

Marine heat waves in the Indian Ocean: Characterizing a major climate impact on microalgae

Abstract

A clearly defined, lengthy (five days or longer) period of extraordinarily high ocean temperatures are known as Marine Heat Waves (MHWs) (above the 90th percentile). These events significantly impact the structural, abundance, cell size, metabolic functions, physico-chemical interactions between microalgae cells and their surroundings in the Indian Ocean. In the tropical Indian Ocean, the average sea surface temperature (SST) increased by 1.0°C (0.15°C/decade) on average between 1951 and 2015, while the global average SST warmed by roughly 0.7°C (0.11 °C/decade). This resulted the incidence of Marine microalgal bloom MMBs (including Harmful Algal Bloom) and the number of causal taxa may grow as SST increase. *Trichodesmium* and *Noctiluca* contributed 34.4% and 31.8%, respectively, to the overall blooms. Such heating phenomenon also triggers dominance of small-sized algal cells, harmful diatoms and pico-plankton. The present paper reviews the Indian as well as global episodes of MHWs such as Western South Atlantic, North-East Pacific, Western Australia, Alaskan Sea etc. and their impact on phytoplankton. The combination of warming and heatwaves triggers blooms of buoyant cyanobacteria and its combined impacts of MHWs and ocean warming/acidification on phytoplankton community structure have not been fully studied in the Indian Ocean.

Keywords: Marine Heatwaves, Indian Ocean, Microalgae, Harmful Algal Blooms, Phytoplankton

1. INTRODUCTION

Microalgae are unicellular, microscopic, photosynthesizing organisms that come in a variety of sizes (nano: 2–20 m, micro: 2–200 m, macro: > 200 m), shapes (single,

filamentous, or colonial), and morphologies [1]. Pelagic microalgae, free-floating or moving in the water column, and benthic microalgae, which have settled on sediment or other substrates, may be present (epiphytic microalgae) [2]. In general, microalgae react quickly to changes in their environment. A significant MHW hot spot with mean MHW intensity, duration, and frequency of 1.54°C, 13.33 days, and 1.97 times is located in a region of the (WEIO) Western equatorial Indian Ocean (48°E-54°E, 2°S-2°N). After removing the long-term trend, MHWs in the hot spot region exhibit significant inter-annual variability that is linked to the primary climate modes of the Indo-Pacific [3]. Less research has been done on and documentation of MHWs in the tropical Indian Ocean (TIO). Sea surface temperature (SST) variability in the TIO is impacted locally by the (IOD) Indian Ocean Dipole and remotely by (ENSO) El Niño Southern Oscillation occurring in the Pacific [4]. The Sumatra-Java coast, the Seychelles dome, and the western TIO are the three major upwelling locations in the TIO that experience considerable SST changes; they are all influenced by the climatic modes through ocean dynamics and air-sea interactions [5].

During the 39-year era of satellite observations, the longest MHWs in these three upwelling zones were discovered in 2015-2016 and 2019-2020, when an extreme El Niño and IOD took place in 2015/2016 and 2019, respectively [5]. One aspect of such a response is a shift in growth that varies between various species or groupings. The Indian Ocean, particularly its western portion, has one of the highest summertime concentrations of algal bloom among the tropical oceans. The intense monsoonal wind blows that promotes ocean upwelling, which transports nutrients from below the surface to the surface and supports increased rates of primary productivity, is the reason for this. These upwelling areas' declining primary production trends may be harmful to the marine food webs and the fishing industry [6]. Extremely warm water episodes are more likely as anthropogenic greenhouse gas emissions raise the global ocean's sea surface temperature (SST) [7].

In the Bay of Bengal, a strong MHW occurred in 2010 from 4th of May to 6th of June month for 34 days the maximum intensity of 3.4°C extra on (15/5/2010) it was spread for an area of 1.1Mkm². El Nino-Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) episodes co-occurred during the 1997–1998 MHW period, weakening the trade winds to the south due to easterly wind anomalies around the Indian Ocean's equator. Less latent heat release from the weaker winds caused the equatorial region to warm, and equatorial Kelvin and Rossby waves that propagated eastward and westward helped the abnormal warming spread throughout the basin. The majority of MHWs in the Andaman Sea happened during or right after powerful El Nino events in the Pacific, which frequently caused Indian Ocean basin warming and negative Indian Ocean Dipole circumstances after El Nino conditions. Along the coasts of India and Sri Lanka, El Nino also causes warming occurrences, which are probably brought on by a weaker South Asian summer monsoon [8]. While nutrients and phytoplankton in warm eddies migrate toward deeper waters, those in cold eddies are carried to shallower seas.

Due to climate change and temperature effects, 90% of the taxa of Atlantic diatoms shift eastward at a median pace of 42.7 km per decade (km.dec⁻¹), whereas the central positions of the core ranges of 74% of the taxa shift pole ward at a median rate of 12.9 km per decade (km dec⁻¹) [9]. Tuna and other fish are widely distributed, and this is related to the availability and abundance of diatom. According to FAO data, the Indian Ocean is the second-largest supplier of tuna to global markets, accounting for 20% of the total catch, particularly the big eye tuna, which is the most valuable economically. It's interesting to note that the Indian Ocean region with the highest microalgae densities also has the highest ocean surface warming. These MHWs were produced by a variety of regional processes, including as air-sea heat transfer, turbulent mixing, and ocean advection. Up to 1.2°C of warming has occurred during the last century, which is significantly more than the 0.8°C global surface

warming that occurred during the same time period. However, past research was unable to determine the effect of the fast-rising Indian Ocean because of the absence of long-term data.

