6.1 Introduction

The outbreaks and termination of algal blooms in the marine environments are influenced by physico-chemical and biological factors. Of the biological factors that regulate bloom dynamics, algal-bacterial interactions are of great importance as they are potential regulators of both, enhancing and decreasing algal blooming (Doucette, 1995; Doucette et al., 1998). Algal blooms have an ordered and structured bacterial community associated with it rather than a random assemblage of species from the marine bacterial community. The algal-bacterial association is very specific, with this specificity transcending a wide range of taxonomical groups, from algal class (Imai et al., 1995) to specific species (Fukami et al., 1992). The lethal effects of bacteria are influential factors in controlling phytoplankton bloom dynamics (Fukami et al., 1996; Kim et al., 1998; Yoshinaga et al., 1998; Imai et al., 2001).

Algal–bacterial interactions can be classified into 4 types; (1) symbiotic, where both partners benefit from each other’s presence; (2) parasitic, where
bacteria can lyse algae and algal antibiotics can inhibit bacterial growth; (3) commensalistic, where the bacteria have no actual negative effects on the host; and (4) bacteria are competitors for limiting nutrients like phosphate by being loosely associated with algae (Grossart, 1999).

Phycosphere is a mutually beneficial region around the algal cell (Bell and Mitchell, 1972) where growth promoting nutrients are exchanged between phytoplankton and bacteria, the latter are especially found to feed on dissolved organic material released by the algal cells (Riquelme et al., 1988). The presence of the bacterial community and of specific populations have distinct effects on the growth and organic matter release of marine diatoms and other algae (Grossart and Simon, 2007). Apart from influencing algal growth, the secondary metabolites produced by the associated bacteria can also inhibit settlement of potential competitors and antagonise other bacteria (Holmstrom and Kjellebeg, 1994).

Reduced sulphur in the form of the osmolyte dimethylsuloniopropionate (DMSP) is abundantly produced by marine phytoplankton (especially dinoflagellates and coccolithophores) and is rapidly converted to the gas dimethylsulfide (DMS) by bacteria, thereby aiding cloud formation over the oceans, which is important for atmospheric cooling (Charlson et al., 1987). Roseobacter found primarily in association with phytoplankton, are most proficient at converting DMSP to DMS (Gonzalez et al., 1999). Thus, these associated bacteria may also contribute immensely in the microbial loop of the marine biogeochemical cycle.

Apart from these, the bioactive compounds produced by the epiphytic bacteria regulate the ontogenesis of marine organisms which either enable them
Bacteria Associated with Algal Blooms and Hydrolytic Enzyme Production

to survive under adverse conditions or strictly regulate its dynamics. As a control measure against algal blooms, this is important because the physical and chemical methods like yellow loess (Na et al., 1996; Choi et al., 1998) and clay (Sun et al., 2004) employed to mitigate the algal blooms have secondary effects upon the feeding habits and ecology of the bottom-dwelling organisms (Rhoads and Young, 1970; Bricelj and Malouf, 1984). Chemical agents such as copper sulfate, hydrogen peroxide, and triosyn are effective in controlling blooms within a short period after application (Steidinger, 1983; Ryu et al., 1998) but their use can have wide spectrum effects upon even beneficial organisms (Jeong et al., 2000). But, the biological factors especially of bacteria (Imai et al., 1995) have least adverse effect (Kim et al., 2007). The mode of action of these bacteria may be either through direct contact with the algal cell or indirectly through the release of dissolved lytic agents (Lovejoy et al., 1998; Wang et al., 2005). Extracellular protease produced by algicidal bacteria exert their effects on algae as dissolved lytic agent. The algal cells which were treated with algicidal strains probably secreting algicidal proteins showed a change in morphological characteristics, with loss of cell wall integrity, discolouration and disruption of cells, ultimately the cellular substances were decomposed and released (Wang et al., 2012).

