Significance of bacteria in carbon fluxes in the Arabian Sea

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Abstract. In the Arabian Sea, temporal contiguity of highly oligotrophic and eutrophic periods, along with high water temperatures, may result in unique features of bacteria-organic matter coupling, nutrient cycling and sedimentation, which are unlike those in the classical oligotrophic and eutrophic waters. Bacteria-phytoplankton interactions are suggested to influence phytoplankton aggregation and its timing. It is also hypothesized that, within aggregates, hydrolytic ectoenzyme activity, together with condensation reactions between the hydrolysis products, produce molecular species which are not readily degraded by pelagic bacteria. Accumulation of a reservoir of such slow-to-degrade dissolved organic carbon (DOC) is proposed to be a carbon flux and energy buffer, which moderates the response of bacteria to the dramatic variations in primary production in the Arabian Sea. Use of the slow-to-degrade DOC pool during the intermonsoon could temporarily render the Arabian Sea net-heterotrophic and a source of CO_2 to the atmosphere. Stored DOC is also suggested to balance the observed deficit between mesopelagic carbon demand and the sinking particulate organic carbon supply. Knowledge of the significance of bacteria in carbon storage and cycling in the Arabian Sea is needed to understand the response of the ocean's biogeochemical state to strong physical forcing and climate change.

Keywords. Bacteria; aggregation; ectoenzymes; dissolved organic carbon; particulate organic carbon; sinking flux.

1. Introduction and statement of the problem

A fundamental goal of oceanography is to understand how biological forces influence the patterns of distribution of carbon and other bioelements in the ocean, in time and in space. This goal is also central to the discussion of whether, and under what ecosystem conditions, the ocean is a source or a sink for atmospheric CO_2, and therefore it is relevant to scenarios of global change. The Arabian Sea is an exciting ecosystem in which to study the mechanisms linking climate change to carbon cycling, both present and past. The extreme variability of physical forcing of the ecosystem related to monsoonal wind reversals creates dramatic variations in the productivity field and provides opportunities for natural perturbation 'experiments' to understand the mechanisms of coupling between the primary synthesis, decomposition and sedimentation of organic matter.

The purpose of this paper is to discuss the role of heterotrophic bacteria in carbon fluxes in the Arabian Sea. There are only a few published 'modern' studies on this subject (Naqvi *et al* 1993; Ducklow 1993; Wiebinga 1994). However, these studies have uncovered intriguing spatial relationships between apparent carbon supply and bacterial carbon demand. Ducklow (1993) found mesopelagic bacterial carbon

demand to be an order-of-magnitude greater than the sinking flux, suggesting large-scale DOC import into the mesopelagic zone. Naqvi (1994) found an imbalance between surface primary productivity and bacterial carbon demand for denitrification in the underlying oxygen minimum zone. Measurements of electron transport system activity indicated that bacterial carbon demand was highest beneath the oligotrophic waters offshore, suggesting organic matter import at intermediate depths. We will examine these unique issues with the help of generalizations from other parts of the world ocean to characterize the microbially-mediated carbon cycling in the Arabian Sea ecosystem. We will formulate hypotheses which might be of some use in future Arabian Sea biogeochemical studies. Denitrification processes have been covered by Naqvi (1994) and this subject will be mentioned only in relation to bacterial utilization of organic matter. We will discuss these issues in a food web context as well as attempt to provide a mechanistic view.

Studies from other parts of the world ocean have identified two main pathways of biologically-mediated carbon fluxes, the classical grazing food chain (phytoplankton → herbivore animals → carnivores animals) and the relatively recent microbial loop (phytoplankton → DOM → bacteria → flagellates → ciliates → animals). A third pathway of biogeochemical significance might be added, namely, the aggregation and sinking of phytoplankton, since it is believed that the aggregation of diatoms is a major sink in the flux of carbon and nitrogen on a global scale (Walsh 1983). We must point out that these pathways of carbon flow are intimately interwined, structurally as well as mechanistically, and that the 'real world' is more complex than that neatly portrayed by the three pathways. However, we think that this is still a useful way to organize and quantify the fluxes.