2. Consequences of Marine Heatwaves on planktonic productivity

Recent heatwaves have changed the extreme summer temperatures, and they have also become powerful drivers of ecological socioeconomic impacts [10]. Such occurrences occur in both the water and the atmosphere, and marine heatwaves (MHWs) can have significant effects on ecosystems. According to (Cavicchioli et al., 2019) Frolicher *et al.* (2018), 87 percent of MHWs are attributable to human-induced warming, with this ratio increasing to nearly 100 per cent under any global warming scenario exceeding 2 degrees Celsius. Humans and other marine creatures may be severely impacted by changes in plankton production [11]. Any alteration in primary production may have higher effects on biogeochemical cycling and ecosystem processes. Under conditions of climate change, MHWs will increase in frequency and intensity, likely pushing marine creatures and ecosystems to the edge of their capacity for resilience and possibly beyond, which may result in permanent alterations [12]. Additionally, it is likely that these modifications feedback on the dynamics of the ocean and atmosphere, possibly modifying the ocean circulation on longer time scales. Only in waters with a mean annual surface temperature of less than 26°C will an increase in heterotrophic prokaryoplankton biomass due to ocean warming of 1°C be seen [13]. A decline in diatom species richness downstream, which was more pronounced in 2003's hot summer than in earlier, colder summers [14].

The MHWs occurred with longer duration, higher frequency, and more total days in 1982/1983, 1983/1984, 1987/1988, 1997/1998, 2006/2007, 2009/2010, 2011, 2012/2013, 2014/2015, 2015/2016, and 2019/2020 as per shown in fig.1 [5]. These years coincide with either an El Nino event, a favourable Indian Ocean Dipole, or both [3].

Specific primary production is thought to rise with temperature due to higher rates of carbon assimilation in light-saturated environments [15]. The net primary productivity was reduced as a result of the phytoplankton loss processes brought on by zooplankton grazing [16], sinking [17], and respiration [15]. As a result of current climate warming, changes in temperature and physical mixing have also impacted the competitive advantage of small-sized diatom cells in Lake Tahoe. Changes in the thermal structure of the water column will cause reorganisations within the phytoplankton community, which will favour small-sized algal cells and species that can control their buoyancy [18]. Tiny *Cyclotella* genus cells grew larger with greater stratification, but giant diatoms predominated under higher turbulent mixing conditions and shrank across the sample period [19]. In experimental mesocosm experiments, a tendency towards decreased phytoplankton size with warming has also been noted [20]. Particular algal cell types are superior competitors for nutrients and can maintain their vertical position in the surface water, changed mixing regimes have an impact on their ability to compete [21].

In series of experiment conducted by [22], with *Cylindrotheca closterium* as the conquering opponent, diatoms dominated the 22 °C heat wave treatment. Heat waves have an intensity-dependent impact on the stability of phytoplankton. Minor biomass loss and hastened competitive exclusion are the results of moderate heat waves. Strong heat waves significantly reduce biomass and promote compensatory growth [22]. The impact of heat waves on community stability is lessened by turbidity. Due to the coexistence of high levels of biodiversity, the predominance of species found at their warm range edges, concurrent non-climatic human impacts, or any combination of these factors, numerous regions in the Pacific, Atlantic, and Indian Oceans are particularly vulnerable to MHW intensification [23].

According to new satellite data, the western Indian Ocean has declined algal abundance up to 30% over the previous 16 years. Fig.2. depicts the Annual and June to

September months occurrences of Marine heatwaves from 1982-2008 in the (a) western Indian Ocean and (b) eastern Indian Ocean. The concept behind ocean warming suppressing the marine productivity is stratification. Stratification, a phenomenon caused by increasing ocean surface temperatures, occurs when the underlying water becomes denser and the surface water becomes less dense. Such stratification prevents nutrient-rich subterranean fluids from vertically mixing their way to the surface. A vital step in supplying nutrients to the top zones, where there is enough light for photosynthesis, is vertical mixing. Along with inhibiting vertical mixing, a crucial method for delivering nutrients into the euphotic zone where there is enough light for photosynthesis, is one of the effects of rising sea surface temperatures (SSTs). Lower phytoplankton production due to warming of surface waters is potentially alarming, especially at low latitudes. The creation of a shallow water column stratification due to a rise in sea surface temperature may keep marine planktonic organisms close to the surface and expose them to high irradiation [24].

Increased commercial and unsustainable fishing is a significant factor in fish stock precipitous drop. However, the decreased microalgae communities could accumulate as a stress element; using a resource that might be depleting can push it over the brink of extinction. It is very important to note that, in the recent decades, the coastal winds over this region have strengthened, and ideally, this should enhance the nutrient mixing and phytoplankton blooms. On the contrary, the current study using quality-controlled blended chlorophyll data and Earth system model simulations points out an alarming decrease of up to 20% in marine phytoplankton during the past six decades. Subtropical and tropical herbivores may migrate their ranges pole ward as a result of MHWs, which would increase grazing pressure.

3. Global Ocean colour satellite reactions to marine heatwaves

High-resolution satellite-derived global ocean colour datasets effectively used to examine the overall pattern of global MHWs related chlorophyll responses. The level of chlorophyll-a serves as a stand-in for primary production [25]. MHWs typically decreases chlorophyll concentrations in the tropics and mid-latitudes, with increases at high latitudes [26]. The magnitude of chlorophyll responses to MHWs is increased in response to higher intensity and longer duration of MHWs. Negative chlorophyll responses are more prevalent in tropical and subtropical climates showing a marked decline in biomass of microalgae in response to MHWs. These trends in chlorophyll are driven by enhanced ocean stratification due to the rapid warming in the Indian Ocean, which suppresses nutrient mixing from subsurface layers [27]. The western Indian Ocean is showing negative trends in the spatial distribution of the chlorophyll trends derived from the measurements and historical simulations. The worldwide marine phytoplankton biomass (chlorophyll) assessed by satellite ocean colour and its reaction to MHWs on global and regional scales were the subject of numerous research. Because of the shallower climatological mixed layer in the warm season compared to the cold season, the latitudinal disparity of the chlorophyll response is more noticeable.

