Water-column dark CO₂ fixation and bacterial-mat growth in intermittently anoxic Saanich Inlet, British Columbia

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ABSTRACT: Saanich Inlet in British Columbia, Canada, is a frequently cited example of an intermittently anoxic fjord, where annual or less frequent deep water renewal events abruptly alter geochemical stratification in the water column. We examined the potential of chemosynthetic bacteria to exploit productively the variable oxic-anoxic interface in the inlet. An intensive zone of water-column dark CO₂ fixation was associated with the oxic-anoxic interface, where rates of dark CO₂ fixation up to 24 mgC m⁻³ d⁻¹ were recorded. This activity closely followed horizontal and seasonal developments in the oxic/anoxic interface. Extensive *Beggiatoa*-like bacterial mats, exceeding 100 ha in area, were observed by submersible on sediments below 105 m. The distribution of bacterial mats was also affected by deep-water stagnation and renewal. Physiologically-oriented investigations are now required to clarify the energetic basis for water-column dark CO₂ fixation and bacterial-mat growth in Saanich Inlet, and thus confirm the significance of chemosynthesis in organic matter production.

INTRODUCTION

Saanich Inlet, a fjord-like embayment in the south-eastern coast of Vancouver Island (Canada), is one of the classical localities among chemically-stratified fjords with intermittently anoxic bottom water. Its hydrography and chemical zonation have been extensively studied during the past 3 decades, and the general features of deep-water renewal and stagnation are now well understood (Anderson & Devol 1973, Stocchi & Giovando 1984). Oxic-anoxic interface zones in stagnant marine basins often provide an environment favorable to the growth of chemosynthetic bacteria, which oxidise H₂S and other reducing substances to obtain energy for dark fixation of CO₂. However, the oxic-anoxic interface in Saanich Inlet is much less stable than that of the Black Sea or the Cariaco Trench, where extensive zones of bacterial dark CO₂ fixation have been found (Sorokin 1972, Tuttle & Jannasch 1979). Previous studies in Saanich Inlet demonstrated or suggested the presence of a number of bacterial chemolithotrophic processes (Lilley et al. 1982, Anderson 1984, Seki et al. 1984, Tebo et al. 1984) but the

extent of this activity and the relation of these organisms to the 'cycle' of anoxia in the inlet is not known. This paper describes the influence of the anoxic cycle on water-column dark CO₂ fixation and bacterial-mat growth in Saanich Inlet, with a view to assessing the potential of chemosynthetic bacteria to exploit temporary oxic-anoxic interface conditions in this fjord and contribute to the production of organic matter.

Saanich Inlet has a single central basin with a maximum depth of 228 m, rising to a sill at the mouth of 70 m depth. Restricted deep-water renewal results in bottom waters being anoxic for much of the year (Anderson & Devol 1973). Anoxia is frequently relieved in late summer/early autumn when dense oxygenated water intrudes over the sill and cascades into the lower depths of the basin. Deep-water renewal is not an annual event in Saanich Inlet; there are many years when the anoxia is not relieved at all (Stocchi & Giovando 1984). Following a renewal event, the bottom waters generally remain oxic until late winter or early spring when decomposition of sedimented organic matter consumes available dissolved oxygen. As the anoxia progresses, the oxic/anoxic interface rises from near the bottom to a mid-depth position in the water column at 110 to 140 m, where it remains until disrupted by a deep water renewal event.

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Renewal events at mid-depth occur more frequently than full-depth renewal in Saanich Inlet (Stucchi & Giovando 1984), and likely prevent further upward movement of the anoxia.

The development of anoxia and associated dark CO_2 fixation in Saanich Inlet was monitored between April 1983 and November 1984 by water-column sampling and *in situ* benthic observations. *In situ* observations and most of the water column sampling were conducted during a series of 38 dives with the manned submersible *Pisces IV*, based at the Institute of Ocean Sciences at Patricia Bay, on Saanich Inlet. Water column sampling was mainly confined to the period of April to November 1983, but submersible observations of the growth of benthic bacterial mats continued through to November 1984.

