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The rising swarms of jellyfish in Indian waters: the environmental drivers, ecological, and socio-economic impacts

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ABSTRACT

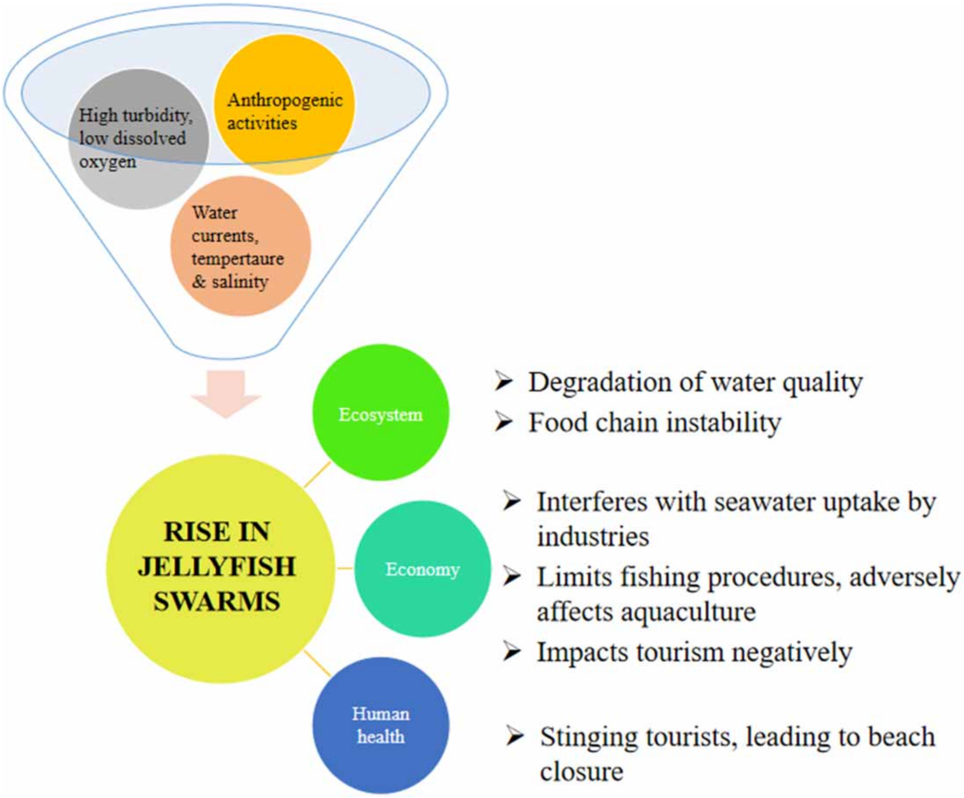
A four-decade data of jellyfish aggregation from 1980 to 2020 were taken to discern whether there has been an actual rise in jellyfish swarm in Indian coastal and estuarine waters. Despite frequent jellyfish aggregations and beach strandings in Indian waters, jellyfish aggregations have been poorly investigated and there is a dearth of information on the swarm-forming jellyfish, their preferred season, and the location of swarming. Therefore, our review aims to account for the frequency of swarming phenomenon annually and the appearance of new swarm-forming jellyfish species. The term 'jellyfish' refers to the medusae stage of phylum Cnidaria (Cubozoa, Hydrozoa, and Scyphozoa) only in this review. The present work postulates a geospatial spread and swarm-forming jellyfish species to increase in recent times. More than 23 coastal locations of India have witnessed jellyfish aggregations and beach stranding in the last four decades. Seasonal oceanographic conditions prevailing during the summer monsoon, fall, and early winter promoted jellyfish aggregations and swarming. Only two jellyfish species were known to form aggregates during 1981–1990, but the diversity of jellyfish species increased to nine by 2011–2020. The development of predictive models from remote sensing data can be useful to warn humans and coastal industries of the approaching swarm.

Key words: anthropogenic activities, climate change, cnidaria, gelatinous zooplankton

HIGHLIGHTS

- Geospatial spread, frequency of jellyfish swarms, and the number of swarm-forming species increased in the coastal and estuarine waters of India.
- More than 23 locations along the coast of India have witnessed jellyfish aggregations, swarms, and beach stranding in the last four decades.
- Seasonal oceanographic conditions during the summer monsoon, fall, and early winter promote jellyfish aggregations.