Depending on latitude, MHWs alter different chlorophyll responses to MHWs, presumably as a result of various limiting conditions. The locations of the strongest meridional gradients in the mean nitrate concentrations are correlated with the dramatic changes in the chlorophyll response to MHWs, indicating that the background levels of nitrate concentrations are the main environmental factor influencing the direction of the global chlorophyll response to MHWs. The effects of MHW-induced mixed-layer shoaling on phytoplankton are supported by the seasonal differences in the chlorophyll responses to MHWs. Plankton functional types (PFTs) respond to global warming in a variety of ways depending on their compositions because phytoplankton communities have varying growth

rates and varied nutrient limitations [28]. When extreme nitrate depletion happens in the future climate, it may have an impact on the poleward shift of the latitudinal band where the sign of chlorophyll responses to MHW changes or even flips the positive chlorophyll responses to negative in the high-latitude regions. Strong MHWs in the northeastern Pacific Ocean have reportedly caused the phytoplankton community composition to shift from bigger species to smaller pico- and nano-plankton. It was specifically expected that the Arctic and Southern Oceans plankton will be far more diversified [29][30]. Additional research is necessary to understand how phytoplankton reacts to MHWs while taking into account the various effects of each PFT in high-latitude locations. According to projections, MHWs will intensify and occur more frequently, making the ecosystem more vulnerable to them [31]. This means that the effects on marine organisms will be more severe as MHWs change other parts of the marine ecosystem like coral, sea grass beds, seabird, and fish colonies and can even cause regime shifts in the marine ecosystem.

4. Algal Blooms and Marine Heat waves: Causes and Effects

So-called "bloom" is a phenomenon that occurs when specific physicochemical circumstances, predominantly temperature, salinity, nutrients, etc., are changed in a way that encourages the growth of opportunistic micro-algae into huge biomass or other cell numbers that might affect the environment. Recurrent microalgae blooms are having an impact on the ecological products and services of the Indian peninsula's shallow coast and marine environment. The research of [32] gives proof that rising ocean temperatures have already made it easier for HABs to intensify and, as a consequence, contribute to an increased threat to human health. It is anticipated that the distribution and range of phytoplankton and HABs will alter when global ocean temperatures rise and the distribution of ocean temperatures changes. The incidence of Marine microalgal bloom MMBs (including HABs) and the number of causal taxa may grow as SST and anthropogenic effects increase near the Indian

peninsula. *Trichodesmium* sp. (Cyanophyceae) and *Noctiluca* sp. (Dinophyceae) contributed 34.4% and 31.8%, respectively, to the overall blooms. [33] revealed that high sea surface temperature (SST) and salinity were significant driving forces for *Trichodesmium* sp. blooms formation. Most variations in micro-climate, which often vary from one geographical place to another, are what cause changes in the physicochemical conditions of the water (temperature, salinity, and dissolved nutrients). Most of the MMBs dominated by cyanophyceae occurred during high SST. Coincidentally, a significant increase in SST condition along the coast of India between 1938 and 1947 matched with the first record of blooms of Cyanophyceae [33]. Similar to this study, SST and salinity have been reported as significant parameters influencing the abundance and distribution of Cyanophyceae (*Trichodesmium* sp.) in different oceans.

Since the Cyanophyceae (*Trichodesmium* sp.), Trebouxiophyceae (*Chlorella marina*), and ciliata (*Mesodinium rubrum*) can grow well in warm water the frequency of their blooms could rise in the near future along the Indian Peninsula coast. The Indian Ocean is warming, and the microalgal strains that bloom there are accustomed to high temperatures and salinity. Therefore, given ideal environmental conditions of high nutrients and prey abundance, the rising SST and salinity conditions around the Indian peninsula might not hinder growth and the production of their blooms. SST may be encouraging Dinophyceae blooms along India's coast by accelerating eutrophication.

In 2013, MHWs in South Australia experienced unusually high and variable water temperatures (5°C above the historic average), lasted for 1 week and led to the algal bloom dominated by a harmful diatom, *Chaetoceros coarctatus* [34]. Due to its tolerance of high temperatures, *C. Coarctatus* may become the dominant species [35]. Extreme HABs may result from extreme MHWs. *Pseudonitzschia australis* possesses a high tolerance to heat and a nitrate affinity and ammonium, which give this species its nutrients [36] has an edge in the

market for obtaining nitrogen (N) under N depleted circumstances [37]. These dangerous diatom produce harmful toxins named biotoxindomoic acid (DA). Global episodes of MHWs and their effects at selective locations on microalgae illustrated in table 1. Over the widest geographic area documented by [38], DA was found in numerous animals, including porpoises, whales, dolphins, sea lions, seals, and seabirds. Through food chain transfer, DA can afflict and kill aquatic organisms while posing a risk to human health. In light of the HAB outbreak and related DA, certain fisheries, including those for Dungeness crab, rock crab, razor clams, etc., had to be closed. The suspension of fisheries caused significant losses to the local economy, with a USD\$97.5 million drop in earnings for the commercial Dungeness crab fishery alone in 2015 compared to 2014 [39]. Red tides are frequently brought on by MHWs, which suggests that MHWs may lessen the biodiversity of microalgae and even raise trophic levels via the food chain.