MATERIALS AND METHODS

Water-column sampling. Water-column sampling was conducted over 3 to 5 d periods at 3 main sites in Saanich Inlet during the third weeks of April through July and September 1983. These sampling stations (Fig. 1), – Christmas Point, Bamberton, Mill Bay, – represented the upper, middle and lower reaches,

Fig. 1. Location of sampling sites in Saanich Inlet, British Columbia (Canada). Main sampling stations are marked by larger, occasional stations by smaller circles

respectively, of the inlet. Additional profiles were taken at Elbow Point, McCurdy Point, and Tozier Rock in June 1983. Water samples were taken with a through-hull sampling system on the submersible or from a surface vessel, the MV *Raymont*, using a Niskin sampler. The submersible's through-hull sampling valve allowed scientific observers to fill sample bottles inside the submersible with seawater drawn directly from the exterior. Water samples were collected at 10 m intervals from 30 to 40 m above the previously determined oxic-anoxic interface to the bottom. Sample bottles were allowed to overflow by twice their volume before capping, to avoid introduction of atmospheric oxygen into the samples.

Water-column chemistry. Development of anoxia in the inlet and movement of the oxic-anoxic interface were monitored by profiling dissolved oxygen and H_2S in the water column. Continuous profiles of conductivity, temperature and dissolved oxygen with depth were recorded with a Guildline CTD- DO_2 instrument mounted on the submersible or cast with a Niskin bottle from the surface vessel. Several submersible-collected or Niskin samples were also immediately fixed with Winkler reagents for verification of electrode dissolved oxygen measurements. Total H_2S was measured by the colorimetric method of Cline (1969).

Dark CO_2 fixation. Triplicate 130 ml samples from each depth and Formalin-killed controls were incubated with 8 μCi of $\text{NaH}^{14}\text{CO}_3$ in light-tight glass-stoppered bottles at 10 °C (*in situ* temperature) for 24 h. A previous study in Saanich Inlet found no significant difference in dark CO_2 fixation between Formalin-killed and zero-time controls (Seki et al. 1984). Time-course incubations showed CO_2 fixation to be nearly linear for ca 30 h, after which activity began to drop off, presumably due to a lack of dissolved oxygen (Jørgensen et al. 1979) or some other deterioration of growth conditions.

Addition of isotope to samples was conducted in a glove bag under an atmosphere of oxygen-free nitrogen. Incubations were terminated by filtering samples through 0.22 μm Millipore filters, which were then rinsed twice with 10 ml of filtered seawater. Filters were routinely fumed with HCl before measuring ^{14}C activity by liquid scintillation counting, although occasional checks revealed no significant amounts of HCl-volatile ^{14}C remained on the filters after rinsing.

Distribution and growth of benthic bacterial mats. All major mudslopes and cliffs of the inlet basin were explored with the submersible to determine the distribution of benthic bacteria mats. Subsequently the largest area of mat growth was mapped by a series of submersible transects, and major changes in area were monitored from November 1983 to November 1984. Mat samples were collected with a suction sampler on

the submersible for microscopic examination. Additionally, on several occasions, bottom water overlying the mats was sampled with the through-hull sampling port on *Pisces IV*. The position of the sample inlet when the submersible was resting on the bottom limited sampling to water 0.5 m above the sediment surface. Dissolved oxygen was measured by a modification of the Winkler method which improved detection at lower concentrations. Dissolved oxygen was eliminated from reagents by flushing with oxygen-free nitrogen (Broenkow & Cline 1969), and reagents were stored in syringes under an atmosphere of N₂ until usage. Titration with thiosulfate was performed with a Brinkman automatic titrator, which considerably improved end-point determinations. While less sensitive than the colorimetric method of Broenkow & Cline

(1969), this modification was more suitable to the broad range of dissolved oxygen concentrations encountered during our surveys of the bacterial mats.