Usually, algicidal bacteria have repeatedly been observed in coastal environments where harmful algal blooms often occur (Imai et al., 1993; Lovejoy et al., 1998). Bacteria having algicidal effects are vivaciously involved in the termination and decomposition of algal blooms (Liu et al., 2008). In the present study, the bloom associated cultivable bacteria were isolated, identified and their ability to produce extracellular enzymes such as amylase, lipase, protease, cellulase, ligninase, phosphatase and alginase were ascertained.
6.2 Review of Literature

Interactions between algae and bacteria are commonly observed in both freshwater and marine ecosystems with bacteria increasingly cited as responsible for the regulation of growth and dynamics of phytoplankton blooms (Doucette et al., 1998; Hold et al., 2001; Mayali and Azam, 2004). Bacteria are inherent part of the physical environment of microalgae both in the laboratory and natural environments (Gallacher and Smith, 1999). The physiological and ecological relevance of the algal-bacterial interactions in stimulating and inhibiting each other’s growth and in the biogeochemical cycling has been reported earlier (Fukami et al., 1996; Lovejoy et al., 1998; Imai et al., 2001). By means of direct or indirect modes of action (Mayali and Azam, 2004) associated bacteria can influence toxin production in algae (Bates et al., 1995). Kim et al. (1998) observed that the population dynamics of algicidal bacteria has a close relationship to the blooms of the phytoplankton and that in the marine ecosystems, algicidal bacteria targeting specific phytoplankton may be one of the agents which regulate the change of species structure of phytoplankton communities.

6.2.1 Bacteria associated with bloom-forming microalgae

Simidu et al. (1971) observed that free living and algal associated bacteria are very different from each other and the latter are usually gram negatives, with Vibrio sp. and Aeromonas sp. constituting 70% of the bacterial flora. As part of the association, the microalgae benefits from bacterial products, mainly remineralized nutrients (Golterman, 1972) while the bacteria benefits from phytoplankton products, such as exudates (Bell et al., 1974; Cole, 1982). The association of the bacteria with the physical environment of the microalgae may be either loose or close (Caldwell, 1977; Alavi et al., 2001) and can also be intracellular (Cole, 1982; Franca et al., 1995).
The bacteria mainly associated with algal bloom were dominated by alpha-proteobacteria, beta-proteobacteria, gamma-proteobacteria and Cytophaga-Flavobacter-Bacteroides (CFB) (De Long et al., 1993; Gonzalez and Moran, 1997; Meusnier et al., 2001). *Pseudomonas* and *Moraxella* were found to be associated with *Amphidinium carterae* while proteobacteria and Cytophaga group were found in association with *Alexandrium catenella* (Nayak et al., 1997). *Marinobacter hydrocarbonoclasticus* associated with *Alexandrium fundyense* was able to metabolise complex unusual hydrocarbon molecules associated with the algae (Rontani et al., 1997).

Liu et al. (2000) reported extracellular and intracellular bacteria associated with *Alexandrium minutum*. Maki and Imai (2001) reported the presence of bacteria in the cytoplasm and the food vacuoles of *Heterocapsa circularisquama*. Dinoflagellate *Pfiesteria* showed the association of as many as thirty bacterial genera including *Pseudomonas, Vibrio, Nocardia, Moraxella, Cytophaga, Acinetobacter* and *Roseobacter* (Alavi et al., 2001).