5. How marine heatwaves cause microalgal bloom?

Increased stratification of the upper ocean due to warming and MHWs may prevent nutrients from being transported from deeper to surface waters, reducing the amount of nutrients available in the upper waters. Therefore, under these nutrient-limiting conditions, phytoplankton species with distinct nutrient acquisition mechanisms can successfully outcompete one another and grow into blooms. These techniques include increased macronutrient "surge" absorption rates, distinct trace metal uptake capacities, mixotrophy, and swimming to locations with higher nutritional concentrations [40]. Additionally, bloom-forming algae can create and secrete poisons that can kill other algal species in addition to their grazers [41]. By eliminating the nutrient-competing microalgae, dangerous species can freely use the scarce nutrients. The lessened competition and grazing pressure let the toxic algae establish a dominating position. Therefore, a key link between marine heatwaves and microalgal blooms/composition and increased severity of stratification or ocean mixing and

the ensuing changes in nutrient availability. Longstanding and large-scale algal blooms must be supported by enough nutrient availability which is present in many patches of Indian ocean. According to satellite data and in-situ climatology assessments of SST, chlorophyll a, and nitrate, algal blooms linked to MHWs are less in nutrient-poor seas and stronger in nutrient-rich waters [42]. In future, oceans stronger stratification and a reduction in the availability of nutrients in the upper waters could increase the likelihood of weaker blooms brought on by marine heatwaves. Some marine organisms exhibit MHW adaptation or ecological memory. In 2016, an exposure to 8–9°C MHWs led to over 90% probability of severe corals (microalgal symbionts) bleaching on the Great Barrier Reef while the same intensity of MHWs in 2017 induced a 50% probability of severe bleaching [43].

6. Microalgal carbon sequestration under marine heat waves

The process by which CO₂ is collected and fixed by algae and subsequently kept in the oceans for a long time (often more than 100 years) in the form of sediments or refractory dissolved organic carbon is known as carbon sequestration by algae. Unfortunately, there aren't many documents available that discuss how much CO₂ algae sequester in the context of MHWs. Wild macroalgae and phytoplankton sequester carbon to the tune of 11.4% and 1.2–2.4% of their respective net primary output. All three El Nino events—1997–1998 and 2015–2016—had a negative impact on the northeast Pacific's phytoplankton biomass and primary productivity and some similarities in Indian Ocean too. Weak upwelling and/or a deep pycnocline/nutricline brought on by warm occurrences, both of which restricted nutrient availability to the surface mixed layer, could be blamed for the decreased primary output [44]. On the other hand, [44] investigated the effects of 19 extreme summer MHWs on chlorophyll a (chl- a) concentration in the Southern Ocean (SO) and discovered that the strongest effects were observed in the coldest regions, where surface chl-a was increased by 80% in comparison to control sites. Different effects of the MHWs on primary production

were seen in the New Zealand region; in general, surface phytoplankton biomass was decreased in the north of the Subtropical Front but rose in the south [45]. The local temperatures may have an impact on the differential effects. North of the Subtropical Front temperatures are significantly higher than those in the south of the Subtropical Front. Therefore, a change in temperature may benefit microalgae at lower temperatures but push it above its thermal limit at higher temperatures.

Regionally dependent surface chlorophyll-a concentration responses to these events and systematically found similarities in the local processes and atmospheric variables that originate and terminate extreme MHWs between 1982 and 2017 [46], keeping this in view the major breakdown of MHWs globally is shown in Table.2 (https://en.wikipedia.org/wiki/Marine_heatwave). The findings revealed that the majority of extreme MHWs had lower chlorophyll-concentrations. On the other side, during some MHWs, improved production was also observed. The effects of MHWs were greatly influenced by latitude. Positive impacts emerged at high latitudes, while negative effects tended to appear at low and mid-latitudes. The cause may be due to enhanced stratification, which kills phytoplankton in oligotrophic tropical and subtropical waters with extremely low nutrient levels by stifling the supply of nutrients from deeper to the upper oceans. Contrarily, stratification can restrict mixing and expose algae to more solar radiation, increasing light availability and aiding photosynthesis and development of phytoplankton at high latitudes where phytoplankton is typically light rather than nutrition limited [47].

7. Microagal cell size and elemental stoichiometry under influence of MHW

Over a mild temperature increase, microalgae show an increase in enzymatic reaction rates and growth rates. Therefore, if no other factors are limiting, an increase from the current temperature of 18°C to 21.5°C could result in an increase of about 25% in growth rate. This

crucially also presupposes that the taxonomic and clonal makeup are unaltered [48]. Because of temperature ranges and development optimums that are specific to different species or ecotypes, the real impact of temperature on metabolic rate is complicated. Beyond the temperature optimum, a rise in temperature can harm cells, slow down their rate of growth, and ultimately kill them. Smaller species have an advantage in an environment without turbulence to resuspend all planktonic species due to thermal stratification and vertical mixing's rapid effect on phytoplankton sinking velocities. In eutrophic settings, bloom-forming cyanobacteria compete more successfully than other phytoplankton groups at higher temperatures. At temperatures above 23⁰C, cyanobacteria develop at a faster maximum specific rate than diatoms and green algae [49]. Rising temperatures will result in steeper nutritional gradients in the thermocline, which benefits phytoplankton that migrate vertically effectively, such cyanobacteria and dinoflagellates. Many lakes with various mixing regimes have observed an increase in cyanobacteria at increasing temperatures [50].

Worldwide increases in greenhouse carbon dioxide and temperature are linked to modifications in ocean circulation and chemistry, which shift the patterns of light and nutrients. Changes in the microalgae community structure that result from this are predicted to have a domino impact on primary and export production, the dynamics of the marine food web, its structure, and the biogeochemical cycling of carbon and bio-limiting elements in the sea. In consisting of many [51] trials dominated by copepod grazers that prey primarily on intermediate phytoplankton size classes, it has been demonstrated that intensified grazing at higher temperature can also change phytoplankton species composition and size structure. Numerous dinoflagellate species appear to prefer warmer temperatures, which may be due to mixotrophy and the effect of temperature on heterotrophic metabolism or flagella motility. In contrast, diatoms appear to predominate in temperate to cooler regimes, despite the fact that broad phylogenetic generalisations are very uncertain. These patterns might be brought on by

secondary variables that are interrelated, such as stratification, light, and nutrient availability [48]. To better understand the physiological underpinnings of the species-specific temperature maxima, the distinctions between species and taxonomic groups, and the real importance to community organisation, more information is needed. Phytoplankton populations may vary as a result of the metabolic response of marine animals at all trophic levels to variations in average and severe ocean temperatures. Increases in ocean stratification and the development of ocean gyres have both been linked to an increase in phytoplankton communities dominated by small picoplankton species [52].