RESULTS

Oxic-anoxic interface dynamics

Anoxic conditions had already developed in the upper reaches of the inlet when sampling began in late April 1983. The bottom 25 m were anoxic at Christmas Point, while only the bottom 10 m were anoxic at Bamberton in the central basin, and dissolved oxygen was absent only on the bottom at the Mill Bay site (Fig. 2). This difference between the upper and lower reaches

Fig. 2. Profiles of H₂S and dissolved O₂ at main sampling sites in Saanich Inlet; Apr to Sep 1983. Hatched areas: zones containing both detectable H₂S and dissolved O₂.

of the inlet also characterised the upward expansion of the H_2S -containing zone through May and June. The Christmas Point site developed a broad H_2S zone very quickly, while development was slower at the Bamberton and Mill Bay sites (Fig. 2). The earlier development of anoxia in the upper inlet was examined more closely in June 1983, when 6 stations were sampled. The build-up of H_2S appeared to be most extensive at the 2 stations in the upper arm of the inlet, Christmas Point and Elbow Point (Fig. 3, see Fig. 1 for station locations). Also, even within the central basin itself, there was some suggestion of more extensive H_2S accumulation further from the mouth of the inlet than closer to the sill (Fig. 1 & 3).

Fig. 3. Horizontal variation in H_2S profiles in Saanich Inlet in Jun 1983. H_2S concentration in $\mu M\ l^{-1}$

There was also an apparent horizontal progression in the development of an H_2S - O_2 interface zone in the water column. A zone containing both detectable O_2 and H_2S had already developed at Christmas Point in April 1983 and persisted throughout the sampling period (Fig. 2a), varying in breadth from 5 to 35 m. Lower in the inlet, an H_2S - O_2 interface zone was not detectable until the June-July interval (Fig. 2b & c). Separation of H_2S and O_2 gradients in the water column would require an alternative electron acceptor to O_2 for the oxidation of H_2S . This phenomenon has been observed before in Saanich Inlet (Anderson 1984), and at that time NO_3 and H_2S profiles suggested that NO_3 was the oxidising agent for H_2S . This reaction is known to be thermodynamically favourable.

The bottom waters in the shallower, upper reaches of the inlet appeared to be affected by different renewal events than those in the central basin. No full depth deep water renewal was observed in the central basin of the inlet in 1983. The anoxic layer continued to develop at the Bamberton and Mill Bay sites through to late September 1983. Further observations in November 1983 and February and March 1984 confirmed that the anoxia persisted through the following winter in the central basin. However, there is evidence

of a renewal event between July and September 1983 that extended to a depth of 140 m. This event noticeably depressed the anoxic layer at Christmas Point, where the bottom depth is 151 m (Fig. 2a) but had little if any detectable effect at the Bamberton and Mill Bay sites where anoxic waters lay mainly below 140 m (Fig. 2b & c). Evidence of this disturbance is also visible in profiles of available density (σ_T) calculated from CTD data (Fig. 4). The convergence of σ_T values in the 110 to 140 depth range between July and September

Fig. 4. Available density (σ_T) at the 3 main study sites in Saanich Inlet; Jul, Aug, Sep 1983

1983 for all stations is suggestive of an intrusion of water and associated mixing. Dissolved oxygen anomalies at 80 to 110 m in July 1983 and 105 to 115 m in September 1983 (Fig. 2) may have been related to mid-water renewal events, as may have been the deepening of the upper H₂S isopleths between May and June 1983 at Christmas Point.

A full-depth deep-water renewal eventually occurred in late summer 1984. This event was first detected during a dive in the central basin in early August. Instrument failure prevented dissolved oxygen measurements at that time but a recent deep water intrusion was evident in the presence in the bottom waters of the milky-colored suspension, likely BaSO₄, normally seen only at the O₂-H₂S interface. Water samples collected on September 21, 1984 confirmed that deep-water renewal had occurred. The dissolved oxygen concentration at the bottom of the central basin (191 m) was 0.45 mg l⁻¹. Similar concentrations were measured in a series of dives in the basin in November 1984. A dive at Christmas Point during that period indicated that the shallower upper reaches of the inlet had not been affected by this renewal event. There the O₂-H₂S interface was near 105 m and H₂S was detectable from that depth through to the bottom at 155 m.

