3,24)} = 11.12, p < 0.0001; \text{NH}_4: F_{(3,24)} = 3.78, p < 0.023; \text{PO}_4: F_{(3,24)} = 3.49, p < 0.031 \), a difference that reflects the significant reduction in macrofauna biomass, while concomitant \( \text{O}_2 \) uptake and nutrient fluxes under mussel culture could not be separated from those of the references. This discrepancy highlights the complexity of biogeochemistry in organically enriched sediments and the difficulty in interpreting the integral role of macrofauna in nutrient regeneration via metabolism and bioturbation in such sediments. Clearly,
the role of macrofauna in sediment is not a simple ratio of rate against a unit of body mass.

Another way of viewing these data is to regress in situ flux rates (micromoles per square metre per hour) to in situ macrofauna biomass (grams dry weight per square metre) measured in any one chamber irrespective of season or site \((n = 32)\). There was a weak positive and significant relationship between macrofauna and \(O_2\) uptake \((r = 0.48, p < 0.0047)\), but no such correlation existed for \(P_0\) flux rates \((r = 0.24, p < 0.18)\) or \(N_4\) \((r = 0.15, p < 0.4)\). Heavy biodeposition that results in high POC, TRS, and C:N ratios (Fig. 2) in sediments generates complex biogeochemical processes that cannot be decisively interpreted from the data in this study.

**Discussion**

**Core profiles**

Heavy biodeposition under rafts in Saldanha Bay created organic enrichment and anoxic conditions \(\geq 10\) cm downcore. This loading can be attributed to high biomass production of about 105 t wet weight-raft\(^{-1}\)-year\(^{-1}\), inclusive of mussels and foulers, principally the tunicate *Ciona intestinalis* (Heasman 1996; Grant et al. 1998). Since *C. intestinalis* is a suspension feeder like *M. galloprovincialis*, ingestion and assimilation of phytoplankton would generate enormous quantities of faeces and pseudofaeces deposits, as found in other culture farms (Dahlbäck and Gunnarsson 1981). On one occasion, the biodeposition rate under R28 was measured as 845 g organic C-m\(^{-2}\)-day\(^{-1}\); this is three times the rate measured outside the farm (P. Monteiro, Centre for Scientific and Industrial Research, South Africa, unpublished data). This value is higher than those reported for other shellfish suspended culture sites (10–508 g C-m\(^{-2}\)-day\(^{-1}\)) (Smaal and Prins 1993). Clearly, however, the quantity and rate of faecal deposition would vary with filter-feeding biomass, seston concentrations, and feeding efficiency of *M. galloprovincialis* (van Erkom Schurink and Griffiths 1992; Grant et al. 1998) and *C. intestinalis* (Kjerulf-Petersen and Riisgård 1992; Lesser et al. 1992; Grant et al. 1998) as well as food acquisition, which would be strongly dependent on the nature and magnitude of particle transportation (Labarbera 1984) and resuspension (Prins and Smaal 1994). Besides faeces, further deposition arising from the dislodgement of mussels and foulers during harvesting and storms can amount to 20% of annual total harvest (Heasman 1996).

High POC in raft sediment also reflects an accumulation over the 10 years that the raft has been in position, the relatively high C:N ratios to reference suggesting aggregation of refractory organic C. Fabiano et al. (1994) showed that labile POC originating from the faeces of *M. galloprovincialis* was degraded by colonising bacteria and protozoans within 4 days, while the somatic tissue took longer, 42% being decomposed within 11 days. The raft sediments in Saldanha Bay thus appear to act as a sink for the less labile POC and PON that are resistant to diagenetic decomposition (Grant and Hargrave 1987). Fichez (1991), studying the biogeochemical C budget in submarine cave sediments, found that 80% of buried biodeposits (up to 15 cm) was complex structured organic matter, composed mainly of carbohydrate–protein aggregates requiring substantial energetic investment to fractionate into simple degradable organic compounds (Tenore et al. 1984).