Different trophic levels appear to respond differently to temperature fluctuations, which could vary the species makeup of the phytoplankton and the timing of blooms. This might be fatal for higher trophic levels, which might be triggered by environmental causes other than temperature [53]. Although there is a strong correlation between these changes and temperature changes, it is not clear whether these changes are a direct metabolic reaction to temperature changes in the ocean or whether they are caused by indirect changes in light and nutrients as well as other abiotic or biotic factors linked to changes in ocean circulation and climate [54]. The elemental makeup of particulate matter may change as a result of these changes in community organisation, which are overlaid on intra-specific responses. With each degree Celsius increase in temperature, cell volume decreases by 2.5% intra-specifically, among other temperature-related consequences. The adaptation to lower oxygen, CO₂ or other nutrient concentrations associated with rising temperatures, or reductions in cell size linked with quicker generation times are some potential evolutionary factors for cell size decline [55]. Differential effects of temperature on the biochemistry of microalgae are known, particularly for N-assimilation [56]. The intensity and sign of the combined effect of nutrient, CO₂ concentration, and temperature on particulate C:N:P are significantly different from the effects of any of the components acting alone. Additionally, changes in the elemental

composition of communities and their corresponding differences may be more significant than intra-specific variations in elemental composition in response to temperature. It is obvious that changes in temperature will have a significant impact on both metabolic functions and physico-chemical interactions between microalgae cells and their surroundings. Such effects interact clearly with cell size.

8. Effects of the medium's physical properties being temperature-dependent

According to a model by [57], the average sea surface temperature (SST) will rise from 18°C to 21.5°C by the year 2100 AD, with a corresponding freshening of the sea surface salinity (g salt per kilogramme saltwater) from 34.71 to 34.53. This is most likely due to greater precipitation and glacier melt countering increasing evaporation from the surface ocean. The rate at which, because to variations in densities, spherical, immobile cells move either down (cells denser than the surrounding water) or up (cells less dense than the surrounding water) in the water column. A spherical organism's terminal velocity is directly correlated with the density difference, inversely correlated with the dynamic viscosity, and correlated with the square of the organism's radius when first sinking and flotation without the assistance of flagella activity are taken into account. Because the dynamic viscosity of saltwater at 21.5°C is 4.4% lower than at 18°C, an organism will move vertically 4.4% faster at 21.5°C than at 18°C. This is equivalent to the increase in speed found with a 2.2% increase in cell radius. The force required to drive a spherical organism at a given speed is proportional to the cell radius and the viscosity of the medium in flagella motility [48]. A 4.4% decrease in viscosity between 18 and 21.5°C would result in a pro rata decrease in the energy cost of motility, comparable to a 4.4% decrease in the organism's radius [58]. Temperature also has an effect on metabolism in terms of diffusion through the boundary layer surrounding the organism in terms of the acquisition and assimilation of nutrients, particularly inorganic carbon, when their rate of supply is limiting for growth. Climate

change will most certainly cause a temporary rise in icebergs, a drop in sea ice cover, and a decrease in salinity at the poles, altering circulation, water column stratification, and mixed layer depths.

9. Combined effects of Ocean warming, Acidification and Marine Heatwaves

Climate change brought on by rising CO₂ clearly affects the size structure and species composition of phytoplankton. Over a 50-year (1960-2009) time period, dinoflagellate abundance fell while diatom abundance grew in the northeast Atlantic and North Sea [45]. This change was ascribed to the interaction of the warming ocean and summer winds becoming more intense. On the other side, future open oceans are expected to see cyanobacteria gain more competitive advantages over diatoms. These may be due to the result of a change in turbulent mixing. Due to the increased heat contrast between the continents and coastal oceans brought on by global warming, wind-driven upwelling may be strengthened in coastal oceans, increasing the competitive advantage of diatom [59]. Diatoms adapt well to environments with pulsed nutrient supplies because they contain a storage vacuole for nutrients [60]. Diatoms also have unique photo protection mechanisms to deal with the fast changes in the underwater light environment. The aforementioned characteristics support the predominance of diatoms in environments with increased mixing. At the worldwide level, the relative abundance of diatoms has decreased by more than 10%, and in the North Atlantic and sub-Antarctic Pacific, it has decreased by as much as 60%. By decreasing the effectiveness of the biological pump, this simulated change in ecosystem structure affects marine carbon uptake and contributes to the positive feedback between climate change and the ocean carbon cycle [61]. Warmer-water species are being favoured at the expense of cold-water species as a result of the current warming of the northeast Atlantic region, with corresponding range expansion and contraction. Certain common diatoms, both HAB (like *Pseudonitzschia* spp.) and non-HAB (like *Thalassiosira* spp.) taxa, have increased

in number, indicating that the overall population of diatoms has not decreased. The relative abundance of diatoms vs dinoflagellates has increased significantly overall as a result of these changes. This flip is caused by an interaction between rising sea surface temperatures and rising summer wind speeds [62].

Future open oceans would have stronger stratification and weaker mixing than coastal oceans, which would result in a decrease in the amount of nutrients coming from deeper waters. Because they have higher ratios of cell volume to surface area and higher nutrient uptake efficiency, smaller phytoplankton like cyanobacteria would be preferred in a nutrient-limited environment. Although the combination of warming and heatwaves triggers blooms of buoyant cyanobacteria and its combined impacts of MHWs and ocean warming/acidification on phytoplankton community structure have not been fully studied. In the future, diatoms would have an advantage over other cyanobacteria in coastal oceans, but smaller cyanobacteria like *Prochlorococcus* sp. and *Synechococcus* sp. would encroach on their territory in open oceans [45].

