Chapter 17

The Mechanism of Ecosystem Restoration and Resilience of Present-Day Coastal Lagoons by Coastal Diatoms and Their Implications for the Management of Successional Diatomite Landscapes

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Abstract Diatoms of coastal lagoons have been known to be excellent proxies of their environmental changes and are excellent proxies for eco-resilience given their capacities for achieving alternate stable states despite being impacted by extreme events such as floods. Thus, the coastal lagoon diatoms can be major agents of the restoration of the ecosystem statuses from a primary production perspective, slowly leading towards natural restoration of the ecosystem services. The present work illustrates this hypothesis through an example of natural restoration and resilience building of a coastal lagoon ecosystem, Pulicat lagoon in the aftermath of the 2015 South India. The factors contributing to the restorative processes and the mechanism of the building of resilience are illustrated. Further, a discussion based on the findings extends this understanding to the ecological successional events and transformation into diatomite landscapes with an abundance of diatom-rich sediments and diatomaceous earth as futuristic natural resources. The implications of the current study with respect to both the present-day diatom-rich lagoons and the possible futuristic diatomite landscapes are presented.

Keywords Coastal diatoms · *Biddulphia* sp. · Pulicat lagoon · Diatomite · Diatomaceous earth · Eco-resilience

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17.1 Introduction

Ecosystem changes pertain to differential spatio-temporal scales and are more dynamic in ecotonal regions where the lateral and vertical changes in environmental characteristics are quite evident. The transitionary nature of the ecosystem changes at ecotones, such as coastal lagoons, makes the biotic indicators such as diatoms quite functional proxies of these changes from the environmental monitoring perspective. From the species assessment perspectives, diatoms also function as keystone species (e.g. *Skeletonema costatum*) influencing the biogeochemistry of the marine and coastal ecosystems with their broad as well as extensive links to silicate and phosphorus recycling within these ecosystems (e.g. Smayda 2011). Some characteristics of diatoms such as cell sizes, formation of the benthic resting states, the xanthophyll cycle pigments, etc. can be used to study the nature of changes undergone by the diatom cells in response to the changes in the ambient environment. Recently, these changes have been linked to stressors of anthropogenic origin and from the climate change perspective, which determine that the extent to which the biogeochemistry of these waters have also been altered resulting in the morphological or functional traits in the diatoms.

From the resilience perspectives, the presence of diatoms is also a unique indicator of the stable and alternate states. For example, the changes in the composition or the abundances of diatoms are indicators of the magnitude of influence of the forcing environmental factors operating within the ecosystem, which cause the changes in the stable states (Seddon et al. 2011). Natural events such as cyclonic storms and coastal flooding can also alter the stable ecosystem states which are well reflected by the diatom assemblages (e.g. Nodine and Gaiser 2014; Santhanam et al. 2018). Changes in ecological stoichiometry, for example, are reflected in the abundances of diatoms which can easily dominate the pelagic algae in the abundances of silicates—a stable proxy of environmental statuses over a long period of time. Santhanam et al. (2018) reported a sudden bloom of *Biddulphia* sp. in Pulicat, a coastal lagoon ecosystem which had been subjected to the effect of acute desalination in the aftermath of the 2015 cyclonic storm event in the Bay of Bengal (Santhanam and Natarajan 2018) which altered the ecosystem status of the lagoon.

Long-term responses of diatoms to changes in the stoichiometry have indicated the onset of nutrient disequilibrium and changes to the biomasses, which lead to the development of long-term stable states. For example, in the case of the blooms of the diatom, *Phaeocystis globosa*, which does not have any grazing pressure from zooplankters such as the copepods, the addition of nutrients to the coastal systems in North Sea translated into a very low transfer efficiency of the biomass (Gasparini et al. 2000). This in turn increased the abundances of the *P. globosa* leading to severe blooms above threshold statuses and probably resulting in low resilience. Figure 17.1 shows the ecological and biological factors related to diatoms which can be considered towards utilising them as robust proxies of eco-resilience in a coastal lagoon ecosystem.