GRAPHICAL ABSTRACT



INTRODUCTION

Jellyfish are gelatinous organisms that form large aggregations in the ocean in response to hydrographical changes (Purcell 2005; Boero *et al.* 2008). Jellyfish blooms are divided into 'true' or demographic blooms and 'apparent' or non-demographic blooms. True blooms occur due to the metagenic life cycle of alteration of generation between sexual and asexual phases. However, apparent blooms are a local increase in abundance, often related to temporary phenomena like fronts and local advection (Graham *et al.* 2001). Aggregation is an assemblage of interacting medusae without any change in their population size or mortality (Hamner & Dawson 2009). Unlike other marine invertebrates, most jellyfish, by their wide environmental tolerance and a benthic–pelagic alternative mode of life, can cope with eclectic fluctuations in temperature and salinity and even programme their reproduction with seasonal changes in these background variables (Miglietta *et al.* 2008). Schnedler-Meyer *et al.* (2018) delineated advective loss to be an important driver of interannual fluctuations in the jellyfish population. They proposed that jellyfish showing a metagenic lifecycle (alteration between benthic polyp stage and pelagic medusa stage) were favoured in comparison to holoplanktic jellyfish. Moreover, Goldstein & Steiner (2020) regarded food availability to be an important ecological driver of jellyfish aggregation along with eutrophication and climate change.

Global warming affects coastal ecosystems by causing an increase in sea water temperature, a rise in sea level, and an increase in the acidity of water (Nazarnia *et al.* 2020). With a rise in anthropogenic activities in the coastal areas, the coastal ecosystems are getting deteriorated. Water pollution from the discharge of untreated industrial effluents, agricultural wastes, and domestic sewage deteriorates the water quality that affects the marine life and the coastal population. In contrast, jellyfish with high tolerance to environmental vicissitudes can take advantage of such ecological imbalance and proliferate into swarms in warm high saline, turbid, and eutrophicated waters (Purcell 2012). Jellyfish species show synanthropy and are favoured by anthropogenic activities (Richardson *et al.* 2009). Robinson & Graham (2013) reported higher jellyfish abundance when winter was warmer and wetter, spring sea surface temperature (SST) was lower, and summer SST higher than usual. Climate change leading to increased sea temperature and westward up-current movement were regarded to be the causative agents for the phenological shift in the swarming behaviour of *Rhopilema nomadica* from the summer to the winter season in the eastern Mediterranean Sea (Edelist *et al.* 2020). Thus, unusual seasonal changes in temperature or climate change-induced ocean warming accelerate the reproduction rate in jellyfish and help them form swarms. Moreover, ichthyofaunal abundance and diversity are greatly impacted by the introduction of invasive species and constant anthropogenic pressure (Ćosić-Flajsig *et al.* 2020). Twelve major estuaries worldwide have suffered more than a 30% reduction in fish stock and a 10% decline in the invertebrate stock and even underwent species extinction due to dense jellyfish swarms (Lotze *et al.* 2006).

The increase in jellyfish abundance has been depicted as a consequence of anthropogenic factors and the hydrodynamics of oceans (Purcell *et al.* 2007; Baliarsingh *et al.* 2015). This perception is mostly based on field research and case studies, but according to Condon *et al.* (2013), there has been no significant indication of an increase in jellyfish globally. Moreover, Pitt *et al.* (2018) also state that anthropogenic stressors leading to jellyfish swarms have been amplified beyond the evidence provided by the data. To examine whether there has been an actual increase in jellyfish abundance in Indian waters this research was undertaken.

A total of 842 species of Cnidaria, containing 212 species of Hydrozoa, 34 species of Scyphozoa, and 6 species of Cubozoa have been recorded from Indian waters (Chakrapany 1984; Saravanan 2018; Nisa *et al.* 2021). More than 23 locations along the coast of India have witnessed jellyfish aggregations, swarms, and beach stranding in the last four decades (Figure 1 and Table 1).

As the United Nations has declared 2021–2030 as the Decade of Ocean Science aimed at restoring degraded ecosystems and sustainably harvesting ocean resources by protecting the life under the water (SDG-14), there is an urgent need to document the causes and processes (physical, chemical, meteorological, and biological) that challenge the healthy functioning of the marine ecosystem. The current review aims at discussing the autecology of swarm-forming jellyfish, highlighting the role of hydrographical, and anthropogenic factors promoting jellyfish swarm; the influence of these swarms on marine ecosystem