10. Interaction between macroalgae and microalgae

Macroalgae and microalgae inevitably compete with one another for resources like nutrients, light, and space when they share the same ecological niche. There was a negative correlation between the occurrence of macroalga *Ulva prolifera* and chlorophyll-a concentration in the Southern Yellow Sea, China. Who will prevail in next oceans? In contrast to studies focused on solitary investigations of microalgae or macroalgae, [45] co-cultured the algae *Skeletonema costatum*, which forms red tides, and *Ulva linza*, which forms green tides, under current and predicted ocean conditions. *S. costatum* exhibited more advantages than *U. linza* in terms of upcoming warming and acidification conditions, which may prevent the formation of green tides brought on by *Ulva* species. This discovery is further supported by the recent

increase in red tides and decrease in green tides in the Chinese [63] seas (China Marine Disaster Bulletin, 2000-2020). Compared to macroalgae, microalgae, and notably some bloom-forming species, have superior temperature tolerance. As a result, one can anticipate that in future oceans with frequent MHWs, microalgae may prevail in the race against macroalgae.

The majority of investigations focused on the effects of MHWs on specific types of macro- or microalgae. In contrast, macroalgae and microalgae coexist and fight for resources in coastal seas. The presence of microalgae on the surface of macroalgae may hinder their growth, especially in young species, mostly by limiting their access to light and nutrients. In the meantime, macroalgae may prevent the growth of nearby microalgae by excreting substances known as allelopathics [63]. Consequently, microalgal blooms are greatly reduced where macroalgae are heavily farmed. On the other side, in recent years, macroalgae farms have occasionally seen microalgal blooms. Given the varied ways that microalgae and macroalgae react to MHWs, MHWs may upset the current balance between the two types of algae. Therefore, it is crucial to look into whether MHWs may affect the interaction of microalgae and macroalgae considering the significance of macroalgae farming and harmful algal bloom.

11. Conclusion

Investigations into how MHW affects microalgal dynamics under the anticipated more intense events of future ocean environments require detection and attribution investigations in both present and future climates. Keeping this in view, in this review an effort was made to elucidate the possible impacts of MHWs on microalgal taxa of the Indian ocean concerning the global picture of microalgae and MHWs. Predominate combined conditions, occurrences, and records of MHWs in the western and eastern Indian Ocean show quite similar environments when compared with the global level but unfortunately unstudied. MHWs

combined with ocean warming and acidification trends promote the growth of smaller phytoplankton and hence limit phytoplankton's role as a carbon sink and sequesterer. Different sites' algae react to MHWs differently. The regulation of other parameters, such as background temperature, nutrition and light levels, desiccation stress, and grazing pressure, maybe the primary driver in addition to the species differences. This paper also lights up about most often the algal blooms are triggered by MHWs and that certain environments are the reason for the domination of respective species. Therefore, more MHWs-simulating research should be carried out to better understand the combined effects of MHWs and other potential stressors and to separate effects induced by the severe temperature increases of MHWs themselves from co-occurring other causes. Furthering our knowledge of how MHWs affect algae in future warming and CO₂enriched oceans is also necessary as a result of climate change.

12. References

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Table 1. Worldwide effects of marine heatwaves on phytoplankton

Country/Ocean	Recorded Year	Impact on phytoplankton	Reference
Chile Antofagasta,	1997/98	Pico-and nanophytoplankton size classes made a significant contribution to the production.	[64]
West Iberia, Portugal	2000	HABs (<i>Dinophysis</i> spp., <i>Lingulodiniumpolyedra</i>) were favored by weaker upwelling during the main upwelling season and warmer water in late summer and autumn;	[65]
Pacific Northwest during spring-summer resulted in	2005	A positive temperature anomaly and a pronounced negative anomaly in surface phytoplankton biomass (chlorophyll <i>a</i>) and primary productivity.	[66]
Terra Nova	2007	Low-chlorophyll <i>a</i> summertime at off-	[67]

Bay and the central and southern Ross Sea		shore waters	
Northeast Atlantic region	2009	<i>Thalassiosira</i> spp and <i>Pseudonitzschia</i> spp dominated through out a decade under favourable conditions of MHWs and rising sea surface temperatures	[62]
Shark Bay, Western Australia	2010-11	Increased nutrient inputs to the water column from degraded seagrass biomass	[68]
South Australia	2013	Algal bloom dominated by a harmful diatom, <i>Chaetoceros coarctatus</i> .	[34]
North Pacific Ocean	2013	Chlorophyll/phytoplankton concentrations are higher in cold than in warm eddies in near-surface water (more than 70 m).	[69]
Western South Atlantic	2013-14	It was responsible for a decrease in surface phytoplankton/chlorophyll a levels.	[70]
Northern California Current (In eastern and central pacific)	2014	MHW event may prevent lipids from phytoplankton and zooplankton from moving to higher trophic levels.	[71]
North East Pacific	2014	Incredibly low chlorophyll levels in the late winter/early spring	[72]
U.S. Pacific Northwest	2014-16	<i>Pseudo-nitzschia</i> (the chain-forming diatom) dominated from due to northeast Pacific marine heat wave.	[39]
The Northern Antarctic Peninsula	2016	A bloom large centric diatom (<i>Odontella weissflogii</i>) by heat waves	[73]
Alaskan Sea	2016	Toxic algal blooms, shellfish poisoning incidents, and seabird mortality incidents are observed.	[74]
New Zealand	2017-18	Surface phytoplankton biomass was decreased	[45]
Tasman Sea coast of Australia	2019	Decreased abundance of a cool-affinity diatom species, <i>Asterionellopsis glacialis</i> and increased abundance of a warm-affinity diatom species, <i>Leptocylindrus danicus</i>	[75]
Santa Catarina Island, south Brazil,	2020	Anoxia was detected and decrease in phytoplankton community richness (growth of <i>Trichodesmium sp</i> favoured).	[76]