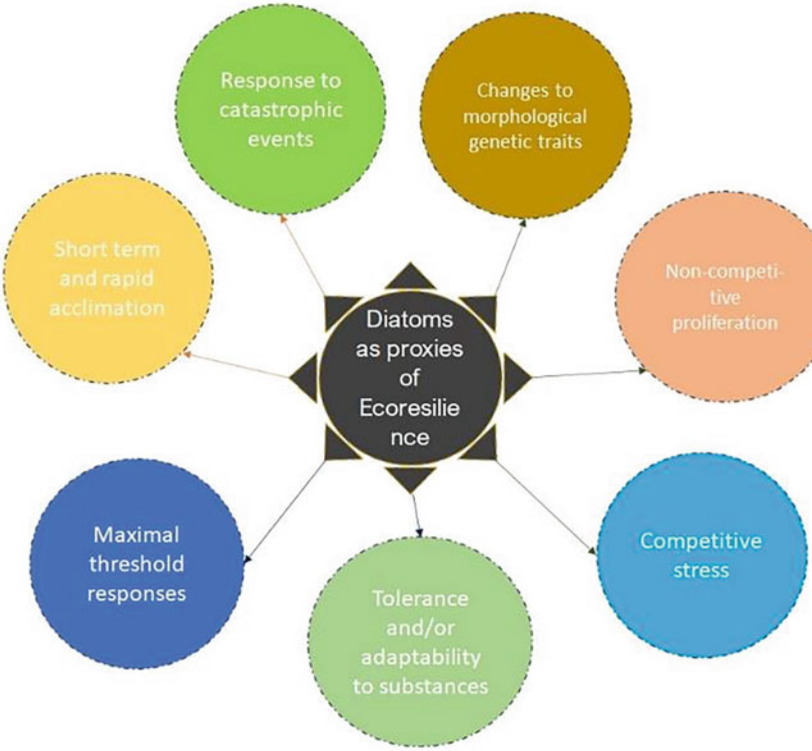

Fig. 17.1 Characteristics of diatoms which render them as suitable proxies of eco-resilience

17.2 Diatoms as Proxies of Eco-Resilience of Coastal Lagoons

The establishment of eco-resilience of coastal ecosystems depends on identifying and quantifying the thresholds and threshold responses to determine the changes in the alternate stable states. Diatoms are significant proxies which can help in identifying the threshold status; for example, Seddon et al. (2011) illustrated that the diatoms' responses to fast and slow processes in coastal systems can help to frame the policies to maximise resilience in coastal systems.

The complexity owing to the highly dynamical nature of the coastal ecosystems can be overcome to determine the changes in the stable states using the abundances and presence of diatoms. Virta et al. (2019) reported that using the diatom linkages to the changes in the sediment organic matter (OM), changes in the ecosystem productivity could be determined. Factors such as changes in the OM, precipitation and run-off quality impact the diatom communities, which directly affect the overall productivity; hence, diatoms can be useful indicators of the low and high production

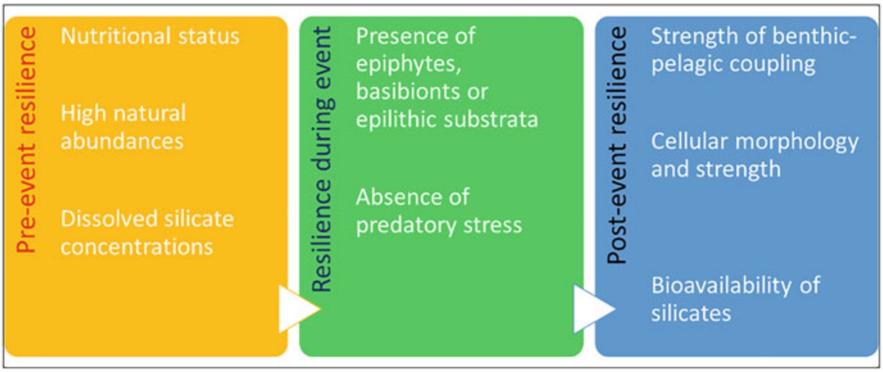

Fig. 17.2 Diatom-specific factors facilitating high resilience to natural hazard events such as floods in the pre-event, event and post-event phases in coastal lagoon systems

rates, which also signify the changes to the stable states. This observation is quite relevant to the relationships of the diatoms to the ecosystem services of coastal ecosystems. Figure 17.2 shows that the presence of dissolved silicates plays a major role in the increases in the diatom abundances or onset of blooms.