Among alpha-proteobacteria, the most frequently associated member is the *Roseobacter* clade (Hold et al., 2001) in microalgal culture (Alavi et al., 2001) and field bloom (Fandino et al., 2001). Within gamma-proteobacteria, *Marinobacter* spp. and *Alteromonas* spp. appear to have an association with dinoflagellates (Hold et al., 2001; Ferrier et al., 2002) and algal cultures (Mayali and Azam, 2004). The bacterial group most often associated with dinoflagellates and diatoms are alpha-proteobacteria and gamma-proteobacteria (Green et al., 2004). Beta-proteobacteria, recorded to be rare in the marine system was found to be dominant as an intracellular bacterial flora of the dinoflagellate *Gymnodinium instriatum* (Alverca et al., 2002).
Rooney-Verga et al. (2005) observed the occurrence of CFB group in association with algal blooms. Grossart et al. (2005) reported the association of Flavobacteria–Sphingobacteria group in diatoms. Alpha and beta-proteobacteria were found in association with *Pseudo-nitzschia multiseries* (Kaczmarska et al., 2005; Sapp et al., 2006). During *Lingulodinium polyedrum* bloom event, 11 associated bacterial taxa were detected, which mainly belonged to the proteobacteria and CFB groups (Mayali et al., 2011). An increased presence of gamma-proteobacteria populations during the bloom of *Akashiwo sanguinea* and its gradual decrease in the post-bloom from Chinese waters was recently reported by Yang et al. (2012).

### 6.2.2 Effect of bacteria on bloom-forming microalgae

Usually bacteria have significant impacts on aquatic biogeochemical processes such as carbon flux and nutrient regeneration (Azam, 1998; Doucette et al., 1998; Copley, 2002) and may influence the initiation, growth, maintenance, and/or termination of bloom populations (Imai et al., 1998, 2001; Kodama et al., 2006). Specifically, a bacterial assemblage can have symbiotic (Silva, 1962), inhibitory (Doucette et al., 1999) or stimulatory effects (Fukami et al., 1991) including algal toxin production during a bloom event (Riquelme et al., 1988; Tamplin, 1990; Simon et al., 2002).

Kodama et al. (1988) reported a toxin producing bacteria associated with dinoflagellate. Yoshinaga et al. (1998) isolated 96 bacterial strains from Hiroshima Bay which have lethal effect on *Heterosigma carterae*. Lovejoy et al. (1998) reported the wide range algicidal effect of *Pseudoalteromonas*, an associated bacterial strain on *Chatonella*, *Heterosigma* and *Gymnodinium* blooms.
and thereby plays an important role in regulating the onset and development of harmful algal blooms.

An algicidal extracellular protease by *Pseudoalteromonas* sp. against *Skeletonema costatum* was reported by Lee et al. in 2000. Skerrat et al. (2002) reported five algicidal bacterial strains, *Pseudoalteromonas*, *Bacillus cereus*, *Zobellia* sp., *Cellulophaga lytica* and *Planomicrobium* sp., from Huon estuary, Australia that were effective against *Gymnodinium catenatun*. Mayali and Doucette (2002) studied the effect of *Cytophaga*, an algicidal bacterium, on *Karenia brevis* and found that there should be threshold concentration to trigger an algicidal response.

Ferrier et al. (2002) reported stimulatory effect of *Alteromonas* sp. on *Alexandrium fundyense*. Amaro et al. (2005) found that in situ environmental condition modulates the algicidal expression in bacteria associated with *Alexandrium catenella*. A bacterial strain *Shewanella* sp. had inhibitory effect (Hare et al., 2005; Pokrzywinski et al., 2012) on dinoflagellate *Pfiesteria piscicida* but stimulatory effect on diatoms and raphidophytes.

Su et al. (2007) isolated *Pseudoalteromonas* which produced a heat tolerant, acid unstable algicidal compound against toxic dinoflagellate *Alexandrium tamarense*. Liu et al. (2008) noted the presence of algicidal effect of bacteria on raphidophyte blooms *Chatonella subsalsa*, *Heterosigma akashiwo* and *Fibrocapsa japonica* and found variability in the taxonomic specificity of the algicidal bacterial effect and raphidophyte susceptibility. Kang et al. (2008) isolated algicidal bacteria *Variorovax paradoxus*, *Acidovorax delafeldii*, *Hydrogenophaga palleronii* and *Pseudomonas plecoglossicida* that have algicidal effects on diatom *Stephanodiscus hantzschii* and dinoflagellate *Peridinium bipes*. *Idiomarina* sp. isolated from the east sea areas of China has algicidal effect on
the toxic dinoflagellate *Alexandrium tamarense* (Su *et al*., 2011). *Aquimarina* sp. under the family Favobacteriaceae (Chen *et al*., 2011) and *Ochrobactrum* sp. (Mu *et al*., 2012) were reported to possess algicidal activity against toxic cyanobacterium *Microcystis aeruginosa*.