Dark CO₂ fixation

Development of dark CO₂ fixation in the water column followed a pattern similar to the development of anoxia: activity progressed upward in the water column over spring and summer, and developed more quickly in the upper inlet than elsewhere (Fig. 2 & 5). Early in the season, activity was most intense in the bottom 5 to 20 m, and later the zone of most intense dark CO₂ fixation shifted upward in the water column (Fig. 5). At its peak in July 1983, the extent of detectable chemosynthetic activity was 50 to 70 m deep.

A broad zone of dark CO₂ fixation had developed at Christmas Point, in the upper inlet, when sampling began and dark activity was detectable from 5 to 10 m above the H₂S-O₂ interface to the bottom throughout the sampling season (Fig. 5A). Elsewhere in the inlet, the development of water dark CO₂ fixation lagged behind Christmas Point. However, by September 1983, both the Bamberton and Mill Bay stations had a broad zone of activity centered at and below the O₂-H₂S interface zone (Fig. 5B & C).

The July–September 1983 renewal event at 140 m had a significant effect on dark CO₂ fixation at Christmas Point, as it did on the H₂S isopleths at this site. Activity decreased sharply between July and September (Fig. 5A), while little effect was noticeable at the other 2 main stations where activity mainly occur-

red below 140 m, the apparent depth limit of this disturbance (Fig. 5B & C).

Benthic bacterial mats

Submersible reconnaissance during spring and summer 1983 revealed the major area of bacterial mat growth to be on the mudslopes of the central basin (Fig. 6). Between June 1983, when it was first observed, and August 1984, mat growth appeared to be confined to areas of the mudslope between 105 m and 135 m. An extensive submersible survey of the mudslope in November 1983 revealed a horseshoe-shaped

Fig. 5. Profiles of water-column dark CO₂ fixation at main study sites in Saanich Inlet; Apr to Sep 1983. Hatched areas: detectable H₂S-O₂ interface zone

Fig. 6. Major areas of benthic bacterial mat in Saanich Inlet. Shading: zones occupied by bacterial mats, where coverage ranged from 60 % of the sediment surface to complete coverage (A) Distribution during from November 1983 to August 1984. (B) Distribution in November 1984

zone of continuous coverage that extended around the western, northern and eastern marginal slopes of the lower basin (Fig. 6A), comprising an area of ca 100 ha. Coverage ranged from a regular hexagonal pattern which covered about 60 % of the sediment surface to a 1 to 2 cm thick pillowing mat that completely covered the bottom (Fig. 7A).

Microscopic examination revealed the mat to consist entirely of filamentous *Beggiatoa*-like cells (Fig. 7B). At the lower limit of the mat, dissolved oxygen was not detectable in this bottom water, and trace amounts of H_2S ($< 2.0 \mu M$) could occasionally be detected. At the upper depth limit of the mat (100 to 105 m) bottom water dissolved oxygen ranged from 0.03 to 0.95 $mg\ l^{-1}$.

The upper depth limit of mat growth on the mud-slopes overlapped with the lower depth range of the galatheid crab *Munida quadraspina*. This animal is noted for its tolerance of hypoxic conditions (Tunnicliffe 1981, Burd & Brinkhurst 1984) and has a lower limit of dissolved oxygen tolerance of 0.15 to 0.23 $mg\ l^{-1}$ (Burd 1984). It was usually the first metazoan to be seen when traversing up-slope from the anoxic zone. Groups and individual crabs were regularly observed grazing on the upper extent of the bacterial mat, and captured crabs consumed mat material introduced to an aquarium. An unidentified amphipod was

often seen swimming in and out of the mat in the zone where *M. quadraspina* were found. These incidental observations suggest that, to some extent, mat production is accessible to some bottom-feeding organisms in Saanich Inlet. In the upper inlet, where mudslopes are smaller in area and *M. quadraspina* more common, grazing activity appeared to noticeably affect mat biomass. Large, bare patches were observed in areas of mat where the crabs were grazing.