Xu et al. (2021) investigated the effects of acclimation and adaptation of coastal diatoms to environmental stressors, which influenced the ecosystem resilience with respect to arsenic. The study illustrated that short acclimation times and mid to high adaptations provided long-term resiliencies to three species of diatoms which are also globally distributed (*Phaeodactylum tricornutum*, *Thalassiosira pseudonana* and *Chaetoceros mulleri*). Coastal diatoms further possess the three criteria which make them robust functional proxies for resilience to climate change, namely, diversity, connectivity and adaptive capacity (Bernhardt and Leslie 2013).

17.3 An Illustrative Example of a Resilient Lagoon Ecosystem from India: Pulicat Lagoon

It is evident from the preceding discussion that factors such as the diatom cell morphologies, strength of the silicate shell, diatom type (whether centric or pennate), propensity for their epilithic and/or epiphytic existence and high nutrient concentrations (Fig. 17.2) provide them with high adaptative responses and the survival rates even under extreme conditions of local weather and/or the effect of high tidal circulation, water currents, etc. Thus, diatoms exhibit an inherent capacity for resilience and can be the drivers of the same within an ecosystem by promoting feedback mechanisms which kick-start the growth and proliferation of other phytoplankter groups, thereby leading the biotic-abiotic environmental responses which help to build the capacity for eco-resilience over the different trophic levels. In this way, diatoms can be considered the ‘model’ biota for investigating and developing nature-based, eco-resilience building measures which can be forged through human-mediated conservation practices for collapsing or collapsed coastal lagoon systems as per the Red List of Ecosystems (RLE) classified by the IUCN (Keith et al. 2013). This central idea is examined using a recent occurrence on the bloom of *Biddulphia* sp. provided in Santhanam et al. (2018) which is discussed in this section.

Biddulphia sp. are cosmopolitan oligohalobous to mesohalobous centric diatoms described as early as 1900 (Boyer 1900). The species of Biddulphia which have been recorded in the coastal waters of India are *Biddulphia mobiliensis*, *B. obtuse*, *B. pulchella*, *B. sinensis*, *B. tuomeyi* and *B. heteroceros* (Subrahmanyan 1946). Of these, *Biddulphia mobiliensis*, *B. obtuse*, *B. pulchella*, *B. sinensis*, *B. rhombus*, *B. longicrurus* and *B. heteroceros* are reported from the coastal waters of Bay of Bengal near Chennai (Subrahmanyan 1946). Redekar and Wagh (2000) reported the presence of two species from the western coast: *Biddulphia regia* and *B. sinensis*. The presence of a protective shell made of silica with concatenating or attached frustules in alternate angles and the presence of valves, well-developed spines and marked reticulations, granules or puncta characterise the diatom (Boyer 1900). The dominance of diatoms in the regions of 13°N latitudinal as well as the monsoon seasonal preference of the species of *Biddulphia heteroceros* and *B. mobiliensis* were observed. The characteristics and morphologies of *Biddulphia* sp. from the coast of India that are important in building its resilience and adaptive capacities are given in Table 17.1.

Pulicat lagoon, a restricted-type coastal lagoon ecosystem of about 450 km^2 situated in the south-east coast of India (13.3 and 13.6°N and 80.23 to 80.25°E), underwent extensive desalination during the recent 2015 South India flood event, owing to an influx of a huge volume of nutrient-laden freshwater from the rivers, which was reported in detail in Santhanam and Natarajan (2018). The salinity variation in the lagoon has been well documented (e.g. Santhanam and Amal Raj 2019). However, the desalination of the brackish water system was found to be phenomenal (~40%) which impacted the ecology and biotic distributions in short term (~ 3 months) before the natural seaward exchanges resumed. These changes were studied using diatoms in the surface sediments as proxies and in the post-flood scenarios; the development of the eco-resilience was largely reported coinciding with a bloom condition of the diatoms of *Biddulphia* sp.

Earlier studies had suggested a large presence of diatoms in sediment cores in general (Farooqui and Vaz 2000) and specifically *Biddulphia* sp. in Pulicat in the southern regions close to a river mixing zone (Araniar river zone). This area, which is within the limits of tidal influence, acts as the ideal niche for marine diatoms travelling into the lagoon from the sea. On the other hand, the northern portions of the lagoon, closer to another zone of river influx (the Kalangi river), were dominated by diatoms such as *Pleurosigma*, *Nitzschia*, *Gyrosigma*, *Navicula* and *Coscinodiscus*, while no dominance of *Biddulphia* sp. in the northern sectors had been reported prior to the 2015 flood event.