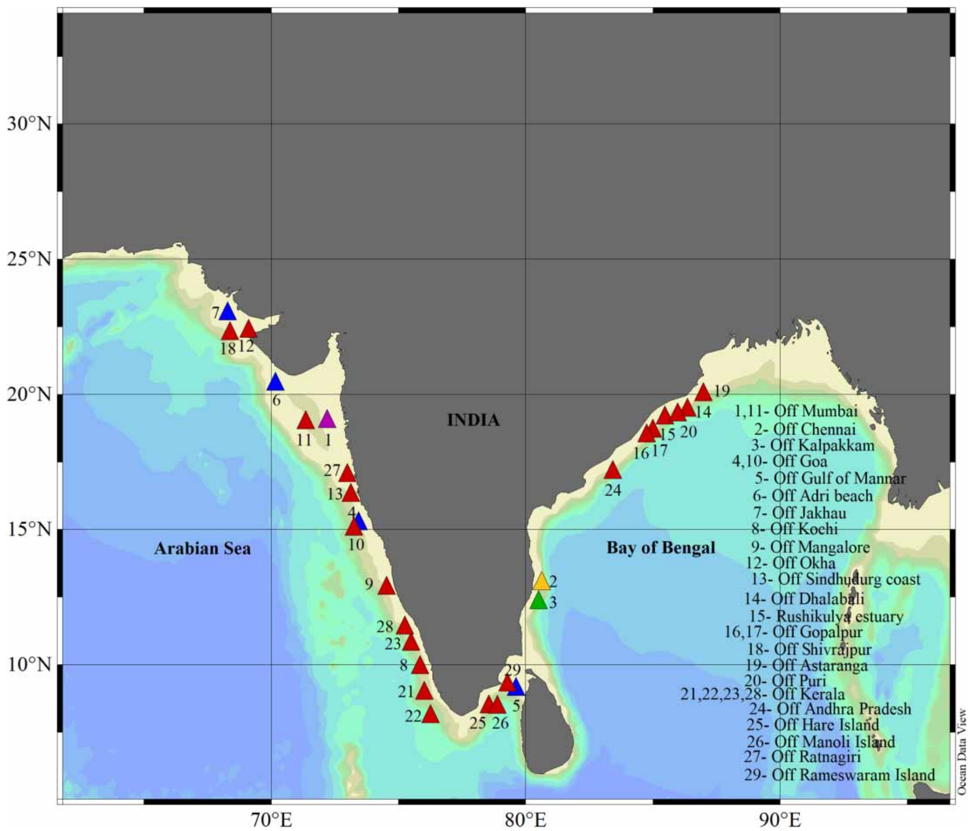


Figure 1 | Incidence of jellyfish aggregations and beach stranding; purple denotes before 1980, yellow denotes 1980–1990, green denotes 1991–2000, blue denotes 2001–2010, red denotes 2011–2020. Please refer to the online version of this paper to see this figure in colour: http://dx.doi.org/10.2166/wcc.2022.245.

Table 1 | Reports on jellyfish aggregations from India

S. no.	Location	Date/Year	Aggregation forming jellyfish species	Features of the aggregation	Economic impact	Reference
1	Off Mumbai, Arabian Sea	1900s		Outburst of medusae		Chopra (1960)
2	Off Chennai coast, Bay of Bengal	1981–1985 (February, March, June, July, August, September)	*Crambionella stulhmanni* and *Chrysaora quinquecirrha*	Aggregations	fish catch was less when medusae were abundant	James *et al.* (1985)
3	Off Kalpakkam, Bay of Bengal	1995–1996	*Crambionella stuhlmanni*, *Chiropsoides buitendijki* and *Chrysaora quinquecirrha*	Aggregations	High revenue loss (~5.5 million Indian Rupees/ day)	Masilamoni *et al.* (2000)
4	Off Goa, Arabian Sea	2006	Rhizostome scyphozoan	Aggregations	Damage to shrimps	Purcell *et al.* (2007)
5	Gulf of Mannar, Bay of Bengal	July–October	*Lobonema smithii*	swarm	Jellyfish exploited commercially for export purpose	Murugan & Durgekar (2008)
6	Adri beach, Gujarat, Arabian Sea	Monsoon	*Porpita porpita*	Beach strandings		CMFRI (2010a)
7	Off Jakhau, Arabian Sea	November–December and April–May	Family: Rhizostomatidae			CMFRI (2010b)
8	Off Kochi, Mangalore, Goa, Mumbai and Okha, Arabian Sea	2010–2017		Swarms		Thomas *et al.* (2020)
9	Sindhudurg coast of Maharashtra, Arabian Sea	October–November 2012		Swarming of jellyfish		Shiledar (2013)
10	Rushikulya, Bay of Bengal	November 2012–February 2013	*Pelagia noctiluca*	Jellyfish aggregates 1–7 nos/10 m^2		Baliarsingh *et al.* (2015)
11	Dhalabali and Gopalpur, Bay of Bengal	December 2012		Jellyfish aggregates with numbers 80–100		Sahu & Panigrahy (2013)
12	Gopalpur, Bay of Bengal	April, 2014		Jellyfish aggregates		Baliarsingh *et al.* (2016)
13	Shivrajpur, Gujarat coast, Arabian Sea	January 2016	*Pelagia noctiluca*	bloom		Padate *et al.* (2020)
14	Astaranga to Puri, Bay of Bengal	May 2016	*Porpita porpita*	Jellyfish aggregates with numbers >100,000; Mass beach stranding		Sahu *et al.* (2020)
15	Kerala coast, Arabian Sea	2016–2019	*Crambionella orsini*, *Lychnorhiza malayensis*, *Chrysaora caliparea*, *Netrostoma coerulescens* and *Cyanea nozakii*	bloom		Riyas *et al.* (2021a)
16	Kerala coast, Arabian Sea	After southwest monsoon (post monsoon)	*Crambionella orsini*	Form blooms		Biju Kumar & Anitha (2017)