The full-depth deep-water renewal event in the late summer of 1984 had a dramatic effect on the growth of the bacterial mat in the lower area of the basin. In August 1984, likely shortly after the renewal event, no mat growth was visible below 135 m. A dive on September 21, 1984 revealed that the mat had recently extended its range to the bottom of the basin. Fresh tufts of mat filaments were growing directly on the surface of the basin sediments, without the underlying layer of discolored, decomposing filaments that were characteristic of areas of more sustained mat growth further up-slope. An extensive survey in November 1984 verified that the mat covered most of the central basin sediments below 105 m, a total area exceeding 1350 ha (Fig. 6B). Moreover, fish (Pacific hake) and amphipods were seen in the bottom of the basin for the first time since the study began in April 1983.

Fig. 7. (A) Benthic bacterial mat in Saanich Inlet photographed from submersible *Pisces IV*; depth 120 m. (B) Light-microscope photograph of sample of benthic bacterial filaments from Saanich Inlet; sample collected by suction sampler on *Pisces IV* submersible

DISCUSSION

Oxic-anoxic interface dynamics

Accelerated development of anoxia in the upper reaches of Saanich Inlet has not been previously recorded, and its cause is not immediately clear. Two

previous sedimentation studies in the inlet suggest that it was not caused by horizontal differences in organic matter sedimentation which supports H₂S production by bottom sediments. Both studies indicate that there is a greater supply of organic material to the sediments in the central and lower inlet, which should support a higher rate of sediment metabolism than in

the upper inlet, thus favoring a later development of anoxia in the upper inlet following the onset of deep water stagnation. Sedimentation-rate data of Matsumoto & Wong (1977), together with unpublished sediment organic carbon data (F. Whitney pers. comm.) indicate an increased input of sediment and organic carbon to the lower basin through horizontal input of particulate matter over the sill. A winter-time sediment trap study by Whitney & Wong (1984) established evidence for translocation of organic carbon to the inlet basin following windy periods, suggested to result from resuspension of sediments in the bordering shallow bays (Fig. 1). The upper reaches of Saanich Inlet have a more classical fjord bathymetry than the central and lower reaches, with no surrounding littoral zone that could supply additional organic material to the deep waters.

Horizontal differences in the impact of the 2 observed deep-water renewal events suggest one possible explanation for the earlier development of anoxia in the upper reaches of the inlet. The renewal event of 1983 was confined to the 110 to 140 depth interval, deep enough to severely disrupt the anoxia at Christmas Point but of little consequence to the central basin stations where the anoxic zone lay mainly below 140 m. The deep-water intrusion in the late summer of 1984 had the opposite effect, introducing oxygen to the extreme depths of the basin, but did not apparently continue upslope to Christmas Point. Past records indicate that deep-water renewal events in Saanich Inlet are more frequently of the type observed in 1984 rather than shallower intrusions (Herlinveux 1962, Richards 1965, Anderson & Devol 1973). If a deep-water renewal event similar to that of 1984 had occurred in the autumn of 1982, it would have resulted in the Christmas Point station having a larger 'anoxic debt' than the central basin stations when our study began in April 1983. Consequently, anoxia would have developed quickly at Christmas Point during spring and summer 1983.

The density of deep-water intrusions into Saanich Inlet and the resulting depth of renewal are apparently determined by seasonal and inter-annual variability in the salinity of the source waters in Haro Strait (Anderson & Devol 1973, Stucchi & Giovando 1984). Thus horizontal patterns in the development of anoxia in Saanich Inlet may vary from year to year, depending on the nature of deep-water renewal events that occur the preceeding autumn. Anderson & Devol (1973) observed a similar variety of deep-water intrusions into Saanich Inlet during cruises in 1962 and 1969. One event was confined to the 75 to 170 m depth interval; and 2 other intrusions renewed the deepest waters in the basin, but by different degrees (Anderson & Devol 1973).