The presence of *B. sinensis* and *B. mobilinesis* from the central portions of the lagoon was observed alongside predominant macroalgal/weed vegetation (about 450 g/L and 230 g/L in the central and north-eastern sectors; Ramesh 2000);

Table 17.1 Species, specific characteristics and habitats of diatoms belonging to Biddulphiaeceae observed at or near the south-east Indian coast (compiled from Subrahmanyan 1946; Venkataraman 1958; Kociolek et al. 1983; Redekar and Wagh 2000)

Species	Cell shape	Horns and processes	Valve spines	Valve surface characteristics	Aerolation	Length of apical axis	Habitat
Biddulphia heteroceros Grunov	Squarish or box-shaped	Presence of strong, polar horns	Presence of small spines	Higher between spines	9–10 areolae in 10 μ	45–48 μ	At the bottom mud of saline pools
Biddulphia mobiliensis Bailey	Linked in small chains	Horns unite the individual cells	Presence of two slender long spines	Surface flat between spines	Yes, sizes not available	26.6–76 μ	At the bottom mud of saline pools
Biddulphia pulchella Gray	Elliptical with undulating cell margin	Not described	Spines with long sutures	Middle part of the valve is raised	5–8 areolae in 10 μ	95–152 μ	Epiphytic on *Chaetomorpha* sp.
Biddulphia rhombus (Ehren)	Elliptical with rectangular girdle view	Presence of stout horns	Presence of two long spines	Siliceous valve with chromatophores, elliptic-lanceolate	On the valve: 9 in 10 μ; on the girdle: 12–14 in 10 μ	26.6–34.2 μ	Epilithic on pebbles immersed in seawater, epiphytic on Lyngbya and Polysiphonia; rarely pelagic
Biddulphia biddulphiana Boyer	Colonial cells united by their angles to form short chains	Swollen margin	Presence of strong coastae described	Elliptic with swollen margins, strongly sculptured, divided into 3 sections by the costae; girdle punctate in longitudinal lines	Yes, arranged in longitudinal and transverse rows, sizes not available	Not available	At the bottom as well as epiphytic
Biddulphia aurita (Lyngbye)	Box-shaped cells united by a thick mucilage pad over	Obtuse, marginal short processes	No central spine	Elliptical-lanceolate valves are present and the girdle zone is divided by a deep	Punctuated aerolae, 8–10 in 10 μ	24–30 μ	Littoral species is epiphytic on *Polysiphonia* sp.

	a zigzag chain that remains attached			groove with distinctive intercalary bands. The valve centres are almost flat but are sub-centrally depressed; strongly siliceous; numerous centrally-aggregated chromatophores			
Biddulphia dubia Cleve	Rhomboid, lanceolate and four sided	A stout horn-like process is observed from the side view of the valve at two angles, a short blunt process is noticed at another angle	Surface of valve may be perceived to either possess small spines or a raised wall of reticulations	Strongly sculptured, valve margins are striated; cell wall is quite strongly silicified and coarsely reticulated which may be irregular/quadrangular/heptagonal and unequal in size about 1.5–3.0 mesh per 10 μm; irregular to short cylindrical centrally aggregated chromatophores	Yes, irregular aerolation; sizes not available	30–55 μm	Littoral and benthic
Biddulphia laevis Ehr.	Zigzag filamentous colonies of short length containing up to 50 cells connected with mucilage	Stalked ocelli-like labiate processes bordered by a thin distal rim containing many porelli on external valve face	Peripheral spines present	Depressed ovoid centre with elevated circular area surrounding it	Yes, radial aerolae; 14–16 in 10 μ	40–60 μ	Epiphytic on *Cladophora glomerata*

however, their abundances are not available. Although short-lived mixed blooms of *Rhizosolenia*, *Chaetoceros*, *Biddulphia*, *Coscinodiscus*, *Thalassionema*, *Thalassiothrix* and *Bacteriastrum* and also species like *Skeletonema costatum* and Asterionella *japonica,* etc., had been reported from the southern sector (Kaliyamurthy 1975), the first record of a dominant *Biddulphia* sp. bloom at Pulicat in a post-flood scenario was evident after the 2015 event (Santhanam et al. 2018).