Flux partitioning among these three pathways influences carbon cycling patterns, because these pathways process phytoplankton biomass in fundamentally different ways. For instance, the grazing chain produces rapidly sinking fecal pellets (high *f*-ratio), the microbial loop efficiently remineralizes the organic matter (low *f*-ratio), while phytoplankton aggregation causes large episodic sinking fluxes of particulate organic matter (POM). Past ecosystem models (e.g. Steele 1974) assumed that the microbial loop did not process a significant fraction of primary production, but it is now well established that a highly variable and often large fraction ($\sim 50\%$) of primary production enters the microbial loop via DOM → bacteria. If one-half of the carbon fixed in the Arabian Sea flows through the DOM → bacteria link, it is obviously important to understand the mechanisms which mediate DOM flow into bacteria. We hasten to add that the 'rule of the thumb' that bacteria use $\sim 50\%$ of the local primary production is now known to be a gross generalization; the actual flux into bacteria may vary from 0% to $> 100\%$ of the co-local primary production. The variability of flux into bacteria actually makes its study more compelling, because of the importance of understanding the variations in flux partitioning in different ecosystem scenarios, such as monsoon versus intermonsoon in the Arabian Sea. This is one of the issues discussed in this paper.

In this paper we develop the argument that, because of temporal contiguity of highly oligotrophic and eutrophic regimes and high water temperature, the Arabian Sea exhibits unique features of bacteria-organic matter coupling, nutrient cycling and sedimentation which are unlike those in the classical oligotrophic and eutrophic systems and may also explain the intriguing mismatch between bacterial carbon demand and sinking flux noted above.

2. Bacteria-phytoplankton coupling

The Arabian Sea experiences sequential 'bloom and bust' productivity regimes caused by the monsoonally driven reversals in circulation. The resulting changes in the magnitude of primary production are the largest in the present day world ocean (Smith *et al* 1991; Banse 1994). Brock *et al* (1994) modeled an annual cycle of primary production for $14 \cdot 36°$N $57 \cdot 38°$E, which ranged from a May–June minimum of ca $50 \, \mathrm{mg \, C \, m^{-2} \, d^{-1}}$ to an August–September maximum of $2500 \, \mathrm{mg \, C \, m^{-2} \, d^{-1}}$. An important question is whether or not the community of heterotrophic bacteria respond in kind to these enormous fluctuations in the level of primary production or whether they lag behind and become 'uncoupled'. Either scenario has dramatic implications for the fate of carbon produced. If bacteria respond rapidly to the phytoplankton bloom and utilize a large fraction of the primary production, this will result in efficient remineralization and reduced sinking flux. The uncoupling of bacterial production from primary production, on the other hand, may lead to mass-aggregation and sinking of phytoplankton.

Pomeroy and Deibel (1986) discovered a dramatic uncoupling during an early spring bloom in coastal Newfoundland waters when bacterial carbon demand or flux into bacteria (F_b) was insignificant relative to the local primary production (PP) and the ratio $F_b/PP (= F_c)$ approached zero. Grazing losses were also minimal as the bloom occurred before significant growth of zooplankton. Without significant consumption, particulate organic matter in the upper mixed layer can sink to the bottom and, as suggested by Pomeroy and Deibel (1986), support rich demersal fisheries. Wiebe *et al* (1992) think the uncoupling in these high latitude waters is due to restriction of DOM uptake by the combined effect of low concentration of utilizable DOM and low temperature.

In the Arabian Sea, grazers may respond more quickly and the high surface water temperatures ($25–30°$C; Brown *et al* 1988) should preclude such restriction of trans-membrane transport and alleviate the bacterial uncoupling, provided the explanation of Wiebe *et al* (1992) is correct. However, high temperature alone cannot support a high F_c, because primary production mainly generates POM (i.e. phytoplankton cells) and it is essential to have mechanisms in place for rapid production of directly utilizable DOM from phytoplankton to achieve a high carbon flux into bacteria.