6.3 Result

6.3.1 Bacteria associated with *Prymnesium parvum* N. Carter bloom

6.3.1.1 Comparative estimation of Total Heterotrophic Bacterial count

During the *Prymnesium parvum* bloom, the total heterotrophic load of associated bacteria was 19.2×10^4 cfu/ml, whereas in the non-bloom sample, the THB was 6.1×10^4 cfu/ml (Fig.53). The variation in total heterotrophic bacterial load between bloom and non-bloom sample was significant (P<0.001, Student-Newman-Keuls-Multiple Comparisons Test).

![Fig.53 Total Heterotrophic Bacterial (THB) count in *Prymnesium parvum* bloom and non-bloom sample](image)

6.3.1.2 Generic composition of bloom associated bacteria

*Flavobacterium* (38%) was found to be the predominant bacterial genera associated with *P. parvum* bloom, which was followed by *Pseudomonas* (19%),
**Vibrio** (13%), 6% each of **Bacillus, Moraxella, Micrococcus, Acinetobacter** and **Corynebacterium** (Fig.54).

![Fig.54 Generic composition of bacteria associated with *Prymnesium parvum* bloom](image)

### 6.3.1.3 Generic composition of bacteria from the non-bloom sample

In the non-bloom sample, the major bacterial genera were **Acinetobacter** and **Alcaligenes** (25% each) followed by **Micrococcus** (17%), **Staphylococcus** (9%), **Corynebacterium, Bacillus** and **Flavobacterium** (8% each) (Fig.55).

![Fig.55 Generic composition of heterotrophic bacteria in the non-bloom sample](image)
6.3.1.4 Hydrolytic enzyme production of bloom associated bacteria

The hydrolytic enzyme production of the heterotrophic bacteria associated with the *P. parvum* bloom showed a high percentage of proteolytic bacteria (31%). The percentage of other hydrolytic enzyme producers were lipases (16%), ligninase and phosphatases (15% each), amylase and cellulase (10% each) and alginase (3%) (Fig.56).

![Fig.56 Hydrolytic enzyme production of bacteria associated with *Prymnesium parvum* bloom](image)

6.3.1.5 Hydrolytic enzyme production of bacteria from the non-bloom sample

Hydrolytic enzyme producers from the non-bloom samples showed the predominance of lipase producers (23%) followed by amylase and phosphatase producers (20% each). 14% of isolates could produce ligninase, whereas only 11% could produce protease. 7% of isolates were able to produce cellulose, whereas alginase producers were only 5% (Fig.57).
6.3.2 Bacteria associated with *Proboscia alata* (Brightwell) Sandström bloom

6.3.2.1 Estimation of Total Heterotrophic Bacterial count

During the *Proboscia alata* bloom, the total heterotrophic load of associated bacteria on the first day was $30 \times 10^4$ cfu/ml, whereas it increased to $40 \times 10^4$ cfu/ml on the last day of observation. However, in the non-bloom sample, the THB was only $12 \times 10^4$ cfu/ml. (Fig.58).
The variation in total heterotrophic bacterial load between bloom and non-bloom sample was significant (P<0.001, Student-Newman-Keuls-Multiple Comparisons Test).

### 6.3.2.2 Genera wise distribution of bloom associated bacteria

On the first day of the bloom event, the generic composition of the bloom associated bacteria showed the predominance of *Flavobacterium* (25%) followed by *Corynebacterium*, *Acinetobacter*, *Micrococcus* (13% each) and 12% each of *Bacillus*, *Pseudomonas* and *Alcaligenes* (Fig.59).

