Chapter 2
Review of Literature

This chapter highlights the major studies and findings of the previous research work carried out on phytoplankton ecology, phytoplankton diversity, size classes, carbon cycling by phytoplankton, their optical properties and its applications for remote sensing.
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Life in oceans has been known since life is known to exist on the earth. Since then evolutionary changes have occurred and ecological stability has fluctuated along with these changes. Ecological and evolutionary revolutions set by the geological shifts, environmental conditions and catastrophic events have caused changes and disturbances in the stability of these life forms from time to time (Zachos et al. 2001, 2008; Knoll 2003). In the present era, environmental conditions influenced by human activities has greatly altered and threatened marine communities and ecosystems (Jackson, 2010). Also the prevailing climate change conditions have severe impacts on species biodiversity and seasonality (Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003; Rosenzweig et al., 2008; Thackeray, 2012).

Among all life forms, planktons are the most sensitive indicators of the climate change as their growth and development are directly dependent on temperature (Taylor et al., 2002; Hays et al., 2005; Richardson, 2008; Adrian et al., 2009). Changes in water temperatures have caused shifts in the seasonal timings of the plankton population growth (Edwards and Richardson, 2004; Adrian et al., 2006; Thackeray et al., 2008, 2012; Berger et al., 2010; Schluter et al., 2010). Recent works of Huber et al., 2008; Thackeray et al., 2008; Feuchtmayr et al., 2010, 2012 and Thackeray, 2012 has shown that in case of phytoplankton, it is not only the temperature but shifts in the seasonal cycles can also be attributed to nutrient loading. Thus it is a set of various environmental factors and their interaction that governs the growth of phytoplankton in a complex ecosystem.

2.1 Phytoplankton ecology:

One of the major challenges faced by the marine ecologists is, to understand the influence of environmental factors, in altering the phytoplankton communities. Phytoplankton assemblages with reference to species richness, stability and succession have significantly shorter operational time scales (Scheffer et al., 2003; Reynolds, 2006). As pointed out by Reynolds (1993), plankton succession sequences accommodated between two winters are comparable to the number of generations that
have occurred since the Weichselian glaciation period in temperate forests. It is therefore practically discernible to observe spatiotemporal patterns of phytoplankton to get a better understanding of the ecological factors influencing it (Reynolds, 2006).

According to the “paradox of plankton”, the violation of Hardin (1960) principle of competitive exclusion from the phytoplankton communities, a large number of species, inhabiting similar environmental conditions, can compete for essentially the same limiting resources. Hutchinson (1961) further explained the plankton paradox by stating that continuous variations in environmental conditions are the most obvious factor that induces non-equilibrium phytoplankton dynamics. Since then, various principles to explain the plankton diversity were put forth. Most of them can be classified into the following three categories (Zhao et al., 2008):


2. Tilman, (1982) and Grover, (1997) highlighted that co-existance of multispecies can be attributed to resource based competition leading to tradeoffs, growth strategies and internal response to resource availability.

3. Diversity can be enhanced by the gradual change of temperature and light during the year (Sommer et al., 1986) as well as small scale advections (Karolyi et al., 2000).

Undoubtedly, there is a complex interplay among physical, chemical, and biological factors on the phytoplankton community composition which can be further influenced by climatic perturbations (Padisak et al., 1993). Apart from these natural factors, various anthropogenic activities have increased the nutrient loading (mainly nitrogen and phosphorus) in the coastal waters over the last few decades (Cloern, 2001). This nutrient enrichment may lead to eutrophication (CEC, 1991; Tett et al., 2007). Generally, during eutrophication, there is a mono-specific dominance, which if becomes massive, may turn into harmful algal bloom (Glibert et al., 2005; Heisler et al., 2008). Coastal ecosystems also receive riverine inputs of freshwater with density
much less than the saline marine waters which causes stratification in the water column. Phytoplankton tends to remain in the upper layers of the water column where relative irradiance is higher due to which the blooms remain at the surface of the water. These surface blooms cause shading of the benthic primary producers and thus reduce their growth. The decomposition of dead matter can then cause de-oxygenation. If the nutrient efflux continues, further eutrophication can intensify the ecological imbalance in the coastal ecosystems (McGlathery et al., 2007; Brito et al., 2010, 2012). Phytoplankton communities are sensitive to anthropogenic pressures such as nutrient loading and therefore they are efficient biological indicators of eutrophiaction and can be used to assess the ecological status of the coastal waters (Brito et al., 2012).