Bacteria could directly attack and solubilize phytoplankton with hydrolytic ectoenzymes. However, it is often assumed that phytoplankton have adaptations to protect themselves (e.g. by secreting antibiotics). It has been proposed (Azam and Smith 1991) that, although bacteria do directly attack phytoplankton cells, phytoplankton shield themselves by continually secreting mucus which bacteria hydrolyze to DOM without killing the phytoplankton. In this case, carbon flux in the pathway phytoplankton → DOM → bacteria is mediated by bacteria themselves via their ectohydrolases. The high temperature of Arabian Sea waters may support high rates of hydrolytic enzyme activities and thereby enhance the role of bacterial enzymes in making the phytoplankton cell-surface mucus accessible to the bacteria. However, much of the phytoplankton carbon would still remain inaccessible to bacteria. A greater fraction of primary production becomes accessible to bacteria when phytoplankton biomass is processed by zooplankton through 'sloppy feeding' (Lampert 1978) and egestion (Jumars *et al* 1989), when cells increase exudation of carbohydrates due to nutrient stress (Mykelstad 1977), or when cells lyse due to

spread of a virus infection (Suttle *et al* 1990). Bacteria can then colonize the dying and dead phytoplankton and grow rapidly on them to cause large-scale carbon flux along the pathway POM → DOM → bacteria as well as cause aggregation (below).

Thus, there are multiple pathways supplying DOM to bacteria. In the warm waters of the Arabian Sea, both bacterial hydrolytic enzymes and transmembrane transport systems should operate at high efficiency, enabling bacteria to efficiently solubilize and procure a substantial fraction of the primary production even during the SW monsoon bloom. Interestingly, bacteria may not only solubilize the particles, but also help aggregate them to generate larger, more rapidly sinking particles. This has implications for regulation of carbon flux into the ocean's interior and for the rates of denitrification and sedimentation.

3. Role of bacteria in phytoplankton aggregation

Mass aggregation is common in the later phase of diatom blooms (Honjo 1982; Billett *et al* 1983; Takahashi 1986; Bodungen *et al* 1986) and, in the Arabian Sea, mass aggregation would be consistent with the observed high sedimentation rates (Haake *et al* 1993). Since it causes large and episodic downward flux of organic matter, it is important to know what mechanisms determine the extent and timing of mass aggregation. We suggest here that, under the conditions found in the Arabian Sea, bacteria could have a major role in determining the timing of mass-aggregation as well as cause solubilization of aggregates with their ectohydrolases. We also discuss the biogeochemical implication of these processes.

In the Arabian Sea, the high sedimentation and the occurrence of an extensive denitrification zone ($\sim$150–1500 m) are consistent with large-scale sinking of aggregates, particularly during the SW monsoon. Aggregation of late-bloom phytoplankton is common, but its mechanism is not clear, nor are the factors known which determine the timing of aggregation. However, these issues are central in carbon flux, since they determine the size, duration, and fate of the bloom. Whether bacteria influence aggregation is not well studied (but see Biddanda and Pomeroy 1988). Below, we argue that bacteria have the potential to profoundly influence aggregation, as well as its timing, and present a hypothesis which focuses on the role of ectohydrolases of bacteria in aggregation.

The significance of bacterial ectohydrolases in regulating the hydrolysis of polymers and particles of phytoplankton origin is well-established (Hollibaugh and Azam 1983; Hoppe 1983; for review, see Chróst 1990). High activities of protease are expressed, as well as activities of α- and β-glucosidases, nucleotidase, phosphatase and chitinase. Thus, bacteria harbor ectoenzymes which can hydrolyze components of phytoplankton surface layers such as polysaccharides, mucopolysaccharide (or proteoglycans) and chitin fibrils (present on some diatoms).

Since the enzyme activities are associated with bacterial surface layers (Martinez and Azam 1993), bacteria must be in contact with the phytoplankton in order to solubilize the phytoplankton surface mucus layer. It has been proposed (Azam and Smith 1991; Smith *et al* 1992) that, because phytoplankton secrete surface mucus, they tend to become 'sticky' and to aggregate. Bacterial enzymes were hypothesized to keep the mucus 'pruned' and thus reduce phytoplankton stickiness. Such enzymatic pruning can produce monomers and, by intramolecular cleavage, could also produce

large polymers, colloids and submicron particles (Smith *et al* 1992). In competition with the hypothesized pruning effect, large polymers produced and released by bacterial enzyme activity may ultimately act as flocculants to enhance phytoplankton aggregation.