Qasim et al. (1973) reported that populations of *Biddulphia sinensis* dominated the Cochin backwaters under high nutrient concentrations of phosphorous and nitrate (singly or in combination) during monsoon months. *Biddulphia* sp., being large celled, possess a primary advantage by virtue of their sizes to attain greater half-life saturation states with respect to nutrient concentrations, outdoing even fast-growing but smaller-sized dinoflagellates such as *Ceratium furca (Ehrenberg)* (see Qasim et al. 1973). Studies by Castenholz (1964) and Humphrey (1979, 1983) suggested that *Biddulphia* sp. favoured underwater spectral illumination at lower wavelengths close to violet regime and shorter photoperiods (15 h) for greater growth and assimilation. Such studies illustrate the ability of *Biddulphia* sp. to grow abundantly rapidly even under low light, high turbidity as well as high flow conditions in the estuaries which are prevalent in the monsoon seasons.

Like most diatoms, *Biddulphia* sp. is known to lead an epiphytic and/or epilithic existence. *B. pulchella* have also been observed to be attached at the valve to another algae, *Lyngbya*, by mucilage and is found to be dominantly epiphytic on *Lyngbya* and *Polysiphonia.* Govindasamy and Anantharaj (2012) described the epiphytic existence of *Biddulphia pulchella* on the leaves of seagrass species *Enhalus acoroides* in Thondi coastal region (Southern Tamil Nadu coast)—a first record ever of such epiphytic existence of *Biddulphia pulchella* observed in January 2010. It is interesting to note that although another genus of seagrass, *Cymodacea serrulata*, is most predominant along the coast, epiphytic *B. pulchella* were observed from the leaves of *E. acoroides*. This interesting result indicates that the 'host' seaweed/seagrasses or macroalgae chosen for epiphytic existence of *Biddulphia* sp. could be quite selective under different environmental conditions.

Aziz (2005) reported planktonic and attached forms of *Biddulphia* sp. from the North-eastern Bay of Bengal along Bangladesh in bloom condition consisting of *B. aurita*, *B. dubia* and *B. pulchella*. While *B. aurita* (in blooms observed in July–September) was observed in a mixed bloom state alongside *Asterionella glacialis*, both *B. dubia* and *B. pulchella* were observed to be largely epiphytic forms: formerly on *Polysiphonia* sp. and the latter with both *Lyngbya* sp. and *Polysiphonia* sp.

Microzooplankton such as the copepods—*Calanus* sp. and *Eucalanus* sp.—are known to extensively feed on diatoms including *Biddulphia* sp. (Corner et al. 1972; Madhu et al. 2007). Other predators include the protozoans, *Tintinnopsis* sp., and exclusive filter feeding molluscan bivalves and oysters such as *Mytilus* sp., *Perna* sp. and *Crassostrea* sp. (e.g. Kasim and Mukai 2006). These predators including copepods and clams such as *Mytilus edulis* and *Perna viridis* are well distributed in Pulicat lagoon; *Crassostrea madrasensis* has been described to be the keystone species (Sanjeeva Raj 2006). However, the absence of these predatory influences as evidenced by the sedimentological analyses presented in Santhanam et al. (2018)

suggests that the diatoms, which were robust survivors of the flood conditions, benefitted by the absence of direct predators. It is interesting to note the low abundances of the resident pennate diatoms such as *Navicula* sp. which are usually quite unaffected by fluctuation in nutrient concentrations compared to centric diatoms as *Biddulphia* sp. (e.g. Mitbavkar and Anil 2002) were quite low in abundances compared to the latter in a post-flood scenario. The extensive reworking of the sediment observed at these sites combined with the habitat preference of pennate types towards the central and northern portions of the lagoon can explain this observation quite well. At site 1 close to the bar mouth, several specimens of tintinnids both separated and unseparated from their lorica were observed (Santhanam et al. 2018).

It is interesting to note the associative factor in the adaptative response to the flood which lead to the survival and resilience of *Biddulphia* sp. The diatoms of this species appear to have found a natural ally surprisingly not a competitor in the robust *Cladophora sp.* compared to other algae (e.g. pelagic diatom *Polysiphonia* or *Lyngbya*) and seagrasses (e.g. *Halophila* sp.). The latter seems to have been the source for its repository of nutrients (especially Si) as well as refuge to *Biddulphia sp*. Such close epiphytic association of *Biddulphia laevis* and *Cladophora glomerata* had been described in detail by Kociolek et al. (1983) in the Ohio river estuary, USA. The latter factor must have offered a comfortable substratum as well as protection from stronger currents (an obvious disadvantage for the pelagic diatoms prominent from their absences as observed during the microscopic survey (Santhanam et al. 2018). Another important consideration is the possible loss of seagrass beds (*H. ovalis*, etc.) observed in the lagoon with lowering of salinities (Lynda Keren and Moses Inbaraj 2013), making them unavailable to *Biddulphia* sp. for epiphytic association as was reported elsewhere (see Govindasamy and Anantharaj 2012).