(*Continued.*)

Table 1 | Continued

S. no.	Location	Date/Year	Aggregation forming jellyfish species	Features of the aggregation	Economic impact	Reference
17	Off Kerala, Arabian Sea	2017–2018	*Chrysaora caliparea*, *Cyanea nozakii* and *Lychnorhiza malayensis*	Bloom		Riyas *et al.* (2021b)
18	Off Andhra Pradesh, Bay of Bengal	March–July 2018	*Crambionella annandalei*		Jellyfish exploited commercially for export purpose	Behera *et al.* (2020)
19	Southern part of Hare Island and Manoli Island, Gulf of Mannar, Bay of Bengal	16 October 2018	*Pelagia noctiluca*	$> 100/m^2$ approximately		Ramesh *et al.* (2021)
20	Ratnagiri, Arabian Sea	December 2018	*Pelagia* cf. *noctiluca*	Bloom		Hari Praved *et al.* (2021)
21	Kerala coast, Arabian Sea		*Acromitus flagellatus*	Bloom		Riyas & Biju Kumar (2019)
22	Vadakadu to Olaikuda Coastline, Rameswaram Island, Gulf of Mannar, Bay of Bengal	7–14 December 2020	*Porpita porpita*	Beach strandings		Tharik *et al.* (2021)

functioning, human health, and the economy of the nation (through its impact on fisheries, tourism, industries, and other sectors) from Indian waters.

MATERIALS AND METHODS

A literature review from authentic search engines like Scopus, Web of Science, Google Scholar, and ScienceDirect was conducted to obtain jellyfish swarm data from Indian waters. The important search terms included 'jellyfish swarm', 'jellyfish bloom', 'jellyfish aggregation', 'gelatinous zooplankton swarm', 'gelatinous zooplankton bloom', 'gelatinous zooplankton aggregation', 'jellyfish beach stranding', 'stinging jellyfish', and 'economic impact of jellyfish bloom'. Ocean Data View (ODV) software (version 4) was used to plot jellyfish aggregations and beach stranding locations along the coastal waters of India.

RESULTS AND DISCUSSION

Since the 1980s, the abundance and sightings of jellyfish swarms have gradually increased. It was reported that jellyfish outbreaks in Jakhau, Gujarat increased three times the previous year (CMFRI 2010b). These swarms have impacted marine ecosystems, human health, and the economy of India.

Autecology of swarm-forming jellyfish

Scyphozoans have a short generation time of two to seventeen months (Pitt & Lucas 2014). Some scyphozoans like *Cyanea nozakii* prefer high temperature (23–26.8 °C) and high salinity (Lu *et al.* 2003), while species such as *Pelagia noctiluca* (8–22 °C) tolerate a wide range of temperature (Morand *et al.* 1992). Similarly, *Crambionella stuhlmanni* shows euryhaline nature, by tolerating a high range of salinity (Perissinotto *et al.* 2013). High temperature and high salinity led *P. noctiluca* to bloom in the Gulf of Mannar (Ramesh *et al.* 2021). Recently, *Acromitus flagellatus* was reported to swarm in the estuarine waters of Sundarbans, Bay of Bengal (Siddique *et al.* 2022). *A. flagellatus* was found to swarm in winters but when the water temperature was comparatively higher (about 25 °C) and when salinity ranged between 24 and 29. Thus, the rise in sea water temperature, accompanied by an increase in salinity in recent years, has facilitated an increase in the incidence of swarming jellyfish in Indian waters.