The presence of free, large, polymer aggregates in seawater was demonstrated by Alldredge *et al* (1993) who found abundant Alcian Blue-staining transparent exopolymer particles (TEP) ranging in size from 3–100's μm. It was then proposed that these polymers cause phytoplankton aggregation (Passow *et al* 1994), although it was speculated that the polymers were released from phytoplankton by abiotic mechanisms. We propose that it is hydrolytic cleavage of phytoplankton cell surface mucus that releases colloids and submicron particles (Smith *et al* 1992) as well as TEP. The released particle populations may interact to form larger agglomerates or be cleaved by enzymes of free bacteria into smaller entities. While glucosidase would cleave polysaccharides, proteases could release larger, complex mucopolysaccharides by cleaving the proteoglycan backbone. If our hypothesis of enzyme mediation of mucus release is correct, then it provides a biotic mechanism of regulation of phytoplankton surface stickiness, as well as TEP production, and has implications for the biological regulation of phytoplankton aggregation.

Combining the above ideas, we propose the following sequence of events during the progression of phytoplankton blooms leading up to aggregation. Early in the bloom, bacterial enzymes keep phytoplankton stickiness under check, as well as keeping the TEP pool at a low level, thus preventing mass aggregation. Later in the bloom, bacteria colonize nutrient-stressed phytoplankton and phytodetritus and, by secreting their own mucus during colonization, actually increase stickiness. Enzymatically-released mucus and TEP are produced too fast for free bacteria to hydrolyze, and therefore accumulate to levels exceeding the enzyme V_{max}. Accumulation of colonized mucus and TEP then act as flocculants to further increase diatom aggregation. Uncolonized and less sticky phytoplankton also become trapped during aggregation. The role of attached bacteria in aggregation envisaged here is consistent with the otherwise paradoxical observation that marine aggregates collected within the surface waters are always highly colonized with bacterial abundances on the order of 10^8–10^9 ml^{-1} (which are 10^2–10^3 times greater than in the surrounding water), but their growth rates are slow (Alldredge and Gotschalk 1990). This has been explained by the proposal that large populations of bacteria develop on microscopic 'source particles', including colonized phytoplankton, detritus and TEP, which aggregate to 'instantaneously' generate highly colonized macroscopic aggregates ('source particle hypothesis'; Azam *et al* 1993).

An important biogeochemical consequence of the action of bacterial ectoenzymes on phytoplankton and TEP is that it can delay the timing of bloom aggregation. This permits the development of a larger bloom than would be expected otherwise. Further, the bloom would persist longer before it aggregates and sinks. The level of expression and environmental (e.g. temperature) regulation of various ectoenzyme activities may provide a basis for understanding the regulation of bloom aggregation. Finally, the higher accumulation of phytoplankton and the delay in its mass aggregation has profound implications for the carbon fluxes and storage during the bloom.

4. Role of bacteria in aggregate solubilization

Earlier studies of bacterial degradation of marine aggregates lead to a consistent yet counter-intuitive conclusion that attached bacteria are not important in particle decomposition (Kirchman and Mitchell 1982; Ducklow *et al* 1982; Ducklow *et al* 1985; Alldredge and Youngbluth 1985; Alldredge *et al* 1986; Karl *et al* 1988; Taylor and Karl 1991). This is based on the finding that if the carbon demand of attached bacteria were the only sink for the aggregate's carbon, it would take months to years to turn over. In order to reconcile the measured carbon demand of free bacteria with the observed depth dissipation of particulate organic carbon in the mesopelagic zone, Cho and Azam (1988) hypothesized that attached bacteria *solubilize* the aggregates with their hydrolytic enzymes. If DOC is produced much faster than its uptake by attached bacteria, most DOC will diffuse into seawater ('uncoupled solubilization') and may be used by free bacteria.