![Fig.59 Generic composition of bacteria associated with *Proboscia alata* bloom on the first day of observation](image)

But on the last day of the bloom event, the generic composition of the bloom associated bacteria showed the predominance of *Flavobacterium* (40%), and *Pseudomonas* (20%), followed by 10% each of *Moraxella*, *Acinetobacter*, *Bacillus* and *Vibrio* (Fig.60).
6.3.2.3 Genera wise distribution of bacteria from the non-bloom sample

In the reference sample, the predominant forms were *Micrococcus* and *Moraxella* (25% each) followed by 13% each of *Bacillus* and *Alcaligenes*, and 12% each of *Pseudomonas* and *Acinetobacter* (Fig. 61).
6.3.2.4 Hydrolytic enzyme production of bloom associated bacteria

The hydrolytic enzyme production of the heterotrophic bacteria associated with the bloom on the first day showed a high percentage of proteolytic bacteria (36%). Other hydrolytic enzyme producers were amylase and phosphatase (14% each), lipase, alginase, ligninase and cellulase (9% each) (Fig.62).

Fig.62 Hydrolytic enzyme production of bacteria associated with Proboscia alata bloom on the first day of observation

On the last day of the bloom event, the presence of proteolytic bacteria increased to 38%. Percentage of other hydrolytic enzyme producers were cellulase and ligninase (12% each), lipase and phosphatase (11% each), amylase and alginase (8% each) (Fig.63).
6.3.2.5 Hydrolytic enzyme production of bacteria from the non-bloom sample

Hydrolytic enzyme producers in the non-bloom samples showed the predominance of amylase and lipase producers (20% each) followed by phosphatase (17%), protease and cellulase (13% each), ligninase (10%) and alginase (7%) (Fig.64).
6.3.3 Bacteria associated with *Chattonella marina* (Subrahmanyan) Hara et Chihara bloom

6.3.3.1 Estimation of Total Heterotrophic Bacterial count

During the *Chattonella marina* bloom event, the total heterotrophic load of associated bacteria ranged from $10.9 \times 10^4$ cfu/ml on the first day to $175 \times 10^4$ cfu/ml on the last day. But in the non-bloom sample, the THB was in the range of $1.2 \times 10^4$ cfu/ml to $4.9 \times 10^4$ cfu/ml (Fig. 65). The variation in total heterotrophic bacterial load between bloom and non-bloom was significant ($P < 0.001$, Student-Newman-Keuls-Multiple Comparisons Test).

![Fig. 65 Total Heterotrophic Bacterial (THB) count in *Chattonella marina* bloom sample and non-bloom sample](image)

6.3.3.2 Genera wise distribution of bloom associated bacteria

The generic composition of the bloom associated bacteria showed the predominance of *Bacillus*, *Micrococcus*, *Vibrio* and *Flavobacterium* on the first day. In the second sampling, species of *Bacillus*, *Micrococcus*, *Staphylococcus*, *Moraxella*, *Vibrio*, *Streptococcus*, *Flavobacterium* and *Pseudomonas* were recorded, whereas on the last day of the bloom event, the predominant genera were *Flavobacterium*, *Pseudomonas*, *Vibrio*, *Corynebacterium*, *Staphylococcus*, *Listeria*, *Micrococcus* and *Bacillus* (Fig. 66).
6.3.3.3 Genera wise distribution of bacteria from the non-bloom sample

The bacteria in the non-bloom sample comprised mainly of *Bacillus*, *Moraxella*, *Listeria*, *Streptococcus*, *Corynebacterium* and *Staphylococcus* (Fig.67).
6.3.3.4 Hydrolytic enzyme production of bloom associated bacteria

The hydrolytic enzyme production of the heterotrophic bacteria associated with the bloom on the successive days of sampling showed a high percentage of proteolytic bacteria, with a gradual increase from 43% on the first day, 45% on the second day to 48% on the last day (mean 45%). Other hydrolytic enzyme producers were amylase (13%), lipase (11%), phosphatase (9%), alginase (8%), ligninase (5%) and cellulase (8%) (Fig. 68).