The general feeding ecology of jellyfish suggests that their most common prey is a copepod. Their feeding rate increases with body size and prey density, and their digestion time is influenced by temperature (Purcell 1997). For *Chrysaora quinquecirrha*, warm waters increase the swimming and digestion rates (Purcell 2009). Nudibranchs, shelled snails, and loggerhead turtles feed on *Porpita* sp. (Sahu *et al.* 2020). Larvae of *P. noctiluca* were investigated to predate on tuna eggs and get predated mostly by Olive Ridley, Leatherback turtles, and fish (Ramesh *et al.* 2021). Diverse prey preference is shown by scyphozoan species belonging to the family Catostylidae (feeding mostly on mesozooplankton; Pitt *et al.* 2008), *Cyanea* sp. (on organisms across different trophic levels including the scyphozoan *Aurelia aurita*; Hansson 1997. Thus, swarms of *Aurelia aurita* can usher *Cyanea* sp. into the system and contribute to their growth and proliferation), *Porpita* sp. (on phytoplankton, carnivorous calanoid copepods, crab megalopa, and fish; Sahu *et al.* 2020). Phytoplankton blooms and the introduction of invasive jellyfish species also cause jellyfish to form aggregates thereby impacting trophic interactions and altering plankton community dynamics spatially.

Factors promoting jellyfish swarms

From an environmental point of view, hydrographical, meteorological, and hydrodynamic changes in the ocean facilitate the swarming of jellyfish. Besides, increased anthropogenic activities in recent years have significantly contributed to jellyfish swarms through habitat modification and coastal pollution (Richardson *et al.* 2009).

Hydrographic, hydrodynamic, and meteorological changes

Surface currents and advection favour jellyfish swarms (Johnson *et al.* 2005). Beach stranding of *Porpita porpita* along the Rameswaram coastline, Gulf of Mannar, might be due to cyclone Nivar, which drifted the swarm of *P. porpita* towards the shoreline (Tharik *et al.* 2021). Shoreward currents and winds also resulted in causing beach stranding of *P. porpita* along the Odisha coast (Sahu *et al.* 2020). Similarly, Padate *et al.* (2020) also observed sea currents to be the driving force behind the drifting *Pelagia noctiluca* bloom along the Gujarat coast. The action of wind, current, tide; fluctuations in jellyfish population, and water movements were considered important factors for the aggregation of *P. noctiluca* along the Odisha coast. Highly turbid and less oxygenated waters offer a hostile environment for mesozooplankton, whereas jellyfish show high resilience to such adverse conditions and increase their population density (Purcell *et al.* 2007). Literature reports suggest that oceanographic conditions during the summer monsoon, fall, and early winter (July–December) promote jellyfish aggregations and swarming in Indian waters (Figure 2).

Ekman pumping, cold-core eddies, coastal upwelling, and mixed layer entrainment during the Indian Ocean Dipole (IOD) induce phytoplankton blooms (Thushara & Vinayachandran 2020), and since nutrients and biological productivity regulate jellyfish proliferation, the bottom-up process may aid in the development of jellyfish swarms. In the summer months, warmer sea temperatures facilitate jellyfish reproduction and growth, causing an increase in jellyfish aggregations (Baliarsingh *et al.* 2020). In contrast to this seasonal trend, the scyphozoan, *C. stuhlmanni,* reaches high abundance during the retreating monsoon (Kumar *et al.* 2017). *Crambionella orsini* abundance had shown rhythmicity with the lunar cycle (Nair 1954). Thus,

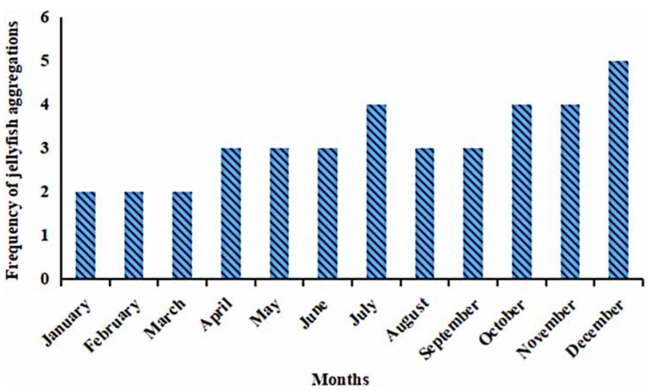


Figure 2 | Temporal variation in jellyfish aggregation along the coastal waters of India.

monitoring of swarms, with the creation of a continuous database that accounts the abundance of jellyfish and hydrographical parameters needs to be undertaken to understand the role of hydrography on jellyfish population.