2.2 Phytoplankton community structure:

Diatoms and dinoflagellates are the most abundant communities of marine phytoplankton (Lalli and Parsons, 1993). Diatoms generally have rapid growth rates (Furnas, 1990) and tend to flourish in upwelling conditions with high nutrient concentrations as well as enough vertical mixing to maintain their position in the euphotic zone which is essential for non-motile diatoms (Smayda, 1970; Margalef, 1978; Mann, 1993). In contrast, dinoflagellates grow in stratified conditions as they can move from the overlying euphotic zone towards the underlying nutrient-rich waters (Margalef, 1978; Cullen, 1982; Mann, 1993). Dinoflagellates can also maintain their position under the weakly turbulent conditions of a stratified water column due to their motility (Margalef, 1978; Mann, 1993).

Diatoms are the dominant group among all phytoplankton types and exhibit seasonal variation during monsoon and non-monsoon periods (Kitner and Poullickova, 2003). They inhabit regions ranging from small fresh water ponds to massive open oceans (Bendley et al., 2005). They are tiny microscopic organisms with sizes ranging between 2 to 500 µm with complex cell walls made up of silica. They serve as powerful indicators of environmental changes as they are sensitive to nutrient concentrations, pH, conductivity and extraordinary preservation in fossil deposits (Sin et al., 1999 and villac, 2008).
Dinoflagellates, similar to diatoms, are of very common occurrence among the phytoplankton communities and are therefore important primary producers (Sangiorgi and Dongers, 2004; Devernal and Marrel, 2007). Their habit ranges from lakes to open oceans and have a spatial distribution in all latitudes ranging from equator to polar seas (Uzar et al., 2010). Saravane et al. (2000) and Sarojini and Sharma (2001) reported that Dinoflagellates dominate in coastal and estuarine waters.

Other groups of phytoplankton such as cyanophyta, chlorophyta and chrysophyta have very less percent contribution to the total phytoplankton diversity (Naik et al., 2009).

2.3 Studies on phytoplankton community structure and diversity in India:

Similar to studies described in section 2.2, several studies on phytoplankton community structure and diversity (Habib and Chaturvedi, 1999; Jena et al., 2008) showed dominance of diatoms and dinoflagellates in Indian waters. Many workers such as Tiwari and Nair, 1998; Ramaiah and Ramaiah, 1998; Padhi and Padhi, 1999; Gopinathan et al., 2001; Tiwari and Chaudhohan, 2006; Mathivanan et al., 2007; Ramalingam et al., 2008; Panda et al., 2011; Palleyi et al., 2011 and Shivaprasad et al., 2012 have studied species composition and seasonal variations of phytoplankton for coastal and estuarine ecosystems of southern India. Redekar and Wagh, 2000a and c; Bijumon et al., 2000; Mathew and Nayar, 2002 studied diurnal, seasonal and spatial distribution of phytoplankton in relation to different physico-chemical parameters for western coast of India. Such studies on phytoplankton need to be carried out on regular basis as phytoplankton have a very short life cycle. In addition, studies on phytoplankton size classes are also important as size affects the overall growth and physiology of the cell.

2.4 Phytoplankton size classes:

Particulate matter are the major constituents that cause sinking of carbon, nutrients and trace elements in the deeper layers of the water column (Broecker and Peng, 1982; Fowler and Knauer, 1986; Hebel et al., 1986; Lee and Fisher, 1993). Rate of sinking is proportional to the size of the particulate matter (Shanks and Trent, 1980;
Alldredge and Gotschalk, 1988, 1989; Syvitsky et al., 1995) therefore particle size is crucial to predict the potential flux in the vertical column of marine ecosystem. Two types of instruments have been used to measure particle sizes (Stemmann, et al., 2004):

1. Impedance instruments which measure a property that approximately corresponds to the volume of the solid particles composing an aggregate e.g. Coulter Counter have been used for particles with 0.5mm to 200mm in water samples after returning back to the laboratory.
2. Optical instruments that measure light transmission and scattering by a particle or the size of its image. Such instruments have been used to measure in situ particles of with less than 50mm.

Jackson et al., (1995, 1997) combined results from multiple instruments as a means to cover the length spectra ranging from 1mm to 1cm. His studies showed that number of smaller particles was higher but contribution to total mass was higher in larger particles.

Among particulate matter present in the marine ecosystems, phytoplankton acts as the most important carbon sequestrating organism and dominates the mass and abundance of particles in both coastal (Peinert and Miquel, 1994; Passow and Wassman, 1994) and oceanic regions (Billet et al., 1983; Lampitt, 1985; Takahashi, 1986; Sancetta et al., 1992).