The presence of organic C at depth in raft sediments suggests that macrofauna may be responsible for mixing sediment downcore, even under anoxic conditions as inferred from the marked increase in percent TRS downcore. Small opportunistic polychaetes, tolerant of such conditions (Ritz et al. 1989), were relatively abundant at 15 cm: species such as *Dorvillea rudolphi*, *Mediomastus capensis*, *Prionospio sexoculata*, and *Eunoe nodulosa*. It has been suggested that greater burrowing activity under mussel culture creates “microsites,” tiny pockets of aerobic decomposition, which enhance nitrification despite the more reduced conditions in
the sediments (Knowles 1978). With more NO₃ available for
denitrification, this process could have played a role in the
elevated release of NH₄ observed at the raft site. Such
bioturbation would, however, also obscure the dissociation
between oxic and anoxic processes, a continuum feature com-
mon to marine sediments (Thamdrup and Canfield 1996).
Notwithstanding, the substantial proportion of TRS com-
pared with the reference site indicates the importance of an-
aerobic metabolism in remineralisation under rafts.

**O₂ uptake and nutrient fluxes**

No conclusive inference could be made on the impact of
biodeposition on O₂ uptake by sediments, all rates being in
the range 24–62 mmol·m⁻²·day⁻¹. These values lie within
ranges measured in embayments impacted by mussel culture
(Baudinet et al. 1990; Hatcher et al. 1994) but are also
within the range measured in unimpacted bays (Hargrave et
al. 1993). This supports the maxim that benthic O₂ fluxes
may not be a sensitive indicator of higher organic input from
mussel culture because of increased activity of the S cycle
(as evidenced by high percent TRS in Saldanha Bay sedi-
ments) concomitant with higher rates of chemical O₂ de-
mand and the storage of end products such as pyrite (Holmer

There are other factors that cloud the sensitivity of O₂ up-
take as an indicator of impact. The mineralisation of organic
matter and the bioturbation activity of macrofauna play a
significant role in sediment O₂ demand (Hopkinson 1987),
as was mentioned earlier in relation to microsites (Knowles
1978). Moreover, benthic photosynthesis can counterbalance
O₂ uptake and can play a substantial role in the absorption
of nutrients (Baudinet et al. 1990; Barranguet et al. 1994).
Our attempt to measure net O₂ sediment uptake by eliminat-
ing photosynthetic activity in darkened incubations was un-
successful. Later surveys in Saldanha Bay have included
nighttime incubations and sediment chlorophyll analyses that
will better quantify the role of phytothons.

From increased biodeposition of organic C and N below
rafts and the concomitant increase in decomposition and
denitrification (Kaspar et al. 1985; Hansen and Blackburn
1991; Hargrave et al. 1993), one may expect more NH₄ and
PO₄ release (Fabiano et al. 1994; Prins and Smaal 1994)
compared with unimpacted sediments. Such distinction was
not consistent between the raft and reference sites or between
seasons. Although NH₄ flux peaked under the raft at
19.8 mmol NH₄·m⁻²·day⁻¹, this rate was only significantly
greater than at one of the reference sites (0.48 mmol NH₄·m⁻²·
day⁻¹). In general, the range of NH₄ flux rates is comparab-
le with that at other sites impacted by mussel culture (Kaspar
et al. 1985; Grant et al. 1995; Mazouni et al. 1996).

NH₄ flux under mussel culture was widely variable in
summer (SE = ±5 mmol NH₄·m⁻²·day⁻¹) and winter (SE = ±500 mmol NH₄·m⁻²·day⁻¹). This precluded identifying a
significant impact using NH₄ flux as an indicator. Heavy
biodeposition of faeces and animal tissue, accumulation of
POC and PON in sediments, and the natural seasonal bloom
and decay of phytoplankton (Monteiro et al. 1998; Pitcher
and Calder 1998) comprise a myriad of factors that can in-
fluence NH₄ flux. In summer, there is often a thermocline
1 m from the bottom, exposing the benthic environment to
NO₃-enriched upwelled water lower in temperature and dif-
ferent in biogeochemical composition. This could influence
the complexity of the relationship between nitrification and
denitrification. Further, in winter, the water column is well
mixed, possibly stimulating greater interchange and NH₄ flux
across the sediment–water interface. The fact that NO₂ and
NO₃ sediment flux rates were consistently low and some-
times negative (uptake by sediments) is indicative of the
complexity of NH₄ production. NO₃ generated by nitrifica-
tion following animal protein degradation (dislodged mus-
sels and foulers) and aerobic decomposition of labile organic
material (faeces) would rapidly enter the denitrification loop,
producing more NH₄ and PO₄.