With both organisms capable of surviving in lower salinities, the rapid growth and sustenance of both species must have been coincidental with the rapid increase in cell size and reproduction of *Biddulphia sp.* being greater than that of *Cladophora sp*. Further, given the fact that benthic diatoms can resuspend into the water column by the wind-stimulated turbulence provided both algal groups with a rich nutrient scape with just sufficient light condition for phototrophic fixation. The competitive stresses from microphytobenthos and phytoplankton could have been quite negligible as is observed during the monsoonal seasons (e.g. Sanilkumar et al. 2011). These factors working in favour of *Biddulphia* sp. has resulted in the formation of a ‘bloom’ condition, which also kick-started the recovery to brackish conditions.

It is also important to relate to the influence of concentrations of the silicic acid on the productivity of the diatoms in the lagoon. The northern regions (site 7 especially; Fig. 17.3) seem to have contributed more to the silicic acid concentrations in the lagoon (Santhanam et al. 2018). Silicate is highly soluble in alkaline conditions, and the higher concentrations of silicate ions in the hydroxide form are observed whenever the pH is found to be alkaline in the lagoon. The more alkaline northern regions thus show higher concentrations than the southern regions; furthermore, the riverine contribution of silicate to the system is higher from the Kalangi river rather than in the Araniar river. Although the availability of silicates is greater in the

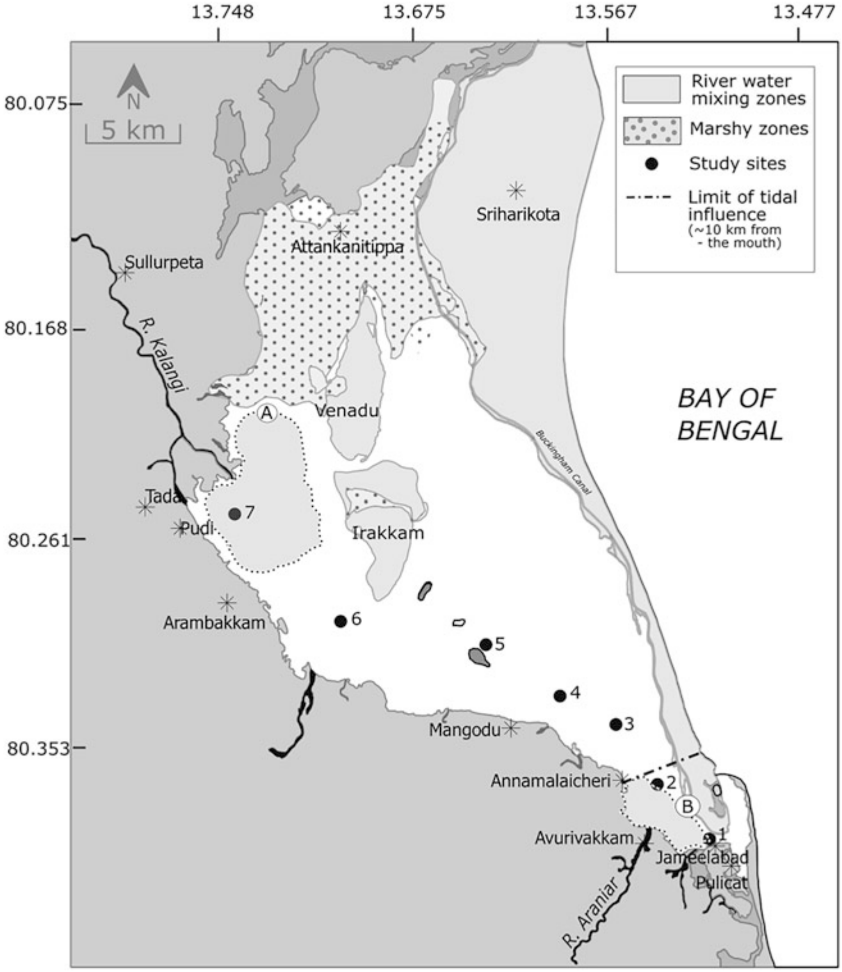

Fig. 17.3 Map of Pulicat lagoon ecosystem in South-east India showing the sampling locations (black dots). The regions under freshwater influence from the rivers Kalangi (NW) and Araniar (SW) are marked A and B with sampling sites 7 and 2, respectively, which are the low saline zones. The predominantly active southern mouth connects the lagoon with the adjacent sea, Bay of Bengal; the dot-dash line shows the limit of tidal influence within the lagoon (~10 km from the mouth; sources: Raman et al. 1977; Thangavelu 1983)