Table 2. Major breakdown of marine heat waves from 1999 to 2019 globally

Name	Duration (days)	Intensity (°C)	Area(Mkm ²)
Mediterranean 1999	8	1.9	NA
Mediterranean 2003	10	5.5	0.5
Mediterranean 2003	28	4.6	1.2
Mediterranean 2006	33	4.0	NA
Western Australia 1999	132	2.1	NA
Western Australia 2011	66	4.9	0.95
Great Barrier Reef 2016	55	4.0	2.6
Tasman Sea 2015	252	2.7	NA
Northwest Atlantic 2012	132	4.3	0.1–0.3
Northeast Pacific 2015	711	2.6	4.5–11.7
Santa Barbara 2015	93	5.1	NA
Southern California Bight 2018	44	3.9	NA

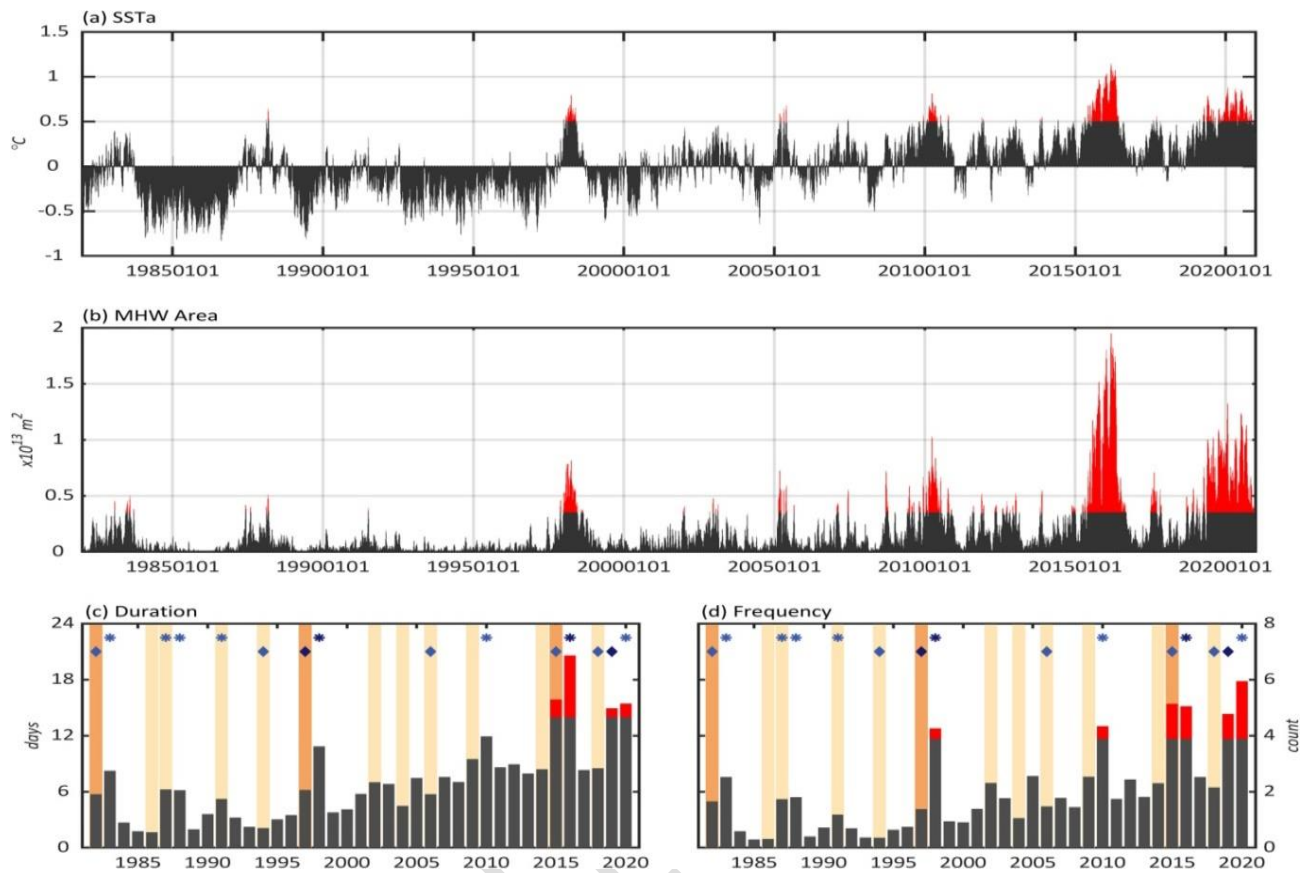


Fig.1. Long-Lasting Marine Heatwaves Instigated by Ocean Planetary Waves in the Tropical Indian Ocean during 2015–2016 and 2019–2020.

(a) Red bars indicate that the daily SST anomalies (SSTa) are bigger than their 1.5 standard deviations in the tropical Indian Ocean (TIO) time series (30°E120°E, 20°S30°N); (b) Time series of yearly mean marine heatwaves; the coverage area of marine heatwaves (MHWs) in the TIO, where red bars indicate the coverage area is larger than 4 times the climatological mean from 1992 to 2020; (c) duration; (d) frequency averaged in the TIO.

- Red bars in (c)–(d) indicate values that are greater than double the full-time series averages. In (c)–(d), years with developing El Niño, warming in the Indian Ocean basin (IOB), and positive Indian Ocean dipole (IOD) are

represented by orange bars, blue asterisks, and blue diamonds, respectively.

Years with extreme events with an index greater than its two standard deviations are represented by dark colours.

Years with extreme events with an index greater than its two standard deviations are represented by dark colours.