In case of phytoplankton, size is an important characteristic in determining both nutrient uptake efficiency and susceptibility to grazing. Smaller size offers increased nutrient uptake efficiency through a greater surface area to volume ratio on the other hand smaller size may also increase susceptibility to grazing (Malone, 1980). To protect themselves from grazing and maintain their surface uptake ability at the same time, some diatoms form chains having hundreds of cells in length (Munk and Riley, 1952). Phytoplankton sizes also correspond with carbon assimilation and sequestration rates especially in the oceanic provinces.
2.5 Carbon cycling by phytoplankton:

In the present conditions, climate change is the most concerning issue of ecologists and policy makers all over the globe. Quantification of carbon cycling through marine phytoplankton is very important to understand the effects and feedbacks of climate change on ocean ecosystems (Emerson and Hedges, 2008; Koeller et al., 2009). Oceans serve as a large area for carbon sequestration but coastal regions are ignored with this respect.

Sequestration of carbon occurs through sinking of particulate matter into the deep ocean floor. After it is utilized by phytoplankton cells for photosynthesis, it passes through various tropic levels, where carbon is released back at intermediate depths due to respiration by heterotrophic organisms. Less than 1% carbon harvested from the atmosphere actually reaches the ocean floor, a very small fraction of it is further sequestered over a geological time scale (Longhurst et al., 1990). To develop a better understanding of ocean carbon cycles, we need to characterize the ecologically meaningful communities of phytoplankton (Gutiérrez-Rodríguez et al., 2010), that although co-exists in similar environment, have different growth rates and physiology (Furnas, 1990; Goericke, 2002; Margalef, 1978). Brown et al., 1999, 2002; Li, 1994; Worden et al., 2004 have investigated the role of different phytoplankton groups in carbon uptake by $^{14}$C –uptake experiments. Atmospheric carbon is fixed as organic carbon through the process of photosynthesis where chlorophyll-a acts as a reaction centre for harvesting light. Chlorophyll-a along with a suit of various other accessory pigments play two important physiological and ecological roles. First, fixing of carbon (through photosynthesis) into organic matter and second is to protect the cell from photodegradation during conditions of intense irradiance. Apart from these two functions pigments also impart a unique property to phytoplankton due to their ability to absorb light at certain specific wavelengths. This property of phytoplankton is termed as optical property and is crucial for their identification through remote sensing.
2.6 Optical studies on phytoplankton:

Pigments present within the phytoplankton cells absorb light which directly contributes to light attenuation in the water column and significantly affecting the optical characteristics of water. The absorption characteristics of phytoplankton population are an important component in models of phytoplankton biomass (Gordon and Morel 1983) and primary production (Platt and Sathyendranath, 1988; Morel and André, 1991; Platt et al., 1995; Sathyendranath et al., 1995) through remote sensing. The spectral chlorophyll \(a\)-specific in vivo light absorption \(a^{ph}* (\lambda)\) provides an estimate of the amount of light absorbed by intact phytoplankton cells from knowledge of ambient irradiance and chlorophyll \(a\) concentration. Chlorophyll \(a\)-specific in vivo light absorption \(a^{ph}* (\lambda)\) also shows significant variations in phytoplankton biomass over regional scales (Hoepffner and Sathyendranath, 1992; Lutz et al., 1996). This variability is due to changes in the abundance of accessory pigments relative to Chlorophyll \(a\) (Bricaud et al., 1983; Sathyendranath et al., 1987; Berner et al., 1989; Sosik and Mitchell, 1991) and changes in cell size as well as pigment concentrations, also known as the package effect (Morel and Bricaud, 1981; Sathyendranath et al., 1987; Mitchell and Kiefer, 1988; Sosik and Mitchell, 1991; Kirk, 1994).