Another contributing factor to an earlier develop-

ment of anoxia in the upper inlet may have been the progressive removal of dissolved oxygen from renewal waters as they passed up the inlet basin. Anderson & Devol (1973) describe deep-water renewal events as the movement of a 'bolus' of dense water which cascades over the sill and moves through the deep water toward the head of the inlet at a level determined by its density. It is likely that some dissolved oxygen would be lost from this moving bolus as it passed through the anoxic zone, a passage estimated to take several days (Anderson & Devol 1973). This would occur through diffusion and limited mixing across the interface of the bolus with resident anoxic water. If this exchange were important, it would result in a renewal event introducing significantly less dissolved oxygen to deep waters further from the sill, setting the stage for an earlier development of anoxia in the upper inlet following deep water stagnation.

Water-column dark CO₂ fixation

Our measured rates of dark CO₂ fixation in the water column of Saanich Inlet, up to 24 mgC m⁻³ d⁻¹, are the highest yet reported for the water column in anoxic basins. Occasional measurements of dark CO₂ fixation in Saanich Inlet by Seki et al. (1984) suggest that our data are not unusual for this fjord. They recorded rates of dark CO₂ fixation of 14 to 17 mgC m⁻³ d⁻¹, with similar results from Formalin-killed and zero-time controls. Two other basins where the oxic-anoxic interface lies below the photic zone are the Black Sea and the Cariaco Trench, where maximum rates of dark CO₂ fixation of 6.0 mgC m⁻³ d⁻¹ (Sorokin 1972) and 3.0 mgC m⁻³ d⁻¹ (Tuttle & Jannasch 1979) have been recorded. The surface waters in Saanich Inlet, which ultimately fuel dark CO₂ fixation, are more productive than in either of these other 2 basins. The average rate of primary production in Saanich Inlet during the anoxic 'season' (Mar to Dec) is 1100 mgC m⁻² d⁻¹ (Takahashi et al. 1977, Whitney & Wong 1984), and appears to be even higher in adjacent Satellite Channel (Parsons et al. 1983) which may supply additional organic carbon to the inlet sediments, as discussed above. Sorokin (1972) gives an average figure of 300 mgC m⁻² d⁻¹ for primary productivity in the Black Sea, and Tuttle & Jannasch (1979) report a range of 140 to 480 mgC m⁻² d⁻¹ for the Cariaco Trench.

Some caution is necessary in interpreting dark CO₂ fixation as 'chemosynthetic activity' where the energy and reducing power for dark CO₂ fixation are derived from oxidation of reducing gases and metal species. Tuttle & Jannasch (1979) point out that gross CO₂ assimilation by aerobic and anaerobic heterotrophic bacteria cannot presently be distinguished from net

chemosynthetic assimilation and must therefore be considered when discussing dark CO₂ fixation data. Our control measurements in the upper oxidised water column indicated that aerobic dark CO₂ fixation, while rather variable, did not exceed 1.0 mgC m⁻³ d⁻¹. Further, measurements of microplankton ETS activity (Devol 1981), microbial incorporation of ³H-thymidine (Hobson 1983, K. Lee pers. comm.) and ¹⁴C-glucose and ¹⁴C-acetate uptake (P. Gillespie pers. comm.) show that microbial heterotrophic activity in Saanich Inlet declines with depth following a maximum in the photic zone, with no local peak associated with the oxic-anoxic interface. While these observations suggest that much of the measured dark CO₂ fixation in Saanich Inlet was a result of chemosynthetic activity, we make this suggestion very tentatively, noting the need to more clearly determine the relationship between measured dark CO₂ fixation and the oxidation of reducing substances by chemosynthetic bacteria.

Microbial dark CO₂ fixation in Saanich Inlet was not clearly confined within the detectable O₂-H₂S interface zone. In fact, the most intense activity was concentrated below this zone and activity developed at the central basin stations before an O₂-H₂S interface was apparent. Since sulfide oxidation by O₂ is the most abundant and most commonly demonstrated source of energy for chemosynthesis, these observations are puzzling. Several other oxidative processes have been demonstrated to exist at the oxic-anoxic interface in Saanich Inlet, some of which are known to be microbially mediated. Tebo et al. (1984) detected microbial manganese oxidation in the O₂-H₂S interface region, and Lilley et al. (1982) suggested, from CH₄ profiles, that microbial CH₄ oxidation occurs there as well. When Anderson (1984) observed a separation of the O₂ and H₂S profiles in Saanich Inlet; he suggested the existence of an upper NH₄-O₂ interface and a lower interface where H₂S was oxidised by NO₃. The NH₄-O₂ reaction is a well-known source of chemosynthetic energy, and the NO₃-H₂S reaction has been shown to support growth of strains of *Thiobacilli* (Kelly 1982). Thus these or other oxidative processes could contribute to expanding and intensifying a zone of chemosynthetic activity beyond that which was supported by H₂S oxidation by O₂.

Another possible explanation for high levels of dark CO₂ fixation below the zone of detectable dissolved oxygen is that the microorganisms themselves may have been more sensitive indicators of low levels of dissolved oxygen than our instrumentation. It is notable that the only observations of the vertical separation of H₂S and dissolved oxygen containing waters in Saanich Inlet, our study and that of Anderson (1984), both employed electrodes for measurement of dissolved oxygen. These instruments allow continuous and

rapid profiling, but they are not noted for their sensitivity to extremely low levels of dissolved oxygen. While our instrument was checked against several Winkler measurements of dissolved oxygen from each profile, the Winkler method itself is not sensitive to extremely low levels of dissolved oxygen (Broenkow & Cline 1969). We therefore cannot rule out the possibility that dissolved oxygen existed at greater depths than we were able to detect, and was thus available for microbial oxidation of H₂S and other substances.

Benthic bacterial mats

Distribution of bacterial mats in Saanich Inlet was restricted to the sediment surface in waters of low oxygen content, where anaerobic conditions prevailed in near-surface sediments. This is characteristic of mat-forming, colorless sulfide-oxidising bacteria which require access to low-levels of dissolved oxygen as well as the products of anaerobic decomposition (Kuenen & Beudeker 1982). Sharp redox gradients form within this type of mat, where sulfide oxidation is often very intensive and largely microbial rather than abiotic (Jørgensen 1982).

Measured levels of dissolved oxygen overlying the bacterial mats do not accurately represent the physiological limits of the mat organisms themselves, but rather are more indicative of conditions under which a low-oxygen microenvironment could be maintained within the mat. Jørgensen & Revsbech (1985) recently used microelectrodes to demonstrate the existence of sharp dissolved oxygen gradients near the surface of *Beggiatoa* mats, maintained by metabolic oxygen consumption within the mat. This boundary layer effect was likely an important factor in allowing these organisms to form mats in Saanich Inlet at depths as shallow as 105 m where significant levels of dissolved oxygen existed in the near-bottom water. This also resulted in the upper mat zone being accessible to grazing by the low-oxygen tolerant galatheid crab *Munida quadraspina*. The contribution of this grazing activity to the nutrition of *M. quadraspina* and its effect on limiting mat growth remain uncertain.

CONCLUSIONS

Despite the uncertainty involved in distinguishing non-chemosynthetic from chemosynthetic dark CO₂ fixation, the observed magnitude and dynamic nature of water column dark CO₂ fixation suggest that chemosynthetic bacteria are able to exploit productively the fluctuating oxic-anoxic interface in Saanich Inlet. Further, more physiologically-oriented investi-

gations are now required to quantify the relation between dark CO₂ fixation and specific oxidative processes. Such studies will permit clarification of the contribution of chemosynthetic bacteria to organic matter production and geochemical processes in Saanich Inlet.

Similarly, although the extent of benthic bacterial mat growth in Saanich Inlet is remarkable, the quantitative significance and energetic basis of their productivity remains to be determined. The unique physico-chemical microenvironment created within bacterial mats requires that such studies be conducted with minimal disturbance. Investigation will be difficult in view of the fact that the bacterial mats in Saanich Inlet are too deep to be studied by means other than submersible.

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