Anthropogenic causes

Anthropogenic activities leading to coastal pollution, eutrophication, habitat modification, and overfishing contribute to the swarming of jellyfish through modification of food-web structure (Richardson *et al.* 2009) (Figure 3). Similarly, the construction of dams and other physical structures in the catchment areas of major rivers impede the natural flow of rivers into the sea, increase the nearshore salinity and help in jellyfish aggregations (Amorim *et al.* 2018). Aquaculture practices may enhance jellyfish proliferation directly by enriching water columns with excess nutrients and indirectly by providing supportive structures for polyp attachment and their strobilation. Plastic waste can also serve as a breeding ground for jellyfish (Gershwin 2013). Overfishing can relax predation and food competition for jellyfish by eliminating organisms higher in the trophic level, causing an ecosystem imbalance that promotes jellyfish proliferation (Boero 2013). Offshore constructions of oil and natural gas platforms have enhanced jellyfish sightings in some areas (Graham *et al.* 2001). The augmented jellyfish population are often linked with hot water effluents from power plants. Invasion of non-native species through ballast water or fouling on the ship also contributes to jellyfish proliferation in areas away from its native habitats (Boero *et al.* 2008). Since jellyfish have a low metabolic rate and some species also store oxygen in their tissues (Rutherford & Thuesen 2005), thus they are more tolerant to hypoxic conditions created by eutrophication and other anthropogenic activities compared to other organisms. During and after the monsoon season, the chances of hypoxia increase in the coastal waters due to riverine influx bringing phosphates and organic matter into the ocean during heavy rainfall. Other anthropogenic factors like wastes from aquaculture industries and domestic sludge are also released in the ocean by rivers during monsoons. Such conditions give rise to eutrophication and coupled with an increase in water temperature (due to climate change) may contribute to hypoxia during and after the monsoon season. Thus, July–December period seems favourable and conducive for jellyfish to aggregate and form swarms in Indian waters as it is evident from literature reports (Figure 2).

There was only one scientific report from Indian waters on jellyfish aggregation before 1980, between 1980 and 1990, and between 1991 and 2000. The reports increased to four during 2001–2010. There was a soar in jellyfish swarms, accounting for 22 reports between 2010 and 2020. Most jellyfish aggregations have been reported from the Indian coastal states of Kerala