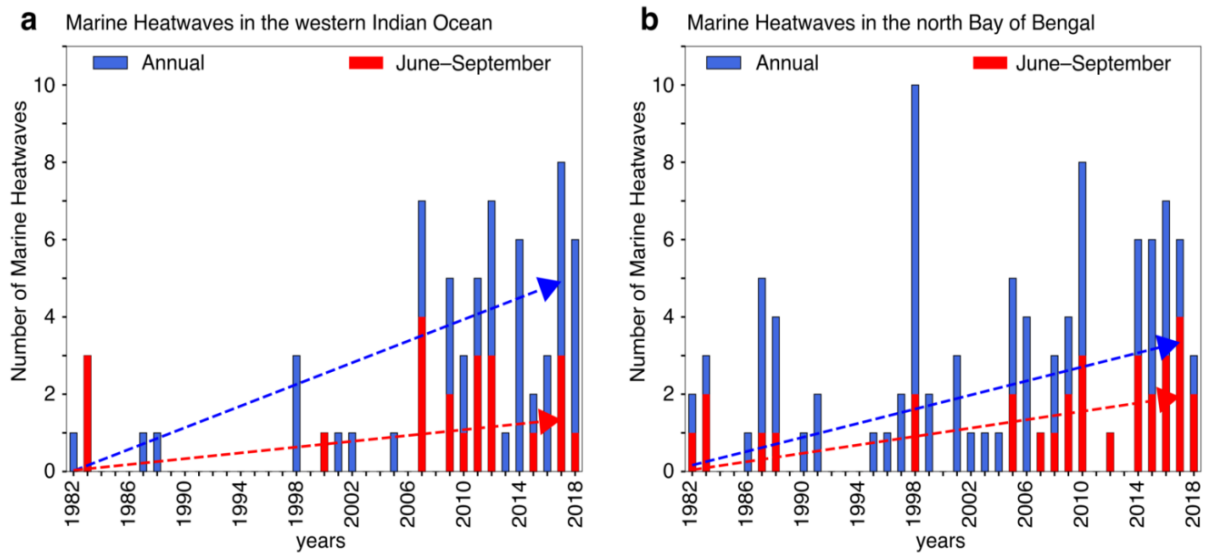


Fig.2. Annual and June to September months occurrences of Marine Heatwaves from 1982-2008 in the (a) western Indian Ocean and (b) eastern Indian Ocean

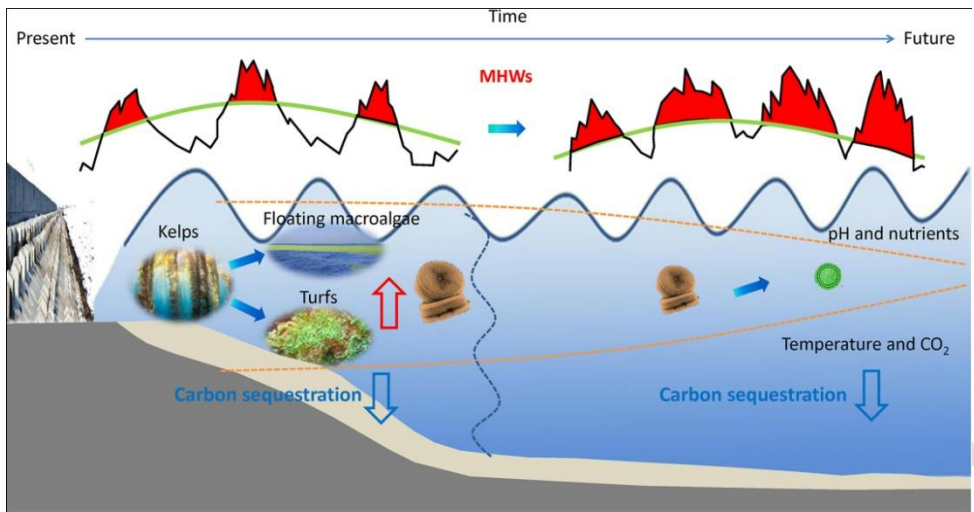


Fig. 3. Comparative effects of normal and heatwave conditions in oceans (Source: IITM, Pune)

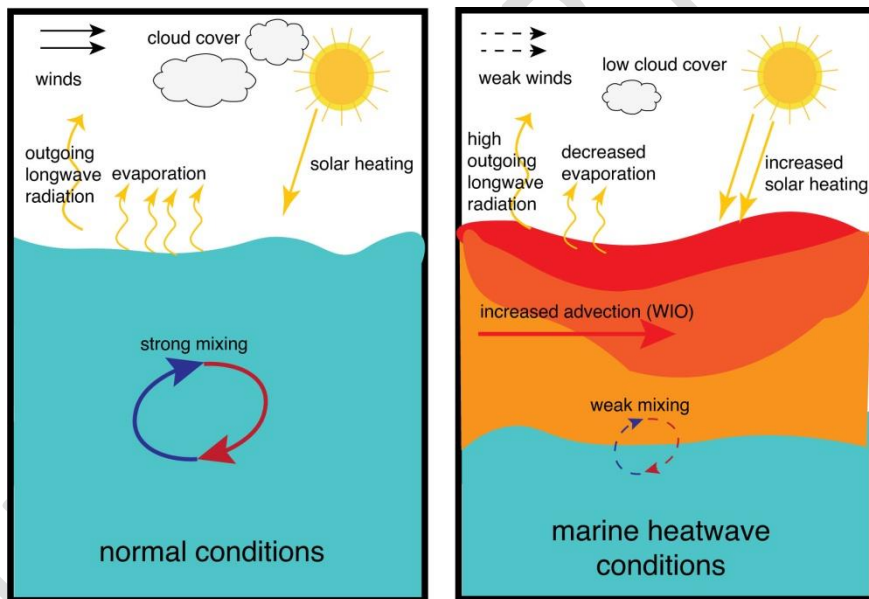


Fig. 4. Warmer, more acidic oceans with frequent heatwaves favor simpler, smaller algae (turfs, diatoms, cyanobacteria) over complex ones (kelp forests). This shift means less carbon gets captured from the atmosphere, potentially accelerating climate change [77].