PO₄ fluxes and molar ratios of N:P presented no conclu-
sive results. This is unexpected, since the anoxic conditions
under the raft provide a strong reducing environment that
should greatly enhance PO₄ release (Balzer et al. 1983), and the decay of mussel faecal material would also be responsible for PO₄ production (Fabiano et al. 1994) relative to the references. However, this argument is counterbalanced by Sundby et al. (1992) having identified interstitial water as a trap for PO₄ due to the adsorption–desorption equilibrium of PO₄ reacting with iron oxides. Iron ore is loaded onto ships in Saldanha Bay, and based on predictive modelling of the transport and fate of trace metals (Monteiro et al. 1999), it is likely that the sediments in and around the farm are high in iron oxides.

**Benthic macrofauna**

Raft biodeposition had a dramatic effect on benthic macrofauna biomass, reducing it to between 5 and 15% of that at reference sites. Such an effect impacts negatively on community structure, as identified in ABC plots and hierarchical cluster analyses in a previous study on the mussel farm (Stenton-Dozey et al. 1999) and as found in other mariculture systems (Kaspar et al. 1985; Hatcher et al. 1994). The raft population was dominated by small r-strategists (e.g., polychaetes) compared with larger K-strategists outside the farm (e.g., prawns, tongue worms). Besides biogeochemical changes, alteration of bottom topography by debris accumulation (ropes, shells, mussels, foulers) provided a multitude of niches that were absent at the reference sites where flat sandy bottoms prevailed. In Saldanha Bay, these niches were occupied by deposit-feeding bivalves and carnivorous/scavenging gastropods that fed upon organic debris.

**Macrofauna, O₂ uptake, and nutrient fluxes**

A weak positive relationship existed between O₂ uptake and macrofauna biomass when these variables were paired within an individual 2-h sediment incubation, irrespective of season or site. Macrofauna represent the largest measured biological biomass in the sediments (Jackson and McGibbon 1991; Stenton-Dozey et al. 1999; J. Stenton-Dozey, personal observation), and their role in O₂ uptake must be substantial. That O₂ flux per gram of macrofauna at the raft site was up to 15 times that at reference sites can be expected, since intersite differences in O₂ uptake were minimal, while macrofauna biomass was substantially less at the raft site. This discrepancy, however, partially explains the extent to which organic debris recently deposited under rafts is responsible for uptake. Grant et al. (1995) estimated that organic deposits could account for 40% of the variance in sediment O₂ uptake below mussel lines. Within the top 10 cm of raft sediment, half the measured organic C content by weight was macrofauna and the other half was organic deposits; at the reference sites, nearly all organic weight measured was macrofauna. In effect, only 50% of the O₂ consumption under the raft could be related to macrofauna compared with nearly 100% at reference sites. The balance of raft O₂ uptake was likely attributable to increased activity of the S cycle (percent TRS) and high rates of chemical O₂ demand (Holmer and Kristensen 1992; Hargrave et al. 1993).

Application of the same approach in quantifying NH₄ release from sediments per unit organic weight is more difficult. The complex interactions between denitrification, ammonification, and decomposition merge with NH₄ excretion by fauna, the degradation of somatic tissue (Fabiano et al. 1994), and the role of bioturbation in accelerating nitrification and the exchange across the sediment–water interface. NH₄ flux could stand on its own as a sensitive indicator of impact without relating to macrofauna biomass, as found in other culture-impact research (Kaspar et al. 1985; Prins and Smaal 1994; Grant et al. 1995). However, in this study, the wide variation in raft NH₄ flux rates (up to 58% of mean) prevented such a conclusive assessment.

In overview, measures of particulate organic matter and anoxia in sediments plus independent assessment of macrofauna biomass proved the most consistent and reliable indicators of impact from mussel raft-culture. Sediments are sinks that accumulate debris and thereby reflect a compounded impact that is not subject to short-term variability as shown by nutrient fluxes. Uptake and (or) release rates of O₂ and nutrients provided no signal of seasonal or intersite differences that were rigorous enough for statistical testing. However, based on trends of the three fluxes measured, NH₄ release was the most indicative of impact and proved significantly greater than that at at least one of the reference sites. Clearly, in situ measures of benthic impact from culture must be based on robust sensitivity indicators, multiple replication of measurements, and, ideally, more than one reference site to account for natural variability in faunal biomass and the dynamics of sediment–water biogeochemistry.

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