![Fig. 68 Hydrolytic enzyme production of bacteria associated with Chattonella marina bloom](image)

6.3.3.5 Hydrolytic enzyme production of bacteria from the non-bloom sample

Hydrolytic enzyme producers in the non-bloom samples were amylase (21%), protease (20%), cellulase (17%), phosphatase (16%), lipase and alginase (13% each) while none of the strains were able to produce ligninase (Fig. 69).
6.4 Discussion

Interactions between bacteria and harmful algal bloom have been considered as an important factor regulating the population of microalgae (Doucette et al., 1998). In the present study, a considerable increase in the culturable bacterial community has been observed in the bloom sample. In all the three bloom events observed, total heterotrophic bacterial count was found to be higher in the bloom samples than in the reference samples. There was a gradual increase in heterotrophic bacterial population from the first day to the last day in the bloom events of *P. alata* and *C. marina*.

THB was found to be maximum during the decline stage of the bloom indicating the probable role of bacteria in bloom termination. Hence it can be assumed that during the algal bloom event, there is a considerable change in associated bacteria, the number slowly increases from the initial stage and reaches its maximum during the decline stage of the bloom. These associated
bacteria must have played a crucial role in bloom dynamics, some acting as beneficial ones supporting the bloom and another group playing a detrimental role in bloom decline. Previous studies have also shown that bacterial community change quantitatively during an algal bloom and this may either play a beneficial or detrimental role in controlling algal growth (Doucette, 1995; Doucette et al., 1999).

The bacterial-algal bloom relationships involve more than just trophic interactions and ultimately reflect a balance between processes inhibitory and/or stimulatory to the organisms involved. Gamma-proteobacteria, beta-proteobacteria and Cytophaga-Flavobacterium-Bacteroides (CFB) are the major bacterial groups reported to have close association with algal blooms (Rooney-Verga et al., 2005). Gamma-proteobacteria frequently encountered in the algal bloom fields act as a potentially significant factor in the bloom decline (Skerratt et al., 2002). CFB group of bacteria are also reported to have algicidal activity (Doucette et al., 1999) and like gamma-proteobacteria, this group also could be important in the bloom termination. Based on several reviews, about 50% of the algicidal strains belong to the CFB group, while about 45% are members of gamma-proteobacteria; the remaining strains represent the gram-positive genera Micrococcus, Bacillus, and Planomicrobium (Fandino et al., 2001; Fukuyo et al., 2002; Mayali and Azam, 2004; Hare et al., 2005; Jasti et al., 2005).

During C. marina bloom, it was clearly noticed that there was a gradual increase in Flavobacterium, gram-negative gamma-proteobacteria such as Pseudomonas and Vibrio, and gram-positive Micrococcus from initial stage to the decline stage of the bloom. The bacterial genera which was abundant especially at the decline stage of bloom was absent or present in very few
numbers in the non-bloom samples. Likewise, it was also noticed that during the *P. alata* bloom event, as the bloom reached its decline stage, the predominance of associated bacteria mainly shifted to *Flavobacterium*, with other members of the gamma-proteobacteria like *Pseudomonas, Vibrio* and *Moraxella* having an increased percentage composition as compared with the first day of the bloom event.

During *P. parvum* bloom also the predominant bacterial genera were *Flavobacterium, Pseudomonas* and *Vibrio*. So, in all the bloom events studied, the predominant associated bacteria comprised of members of gamma-proteobacteria and CFB groups and its abundance was also found to be increased in the successive stages of the bloom event with a peak in the decline stage of bloom. The relative difference in the composition and abundance of the associated bacteria in the bloom samples with non-bloom samples indicated its specific association behaviour. These findings were positively correlated with the recorded reports that in early stages of algal blooms bacteria often are virtually absent or less in abundance (Azam and Ammerman, 1984; Lancelot and Rousseau, 1994), whereas late bloom stages coincide with increased colonization by associated bacteria (Lancelot and Rousseau, 1994; Smith *et al.*, 1995). Recently, Yang *et al.* (2012) also noticed the abundance of gamma-proteobacteria populations significantly during the decline phase of *Akashiwo sanguinea* bloom.