northern regions, its influence as a limiting factor for diatoms is well observed in the southern region which can reflect the trend during high-flood events as in the present case. The stagnation of the central region as illustrated from its salinity characteristics combined it the prevalent N and Si limitations in monsoon seasons renders it impossible for the onset of blooms here. However, the 2015 floods illustrated the alleviation of the generally Si-limited situation prevailing under ambient conditions in the southern zone which in combination with higher nitrates are responsible for sustaining bloom conditions.

17.4 Discussion and Conclusions

The concept of monitoring and assessing the eco-resilience of ecosystem was the central theme presented here. It is interesting to note that among the different diatoms, the strength of the siliceous skeletons of the large, centric diatoms like *Biddulphia sp.* seems to be advantageous to resist damage from impacts and help with sustenance during such high impact events such as cyclone-induced floods. With their established ability to rapidly utilise the available nutrients under a high-nutrient, high-turbid environment, *Biddulphia* sp. produced a bloom as observed during the study. This example illustrates the following implications for building eco-resilience at the ecosystem level even for collapsing ecosystem as Pulicat threatened by anthropogenic activities:

1. Diatoms such as *Biddulphia* sp. are important proxies for post-hazard monitoring of eco-resilience in coastal lagoons. They can hence indicate the levels of success of eco-restoration of the lagoons.
2. The case of Pulicat illustrates the important roles of robust diatoms in supporting primary production of lagoon ecosystems and hence can be explored for their applications as nature-based solutions (NbS) for ecosystem recovery, with special reference to post-flood scenarios in the absence of anthropogenic pressures.
3. The presence of diatoms from collapsed ecosystems which have transformed to dry landscape remains to be good indicators of the flood-bearing capacity of these regions which can be used as excellent markers for planners to build flood-resilient landscapes.

Over longer time periods of the order of thousands of years, the drying up of the lagoon beds with rich accumulation of such diatoms can produce diatom-rich substrata or sediment (DRS), which become diatomite ‘rocks’ (diatomaceous earth, DE; sedimentary layers rich in silicates) of the landscape. Thus, through successional conversion of the erstwhile wetland/lagoon systems into drier landscapes, the fossilised and sub-fossilised diatoms of older wetlands become ‘ores’ of the diatomite.

While diatomaceous earth remain critical substances for inexpensive, inert and durable filtration media over industrial processes and in manufacturing at present, there remain possibilities of their exploitation through excessive diatomite mining in the near futuristic scenarios. It needs to be recognised that though diatomite is deemed to be an extensive and ‘inexhaustible’ resource currently, with most resources located in Rajasthan and Gujarat, continual mining corresponding to demand for industrial use of DE can lead to their exploitation. Unregulated mining in futuristic scenarios may contribute to degradation of the land and the loss of the capacity of the dry diatomite landscapes to act as natural filters for the waters flowing downstream through the floodplains.

In conclusion, it is suggested that the observations presented herein need to be considered as part of the scientific efforts to build diatom-based natural resource management models focussing on the eco-resilience building initiatives of the present-day natural lagoon landscapes:

1. The adaptative capacities of the different diatoms must be researched to reconstruct the manner of natural recovery of lagoon ecosystems to floods and inundations. This will be useful to plan for successful wetland restoration and disaster risk reduction in the present day.
2. The links between diatoms, their epiphytes and epilithic associations are crucial to assess the extent to which successful natural restoration activities can be planned for lagoon systems in India.
3. Assessment of environmental risks associated with diatomite mining from ancient floodplains and coastal lacustrine environments must be extended to the studies on the ecosystem services assessments for present-day lagoon environments with diatom-rich benthic environments such as Pulicat and Chilika.
4. NbS-based assessment to capture the natural asset values of diatoms to wetlands and coastal lagoons must be facilitated in the present-day scenario to avoid any futuristic exploitation of these value resources.

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