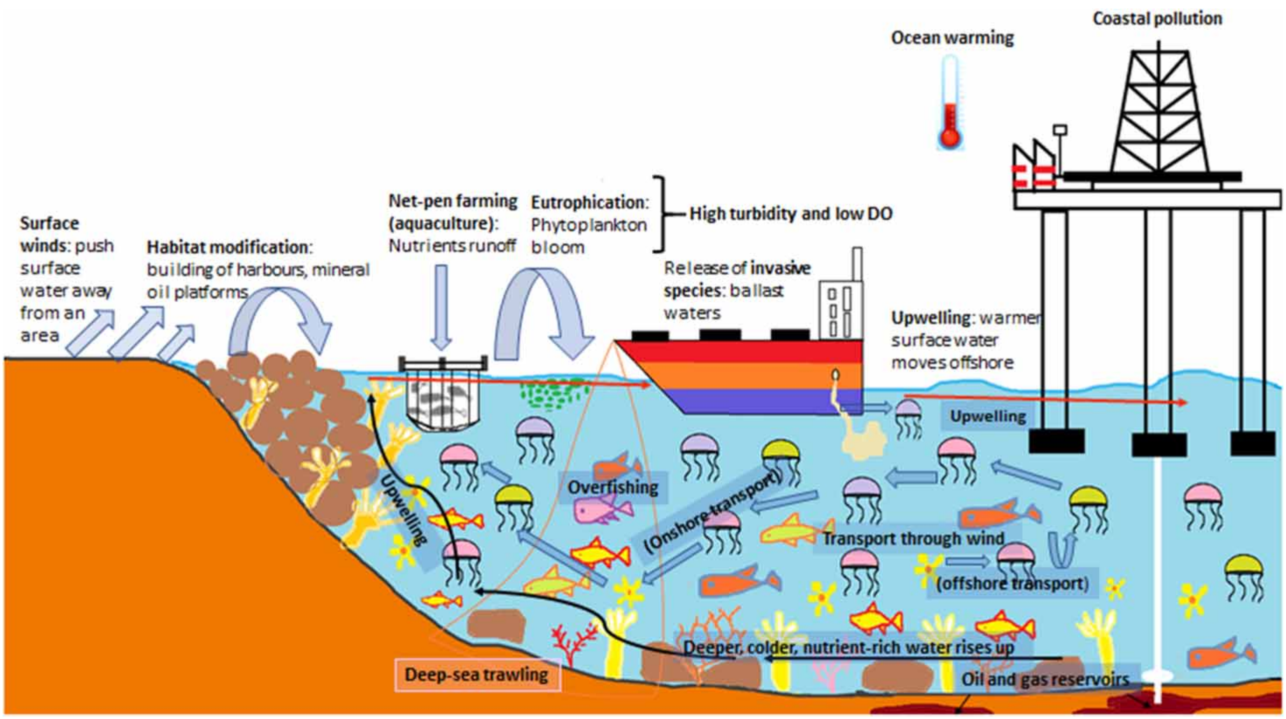


Figure 3 | Schematic representation of factors promoting jellyfish swarm.

and Odisha. The recent years have witnessed a substantial increase in the geospatial spread and frequency of jellyfish swarms. Two jellyfish species (*C. stulhmanni* and *C. quinquecirrha*) forming aggregates, were reported during 1981–1990. In the second decade (1991–2000), *Chiropsoides buitendijki* was also reported to form aggregations. *Lobonema smithii* and *P. porpita* were recorded for swarming and beach stranding between 2001 and 2010. The diversity of jellyfish species increased to nine by 2011–2020; among which eight new species recorded blooms, swarms, aggregations, and beach stranding (Table 2). Our study is consistent with the results of Baliarsingh *et al.* (2020) which state that jellyfish aggregations and beach strandings have become a recurring phenomenon in the coastal waters of India and also revealed environmental factors like winds, tidal fronts, surface currents, dissolved oxygen, water temperature, salinity, and turbidity along with anthropogenic factors like deteriorated water quality, overfishing, habitat change and introduction of exotic species to play a vital role in triggering jellyfish aggregations. Hence, by the increased number of scientific reports, it is evident that jellyfish swarms have increased in recent years. Although, the frequency of jellyfish aggregations has increased in present times, the causative drivers for jellyfish swarms need to be explored further with robust evidence.

Ecological and socio-economic impacts of jellyfish swarming

Jellyfish swarms can be detrimental to the marine ecosystem, human health, and economy of a country in different ways.

Ecological impacts

Irrespective of their adverse impacts on the marine ecosystem, jellyfish perform several crucial ecological functions, like facilitating the mixing of oceans (Leshansky & Pismen 2010), and also as a food source for several fish species, sea birds, turtles, and parasitic amphipods (Pauly *et al.* 2008). During the regression of swarms, the dead jellyfish that sink to the sea bed support several benthic life forms and contribute to benthic nutrient regeneration (Sweetman & Chapman 2011). Amphipods show parasitic association while crabs show commensalism and mutualism with jellyfish (Towanda & Thuesen 2006). Therefore, they are intricately linked to other marine phyla in the complex marine food web. Jellyfish swarms also act as an indicator of monsoons and earthquakes (Mackie 2002). The red tide causing dinoflagellate, *Noctiluca scintillans*, benefits from jellyfish swarm since jellyfish prey upon the predators of *N. scintillans*. Thus, jellyfish swarming might promote harmful algal blooms (HABs) in coastal waters, as reported off Gopalpur, on the east coast of India (Baliarsingh *et al.* 2016).