Smith *et al* (1992) found intense activities (10^2–10^4 times the activities in bulk water) of several hydrolytic enzymes (protease, α and β-glucosidase, chitinase, phosphatase and lysozyme) on aggregates. Particulate combined amino acids (PCAA) were rapidly solubilized (turnover times of 0·2–2·1 d). Attached bacteria, however, were virtually uncoupled from hydrolysis. Bacterial carbon demand was so small that $\geqslant 97\%$ of the PCAA hydrolysate was released into the surrounding water mainly as dissolved combined amino acids (DCAA). Smith *et al* (1992) also suggested that aggregates' protein may undergo more rapid enzymatic hydrolysis than polysaccharide which may explain the increase in the aggregates' C/N ratio with depth as observed with sediment trap material from other areas (Wakeham *et al* 1984; Martin *et al* 1987).

In the Arabian Sea, whether the uncoupled solubilization of sinking particles continues in the suboxic zone could be an important factor in carbon cycling there. If the surface-derived bacteria colonizing the aggregates become metabolically inactive as the particle sinks into the suboxic zone, then POC solubilization is expected to slow as the preformed hydrolases of the surface-derived bacteria are degraded, but are no longer replaced. The turnover time of the hydrolases on marine aggregates is unknown and, therefore, we cannot predict the time course, nor the associated depth-dependence, of such diminution of POC → DOC transition in the Arabian Sea. There is some evidence that the depth dissipation of POM in the Arabian Sea is in fact lower than average for open ocean (Haake *et al* 1992), but currently the role of the oxygen minimum zone in this phenomenon is only speculative.

There is no *a priori* reason why the surface-derived populations of bacteria might not be replaced by those adapted to the environmental conditions in the suboxic zone. If so, then the solubilization of the aggregates' organic matter could continue. Indeed, this latter scenario is consistent with persistence of an extensive denitrification zone in the Arabian Sea. However, Naqvi (1994) has argued persuasively that the carbon demand for denitrification in the suboxic zone cannot be supported by the particle flux alone and hypothesizes that it is fueled by DOC.

If the aggregate solubilization is much reduced in the suboxic zone, it might have the important secondary effect that, without preferential hydrolysis of protein relative to polysaccharides, the C/N ratio of aggregates will not change much during their descent through the suboxic zone. The C/N ratio of particles reaching the bottom of the suboxic zone has implications for N cycling and the nutritional status of the

particulate matter reaching the animals inhabiting the deep, oxygenated layer. This idea can be tested by measuring the C/N ratio of the particles exciting the bottom of the suboxic zone.

Despite the sparsity of relevant data from the Arabian Sea, we state the following tentative hypothesis that in the Arabian Sea aggregates in surface waters are heavily colonized, harbor intense activities of hydrolytic enzymes, and undergo rapid 'uncoupled' solubilization which converts POC to DOC. In the suboxic zone, POC solubilization slows, resulting in slow POC turnover (reduced depth dissipation of carbon) and sustained C/N and C/P ratios.

5. Production and significance of slow-to-degrade DOC from aggregates

The enzyme activity of bacteria on aggregates could generate slow-to-degrade DOC (Smith *et al* 1992) by creating high concentrations of hydrolysis products within the aggregates' matrix. For instance, peptides and sugars produced by protease and glucosidase activities, respectively, can condense (Maillard 1913) to form humic-like products which pelagic bacteria cannot utilize rapidly (Keil and Kirchman 1993). Hydrolysis of complex polysaccharides and proteoglycan may produce a great variety of polymers, many of which may not be recognized by the limited number of ecto-enzymes of bacteria (Azam *et al* in press).

We suggest that simultaneous action of high activities of various enzymes on the structurally diverse and complex particulate matter of the aggregates produces a great variety of molecular species, some of which are not readily utilized. Mass aggregation during a bloom will thus cause large-scale production of slow-to-degrade DOC. Accumulation of a reservoir of this DOC could act as an energy and carbon flux 'buffer', moderating the response of bacteria to the extreme cycles of primary production found in the Arabian Sea.