The association of bacteria on algae was complex and diverse in the sense of many effects on algae (Imai *et al.*, 1995; Lovejoy *et al.*, 1998; Lee *et al.*, 2000). The algicidal effect of the associated bacteria could play a vital role in the algal bloom dynamics especially of the bloom termination (Liu *et al.*, 2008).
In a natural system the algae lytic bacteria closely respond to the algal bloom dynamics; as bloom proceeds through their initiation, maintenance and decline stage, the relative algicidal bacterial abundance also increases (Doucette et al., 1999), ultimately reaching the threshold concentration, where algicidal activity becomes detectable and leads to the rapid destruction of algal cells (Fukami et al., 1992; Mitsutani et al., 1992; Imai et al., 1993). During the decline stage, the abundance of the algicidal bacteria become high in number and maintain a top-down control mechanism (Liu et al., 2008).

The algicidal effect of *Flavobacterium* sp. (Yoshinaga et al., 1997), *Pseudomonas* sp. (Baker and Herson, 1978; Yoshinaga et al., 1997; Lee and Park, 1998; Kitaguchi et al., 2001), *Vibrio* sp. (Ishio et al., 1989; Yoshinaga et al., 1997; Wang et al., 2010) and *Micrococcus* sp. (Park et al., 1998) against different microalgae have already been documented.

Usually the mode of action of algicidal bacteria are of two types, those which attack algal cells through direct contact and others which attack through the release of a dissolved lytic agent (Wang et al., 2005). Approximately 30% of the phylogenetically classified algicidal bacteria attack their target algal species through direct contact, and approximately 70% of algicidal bacteria exhibit an indirect mode of attack where dissolved lytic agents, especially extracellular metabolites, are released into the surroundings that effectively antagonises algal cells without the need of physical contact (Hare et al., 2005).

Many algicidal bacteria exert their effects on algae through extracellular protease (Lee et al., 2000; Wang et al., 2012). So, the hydrolytic enzyme production potential of the bloom associated bacteria was assessed. The percentage of protease producers were very high in the bloom sample. During
C. marina bloom, the percentage of protease producers was significantly higher when compared with the other hydrolytic enzyme producers and a gradual increase in protease producers was noticed from the initial stage to the decline stage of the bloom event. But in the non-bloom sample, such an increase in protease producers was not observed. Similarly, the hydrolytic enzyme production potential of the associated bacteria of P. alata on the successive days showed a significantly higher number of protease producers when compared with other enzyme producers and a gradual increase in protease producers was found in the decline stage of the bloom. Similar phenomenon was also observed during the P. parvum bloom event. Among the various genera associated with HAB, Flavobacterium, Pseudomonas and Vibrio were found to be more potent proteolytic bacteria in all the bloom events. The occurrence of higher number of proteolytic bacteria was found to be unique in all the bloom events. The proteases produced by the bacteria were found to have algicidal activity. Lee et al. (2000) reported the algicidal activity of the extracellular protease produced by the strains of Pseudoalteromonas against the diatom Skeletonema costatum. Recently, Wang et al. (2012) also documented the algicidal effect of the protein produced by two algicidal bacteria, Vibrio and Pseudoalteromonas, against the toxic dinoflagellate Alexandrium tamarense. The unique nature of the associated bacterial composition, abundance, high proteolytic activity and its gradual increase at the time of bloom declination in all the present bloom events pointed out the specific nature of the bloom associated bacteria and its significant role in the bloom dynamics especially of the bloom termination.