Jellyfish are opportunistic feeders and predate on all zooplankters, leading to a collapse of the mesozooplankton population and alteration of pelagic trophodynamics (Niermann 2004). Jellyfish affect zooplankton, the primary production (Kideys *et al.* 2008), and microbial food-web dynamics (Condon *et al.* 2011). By consuming the herbivorous zooplankton, gelatinous carnivores indirectly benefit the phytoplankton community. They convert an enormous amount of carbon (C), fixed through primary and secondary production, into gelatinous biomass, limiting the transfer of C to higher trophic

Table 2 | List of reported jellyfish species forming aggregations/blooms/swarms/beach stranding from 1980 to 2020 in Indian waters

S.No.	Species	Decade I (1981–1990)	Decade II (1991–2000)	Decade III (2001–2010)	Decade IV (2011–2020)
1	*Acromitus flagellatus* (Maas, 1903)	–	–	–	+
2	*Chiropsoides buitendijki* (van der Horst, 1907)	–	+	–	–
3	*Chrysaora caliparea* (Reynaud, 1830)	–	–	–	+
4	*Chrysaora quinquecirrha* (Desor, 1848)	+	+	–	–
5	*Crambionella annandalei* Rao, 1931	–	–	–	+
6	*Crambionella orsini* (Vanhöffen, 1888)	–	–	–	+
7	*Crambionella stuhlmanni* (Chun, 1896)	+	+	–	–
8	*Cyanea nozakii* Kishinouye, 1891	–	–	–	+
9	*Lobonema smithii* Mayer, 1910	–	–	+	–
10	*Lychnorhiza malayensis* Stiasny, 1920	–	–	–	+
11	*Netrostoma coerulescens* Maas, 1903	–	–	–	+
12	*Pelagia noctiluca* (Forsskål, 1775)	–	–	–	+
13	*Porpita porpita* (Linnaeus, 1758)	–	–	+	+

'+' denotes presence and '–' denotes not recorded.

levels since most consumers do not feed on jellyfish. They release colloidal and jelly-based C-rich-labile dissolved organic matter (DOM), which is rapidly metabolized by heterotrophic bacteria. However, since bacteria use this DOM primarily for respiration rather than biomass build-up, there could be a decrease in bacterial growth by 10–15% (Condon *et al.* 2011). Thus, jellyfish swarms may change the pathways of nutrients and carbon flow in the food web, affecting biogeochemical cycles, primary production, and pelagic food-web functioning.

Socio-economic impacts

Incidents of jellyfish swarms causing considerable economic loss to the fisheries sector, coastal industries, and tourism, have been reported from the coastal waters of India.

Fisheries

Jellyfish adversely affects the fish population of an area by predation (on fish larvae) and competition (by preying on zooplankton). Jellyfish aggregations cause physical damages to the fishing gears by clogging the nets and even capsizing boats, thereby decreasing the number of fishing days (Biju Kumar *et al.* 2017). India has sprawling aquaculture activity along its vast coastline (7,500 km). Around 152,600 ha (encompassing nine Indian coastal states) are dedicated to shrimp culture yield ~680,000 metric tonnes of shrimp annually (MPEDA 2020). Aquaculture constructions provide a suitable substratum for the attachment of polyp stages of jellyfish. Jellyfish wreak havoc in aquaculture by fouling the cages, causing fish death by toxic stinging, and creating metabolic stress (Purcell *et al.* 2013). Jellyfish aggregations that occur seasonally (November–December and April–May) are the leading cause of clogging gillnets in the coastal waters of Jakhau (CMFRI 2010b).

Industries

Jellyfish clogs the water intake of the cooling system of nuclear power plants, seabed mining facilities, power and desalination plants, ships, aquaria, and naval facilities, causing a temporary shutdown of the systems (Purcell *et al.* 2007). Blocking of the cooling system by jellyfish caused a temporary shutdown of Madras Atomic Power Station (MAPS) located at Kalpakkam, southeast coast of India. The shutdown caused a massive loss in revenue of >75,000 US$ per day (Masilamoni *et al.* 2000). Jellyfish outbreak in the coastal waters of Kalpakkam near MAPS was related to the coastal water currents during southwest and northeast monsoons (Masilamoni *et al.* 2000).

Marine surveys

Jellyfish swarms have been reported to disturb marine research expeditions by interfering with sampling, obtaining fish bycatch, and acoustic data acquisition. Since jellyfish compete with fish for zooplankton and predate on fish egg and larvae, biological data collection during jellyfish swarms might yield inaccurate data regarding an area's productivity potential and plankton dynamics. Jellyfish may also cause painful stings while collecting biological samples (Aznar *et al.* 2017).

Tourism and human health

Coastal tourism through recreational activities provides significant revenues to a country. However, incidents of jellyfish aggregations jeopardizing coastal tourism have increased in recent times. The most common jellyfish species associated with stinging are *C. nozakii* and *P. noctiluca* (Dong *et al.* 2010; Baliarsingh *et al.* 2015). *Physalia physalis* have been documented from Goa, