

Chapter 5
Summary

Given the sheer range of **phytoplankton-bacterial interactions**, some intriguing aspects have been addressed in this study. Firstly, the role of bacteria in influencing phytoplankton communities at the system level was examined. **Where do bacteria fit in the suite of factors regulating phytoplankton community structure?** To answer this question, the phytoplankton community in a tropical monsoon-influenced environment (Mumbai and Jawaharlal Nehru ports), along the west coast of India, was analyzed over two post-monsoons and the intervening pre-monsoon period. The **seasonal changes in the diatom and dinoflagellate communities** and the **underlying ecological mechanisms** were probed.

Characteristic temporal shifts in diatom community structure were observed across the sampling periods; these were mainly driven by temperature, salinity and dissolved oxygen saturation. The nutrient-poor pre-monsoon period supported low abundance yet high species richness and diversity of diatoms. *Coscinodiscus*, *Cyclotella*, *Triceratium*, *Pleurosigma* and *Surirella* were the most dominant genera. Both the post-monsoon periods, following dissimilar monsoon events, were dominated by *Skeletonema costatum*, a blooming diatom.

The vegetative dinoflagellate community was most diverse during the pre-monsoon period. Heterotrophic dinoflagellates were abundant in the water column as well as sediment. A seasonal cycling between vegetative and resting cysts of autotrophic and heterotrophic dinoflagellates governed by the environmental characteristics of the study area was observed. Temperature, salinity and Suspended Particulate Matter (SPM) were the main factors affecting dinoflagellate community structure in both the water column and sediment. The dominant dinoflagellates in the

water column differed during both post-monsoon periods that followed two dissimilar monsoon events, highlighting the influence of the South West monsoon.

Interactions of diatoms and dinoflagellates with bacteria appear to be most important in the pre-monsoon period, characterized by high temperature, salinity, SPM and low nutrients. Under such conditions, diatoms and bacteria will most probably have a competitive relationship (for nutrients). Such competitive interactions contribute to the autogenic mechanisms regulating diatom communities. *S. costatum* possibly escapes this biological control mechanism in post-monsoon due to the following sequence of events: influx of nutrients subsequent to the monsoons and explosive growth of *S. costatum* past the critical phase where they can be controlled by grazing, ultimately resulting in dominance. This is analogous to the hypothesis put forth by Irigoien et al. (2005) wherein the dynamics of phytoplankton blooms are explained in the context of a 'loophole' in microzooplankton grazing impact.

The increase in heterotrophic dinoflagellates in the water column in the pre-monsoon period was possibly supported by the increased bacterial abundance and SPM (the microbial loop). Therefore, **in the pre-monsoon period, diatoms and dinoflagellates interact differently with bacteria. Diatoms appear to have a competitive relationship with bacteria whereas dinoflagellates resort to phagotrophy, and eat their own competitors** (sensu Thingstad et al. 1996).

The subsequent experiments focused on **whether changes in bacterial communities are reflected in benthic diatom communities**. An indirect method (the 'antibiotics' approach) was used to assess the influence of bacteria on diatoms, at the community scale. Surface sediment (0-5 cm) was treated with penicillin

(0.2 mg mL⁻¹), streptomycin (0.1 mg mL⁻¹) and chloramphenicol (0.02 mg mL⁻¹), individually and in combination. Penicillin inhibits cell wall peptidoglycan synthesis and is effective mainly against gram-positive bacteria (Josephson et al. 2000). Since diatoms have a different cell wall structure, penicillin cannot affect diatoms directly. Thus, any effects on diatom community structure when treated with penicillin, represents the effect of bacteria. Streptomycin and chloramphenicol inhibit protein synthesis, streptomycin by binding to the 30S ribosomal subunit and chloramphenicol by binding to the 50S ribosomal subunit (Josephson et al. 2000). Both have the potential to affect diatoms directly by inhibiting protein synthesis in diatom organelles (70S) (Stanier et al. 1971, Cullen and Lesser 1991). In fact, chloramphenicol is a known inhibitor of photosystem II in diatoms (Ohad et al. 1984), and therefore represents the direct effect of antibiotics. Streptomycin represents the combination of potentially direct and indirect effects of antibiotics. After suitable incubation periods, diatoms were analyzed using the extinction-dilution method (Thronsen 1978), and confirmed as viable through observation of diatom autofluorescence. The extent of bacterial suppression was also determined.

To investigate **whether bacteria can modulate diatom community structure**, surface sediment (0-5 cm) collected from an intertidal sandflat was treated with varying concentrations of antibiotics, ranging from 3X (for only streptomycin), 2X, X and X/10 concentrations [X is 0.2 mg mL⁻¹ for penicillin, 0.1 mg mL⁻¹ for streptomycin, and 0.02 mg mL⁻¹ for chloramphenicol]. 3X and 2X were considered high concentrations, X – moderate concentration and X/10 - low concentration. When bacteria were suppressed to 1-17% in the penicillin treatments, there was a marked reduction in diatom abundance (0.1-38% of control values). Characteristic

shifts in dominance patterns were also observed. *Amphora rostrata* and *A. coffeaeformis* dominated under control conditions. However, when bacteria were suppressed by penicillin, only *Odontella aurita* emerged in the high penicillin (2P) treatment, an unidentified diatom and *Nitzschia* sp. in the moderate penicillin (P) treatment, and *A. rostrata* and an unidentified diatom in the low penicillin (P/10) treatment.

These trends were distinct from those of streptomycin (which inhibited/enhanced diatom growth erratically, and were dominated by *A. rostrata*), chloramphenicol (consistently dominated by *A. coffeaeformis*) and the antibiotic combination (PSC) treatment (which reduced diatoms 100% in 2PSC, 99% in PSC and 82% in PSC/10). These results highlight the relevance of penicillin-sensitive bacteria (mainly Gram-positive forms) in shaping diatom communities, and also clearly show that they are distinct from other antibiotic-mediated influences on diatom communities.

The **concurrent changes in the bacterial community** were analyzed through Denaturing Gradient Gel Electrophoresis (DGGE) profiling. The day-wise changes in the following groups of bacteria were also analyzed throughout the incubation period (7 days): (1) Antibiotic-resistant bacteria (ARB) – they can survive and multiply in presence of the antibiotic, (2) Antibiotic-tolerant bacteria (ATB) – they can survive but not multiply in the presence of the antibiotic and (3) *Vibrio* species that are usually associated with plankton (Seeligmann et al. 2008).

Among the individual antibiotics, penicillin affected diatom community structure to a maximum extent, reiterating the importance of bacteria. Antibiotic tolerance (ATB) predominated upto day 3 in most treatments, followed by a shift towards antibiotic resistance (ARB). In the penicillin treatment, antibiotic tolerance was

overrode antibiotic resistance at the end of the incubation period. The reverse was true for diatom communities subjected to chloramphenicol (C) and antibiotic combination (PSC) treatment. This is reflected in the DGGE profile of the bacterial community, i.e., the bacterial communities in the chloramphenicol (C) and antibiotic combination (PSC) treatments were most similar. However, the trends obtained through cluster analysis of the DGGE profiles did not mirror the changes in the diatom community. The diatom communities in the chloramphenicol (C) and f/2(ASW) treatments were most similar. These trends point to the complexity of diatom-bacterial interactions, and the influence of the shifting dynamics between antibiotic resistance and antibiotic tolerance on diatom community structure.

Vibrio parahaemolyticus proliferated in the penicillin and chloramphenicol treatments that supported reduced diatom abundance, but were sensitive to the higher streptomycin (3S, 2S and S) treatments, which supported erratic enhancement/inhibition of diatoms. From these observations, it can be inferred that *V. parahaemolyticus*, though associated with plankton, may not be essential for diatom growth.

The above aspects deal with interactions at the system/community level. **Are diatom monocultures affected differently compared to *in situ* multiculture conditions?** To analyse this aspect, the effect of antibiotics on near-axenic diatom monocultures (*Coscinodiscus* sp., *S. costatum* and *Thalassiosira* sp.) isolated from the study area, was examined. When recovery of the bacterial population associated with the near-axenic monocultures was suppressed in the different antibiotic treatments, growth rates of *Amphora coffeaeformis*, *Coscinodiscus* sp. and *Thalassiosira* sp. were comparatively lower in all the antibiotic treatments, revealing the importance of

bacteria to these diatoms. The only exception was *Coscinodiscus* sp. in the non-penicillin treatments, indicating species-specific responses to antibiotics.

Similar to the trend observed in experiments with natural diatom communities from sediment, streptomycin seemed to be the least effective in inhibiting diatoms and showed erratic enhancement/inhibition of *Coscinodiscus* sp. *Coscinodiscus* sp. had the lowest growth rates compared to the other diatom monocultures. It also supported the highest abundance of free-living bacteria (FLB), diatom-associated bacteria (DAB) and free-living bacteria after penicillin treatment (FLB_p), probably due to the species-specific nature of these interactions, reported earlier by Schafer et al. (2002). Its DAB isolates had the highest antibacterial activity against both, FLB and DAB.

A marked change in the FLB associated with *S. costatum* was observed when treated with penicillin, from dominance of *Alteromonas* and *Bacillus* to dominance of *Flavobacterium*. Such changes have the potential to impact the interactions of FLB with DAB, which have a wide range of antibacterial activity, from stimulation to inhibition. These results, along with the lower growth rates of near-axenic *A. coffeaeformis*, *Coscinodiscus* sp. and *Thalassiosira* sp. in the penicillin treatments suggest that inter-species interactions among bacteria play an important role in influencing diatom growth, especially in response to treatment with penicillin.

The next aspect addressed was the **spatial and temporal variations in diatom-bacterial interactions**. An intertidal sand flat, a mangrove environment and a port environment, situated in Goa, along the west coast of India, were sampled over an annual cycle: two post-monsoons and the intervening pre-monsoon and monsoon periods.

Diatoms were consistently inhibited in the penicillin treatments in all 3 sites, reiterating the significance of bacteria to diatoms. At the intertidal sandflat, the most striking change in diatom community structure associated with suppression of bacteria by penicillin was observed in the pre-monsoon period. *Thalassiosira*, a centric diatom, dominated the community. *Thalassiosira* is an important member of the microphytobenthic community in the study area (Mitbavkar and Anil 2002), and is an important blooming diatom in both temperate (Durbin 1974, Muylaert and Sabbe 1996, Popovich and Gayoso 1999) and tropical (Patil and Anil 2008) environments. The results of this study reveal that the dynamics of this important blooming diatom is influenced by interactions with bacteria. However, the restriction of *Thalassiosira* dominance to only the pre-monsoon period, characterized by the highest generic evenness and diversity, points to the important role of the interacting diatom and bacterial communities, mediated by seasonal environmental variations.

Chloramphenicol inhibited diatoms as expected, in all the 3 sites. The response of the diatom community to streptomycin appeared to be site-specific. Streptomycin enhanced diatom growth at only the intertidal sandflat. This was inspite of suppression of bacteria to <1% of control values, a shift in culturable bacteria and the potential of streptomycin to inhibit diatoms directly. Possibly, the particular subset of bacteria inhibited by streptomycin, is not necessary for diatom growth. Or else, bacterial inhibition by streptomycin relaxes the constraints on diatom growth, resulting in higher diatom abundance than that in the control. However, the restriction of this trend to only the intertidal sandflat reflects the significance of the interacting diatom and bacterial communities. These variations in the emergence

characteristics of diatoms in the different antibiotic treatments across the sites, probably reflect the differences in the habitat characteristics of the sites.

The intertidal sandflat had a sandy sediment texture, lower nutrient concentrations, and showed a characteristic reverse trend between diatom and bacterial dynamics in surface waters. Sandflats are generally more oligotrophic than silt-rich sediments (Heip et al. 1995), characteristic of the mangrove site, and experience turbulent wave action. The mangrove site has a silt-rich sediment texture, which due to its small size fraction (2-63 μm), tends to have low loss of diatoms resulting from abrasion, a high specific surface area, and consequently, supports high abundance and generic number of microphytobenthic diatoms. The port site had higher dissolved oxygen, salinity, pH and suspended particulate matter compared to the mangrove site. It had a rocky-sandy texture, and was regularly dredged, resulting in the absence of a stable surface sediment layer. Due to this, pennates occurred in low numbers, and tychopelagic, centric diatoms dominated.

The intertidal sandflat and mangrove site are subjected to lesser anthropogenic pressures compared to the port site. Both have stable, pennate-dominated diatom communities, and a hidden repository of diatoms that can emerge when faced with a perturbation. These diatoms, which emerged in only the antibiotic treatments, but not under the control conditions (in this case, the perturbation conditions), were *Cerataulina*, *Melosira*, *Achnanthes*, *Amphiprora* and *Mastogloia* at the intertidal sandflat, *Achnanthes*, *Cocconeis*, *Cylindrotheca*, *Diploneis* and *Surirella* at the mangrove site, and *Ditylum*, *Helicotheca* and *Achnanthes* at the port site. It is clear that the diatom communities at the intertidal sandflat and mangrove site have a higher capacity to respond to perturbations compared to the anthropogenically influenced

port site. In fact, compared to the species-stable intertidal sandflat and mangrove site, the port site showed a range of responses to the different antibiotics, from total inhibition to enhancement, and also differed in terms of effects on community composition.

The habitat characteristics of diatoms influenced their response to suppression of bacteria by penicillin and treatment with the other antibiotics. *Achnanthes*, a monoraphid diatom, was not recorded in the penicillin treatment at all the 3 sites, throughout the sampling period. This suggests that bacteria (mainly the penicillin-sensitive fraction) are essential for the attachment and growth of this diatom. Another monoraphid diatom, *Cocconeis*, appeared to be sensitive to not only the suppression of bacteria by penicillin, but also to the other antibiotic treatments. However, this trend seemed to be site-specific and was restricted to the intertidal sandflat. The requirement for bacteria was also apparent in the sensitivity of *Grammatophora* and *Thalassionema* (both araphid pennates) to the penicillin and antibiotic combination treatments. These diatoms constitute the epipsammic fraction of the microphytobenthic diatom community. The other group of diatoms, the epipelon, is represented by the biraphid diatoms, namely *Amphora* and *Navicula*. They have a higher chance of escaping unfavourable conditions/gradients. These characteristics could explain the comparatively lower sensitivity of these genera to the antibiotics used. Thus, the epipsammic diatoms appear to be more sensitive to suppression of bacteria, as well as antibiotics, compared to the epipellic diatoms.

As mentioned earlier, streptomycin was the least effective in reducing diatom abundance among all the individual antibiotics. When analyzed through cluster analysis, the streptomycin treatments were most similar to the respective control

conditions in all the sampling periods, except monsoon. In the monsoon period, the penicillin treatment was most similar to the control conditions. These observations were restricted to the intertidal sandflat and mangrove site. The port site, with no stable resident diatom community, showed varying clustering patterns, indicating the influence of anthropogenic activities on diatom-bacterial interactions.

As evident from the clustering patterns during the monsoon period, the diatom community in the monsoon period appeared to be resistant to penicillin. The diatom community in the monsoon period was resistant to not only penicillin, but also to all the antibiotic treatments. For e.g., at the intertidal sandflat, all the treatments had a ≤ 1 I:E ratio in the monsoon period. [The I:E ratio is the ratio of the number of genera inhibited to the number of genera enhanced.] At the mangrove and port sites, enhancement of diatom growth was observed only in the monsoon period. This trend was corroborated by the grouping together of all the monsoon period treatments in the temporal cluster, at all 3 sites. Therefore, these modulations are affected by the monsoons, a consistent pattern observed across all 3 sites.

Overall, the results obtained during the course of this study reveal the intricate dynamics between bacterial and phytoplankton communities. In view of the increasing attention towards the role of trophic interactions in shaping phytoplankton communities and the rethinking of the role of phytoplankton and bacteria in ecosystem functioning and trophic dynamics, it is necessary to include interactions with bacteria in future studies on phytoplankton communities, especially in the context of their responses to environmental perturbations.

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