Variations in optical absorption characteristics of opticaical components are well understood and documented for Open Ocean (case 1) waters but very less is known about case 2 waters especially the coastal oceans in terms of its variability and trends (Babin, 2003). With regard to phytoplankton absorption, the sources of variability, pigment composition (Hoepffner and Sathyendranath, 1991) and packaging (Bricaud et al., 1998) are well understood. Many laboratory and field studies over the last two decades have described the extent of variations in optical characteristics and the diversity of spectral signatures for aquatic environments, including Case 2 waters (Mitchell and Kiefer, 1988; Bricaud and Stramski, 1990; Babin et al., 1993, 1996; Johnsen et al., 1994; Sosik and Mitchell, 1995; Cleveland, 1995; Allali et al., 1997; Stramski et al., 2001) but these documentations are not enough to derive trends for coastal waters due to very high variability in biological, physical and chemical conditions.
The Chlorophyll $a$ specific absorption coefficient has been found to decrease from oligotrophic, over mesotrophic to eutrophic waters (Yentsch and Phinney, 1989; Bricaud et al., 1995; Cleveland, 1995). Yentsch and Phinney (1989) suggested that this pattern results from the presence of small cells with high specific absorption coefficients in oligotrophic waters shifting towards larger cells with lower specific absorption coefficients and higher nutrient concentrations in the water. Also Chlorophyll $a$-specific absorption coefficient can vary significantly with different phytoplankton species (Bricaud et al., 1983; Geider et al., 1986; Falkowski et al., 1985; Bricaud et al., 1988). In short, Chlorophyll $a$ specific absorption coefficient is dependent on cellular pigmentation and cell size/morphology, based on interspecies and intraspecies differences, resulting from physiological acclimatisation to varying growth conditions (light, temperature and nutrient availability) (Staehr, 2002). Chlorophyll-$a$ serves as one of the index for estimation of phytoplankton biomass and chlorophyll-$a$ specific absorption coefficient can be used to estimate phytoplankton biomass through remote sensing.

2.7 Relevance of optical properties of phytoplankton for remote sensing:

Interactions between electromagnetic radiation and matter form the base of Remote sensing measurements. The visible region (400 to 700 nm) of the electromagnetic spectrum is the most important band for remote sensing of water quality. Remote sensing has been successfully used to measure chlorophyll concentrations and patterns over open oceans. Most remote sensing studies of chlorophyll in water are based on empirical relationship between band radiances or band ratios and chlorophyll concentration. Measurements from sensors aloft aircraft or satellite have used a variety of algorithms and wavelengths to map chlorophyll of the oceans, estuaries and fresh water. The attenuation of infrared (around 700 nm to 15 m) and microwave radiation (1 mm to 30 cm) is very high in water (Zoloratev and Demin, 1977) and thus can only be used for observing surface phenomena such as algal blooms.

Recent approaches have employed ocean colour data to derive size based phytoplankton functional types, most of which were linked to taxa-specific phytoplankton pigments (Ciotti et al., 2002; Sathyendranath et al., 2004; Alvain et al., 2005). Another classification of phytoplankton functional types was based on
biogeochemical types and included nitrogen-fixers, calcifiers, silicifiers and dimethyl sulphide (DMS) producers (Nair et al., 2008). Conclusively, there are three main streams for developing phytoplankton functional type models: 1) based on size classes (Aiken et al., 2006; Brewin et al., 2010; Ciotti et al., 2002; Ciotti and Bricaud, 2006; Hirata et al., 2008; Kostadinov et al., 2009; Kutser et al., 2006; Uitz et al., 2006, Devred et al., 2011); 2) based on dominant phytoplankton community/genus (Alvain et al., 2005; Bracher et al., 2009; Sathyendranath et al., 2004; Subramaniam et al., 2002) and 3) bio-geochemical types (Nair et al., 2008); but there is no universal definition of phytoplankton functional types.

Following two approaches were explained by Devred et al., (2011) for obtaining information on phytoplankton size classes through remote sensing.

1. The first is based on the phytoplankton absorption characteristics where changes in the spectral properties in association with size structures are exploited. Phytoplankton absorption spectra is equally influenced by cell sizes (Bricaud et al., 2004; Duysens, 1956; Fujiki & Tagushi, 2002; Sathyendranath et al., 2001) and pigments compositions (Ciotti et al., 1999; Hoepffner & Sathyendranath, 1991, 1992; Lohrenz et al., 2003; Sathyendranath et al., 1987, 2005) resulting into the phenomenon termed as packaging effect (Bricaud et al., 2004; Devred et al., 2006a; Sathyendranath et al., 1987) and therefore it is difficult to separate the individual contribution of sizes and pigments on the absorption spectra.

2. The second is based on the measure of chlorophyll-a concentrations (Brewin et al., 2010; Hirata et al., 2008; Uitz et al., 2006) where changes in cell size were observed to change with chlorophyll-a abundance. An established pattern between variations in these two parameters was then used to infer size structure from chlorophyll-a abundance.

Direct attempts for retrieving pico-, nano- and microphytoplankton size classes from absorption coefficients of phytoplankton have been successful (Bricaud et al., 2007). Observations by Aiken et al., 2004; Barlow et al., 2002, 2004; Moore et al., 2005; Fishwick et al., 2006 have shown links between optical properties, phytoplankton
pigment composition and photosynthetic parameters. Besides these, Jeffrey et al., 1997 have shown links between specific pigments and specific taxa.