5.1 *Consequences for the oligotrophic period*

Slow-to-degrade DOM produced during the monsoonal bloom could persist into the oligotrophic period and add significant reduced carbon to the low level of primary production. Since it is almost exclusively used by bacteria, the temporally-imported DOM may support bacterial carbon demand in excess of primary production during the oligotrophic period. The Arabian Sea would thus be fundamentally different from other oligotrophic systems where bacteria are a substantial biomass component, but, as their growth is limited by the fixed carbon supply, their turnover is slow and much of the nitrogen remains sequestered in bacterial biomass. In the Arabian Sea, a large reservoir of DOC fueling bacterial production during the oligotrophic period would result in bacteria not only being a substantial biomass component, but also a significant source of biomass production. The resulting high rates of bacterial turnover, along with a possible decrease in bacterial growth yield (below), would enhance the remineralization of nitrogen and carbon. Remineralization of slow-to-degrade DON should sustain a higher rate of primary production than without DON import. However, depending on the relative proportions of carbon fixation and DOM import, respiration may actually exceed carbon fixation. This will make the oligotrophic period net-heterotrophic ($F_c > 1$) and the ocean would be a net source of CO_2 during this period.

5.2 An energy source for the mesopelagic zone

The envisioned 'buffering' role of the stored DOC may explain the intriguing observations of Ducklow (1993) and Naqvi (1994). At stations in the central and NW Arabian Sea during September–October, Ducklow (1993) found that bacterial carbon demand in the 100–1000 m depth interval was an order of magnitude greater than the downward flux of POC. Shoaling of the pycnocline could transport a substantial amount of DOC below the mixed layer and this could enhance bacterial production in the mesopelagic zone. Additional slow-to-degrade DOC may have been imported horizontally, derived from particles which underwent enzymatic hydrolysis below the upper mixed layer.

Horizontal import of excess slow-to-degrade DOC could also explain the geographical mismatch between high sinking flux and high carbon demand for denitrification found by Naqvi (1994). He hypothesized that a greater fraction of the DOC pool is utilized by bacteria in the denitrification zone than outside. It is possible that the hypothesized reservoir of slow-to-degrade DOC would be more labile for the bacterial communities present in the denitrification zone whose metabolic capacities differ from those of surface communities. DOC which is refractory for surface communities could then support the additional carbon demand for denitrification as proposed by Naqvi (1994).

5.3 Variability of bacterial growth yield

Bacteria utilize DOC with highly variable carbon assimilation efficiency (generally 10–70%), therefore, the fraction of the DOC converted to CO_2 by the bacteria is also highly variable (generally 30–90%). It is believed that the carbon assimilation efficiency reflects the metabolic costs of using DOC pools of different compositions. Consequently, quite different percentages of the metabolized DOC would appear as CO_2 depending on the lability of the substrate, and this point is pertinent to DOC respiration during the course of eutrophic and oligotrophic periods. If the growth yield decreases with gradual depletion of 'better' substrates, then CO_2 production at the expense of the stored substrate would increase during the oligotrophic period, furthering the tendency toward net heterotrophy. Therefore, the measurement of growth yield and its variation is important for understanding the role of bacteria in carbon fluxes.

6. Conclusions

There is only limited information at present on the magnitude and mechanisms of bacterial cycling of organic matter and how they are influenced by the sequential eutrophic and oligotrophic productivity regimes in the Arabian Sea ecosystem. The hypothesized temporal patterns of DOC storage and use, if true, could have a major influence on carbon cycling and community structure during both the oligotrophic and eutrophic regimes. Whether the proposed temporal transfer of DOC and its use during the oligotrophic period actually makes the Arabian Sea a net source of CO_2 is an important issue which can be resolved by the use of off-the-shelf techniques. The significance of hydrolytic enzymes in particle solubilization has so far been studied only in well-oxygenated water columns. Whether or not the enzyme-mediated

POC → DOC phase transitions cease in the suboxic zone could profoundly influence the fate of sinking carbon and nitrogen. The knowledge of the significance of bacteria in carbon storage and cycling in the Arabian Sea will contribute to concepts and models of the response of the ocean's biogeochemical state to strong physical forcing and climate change.

Acknowledgements

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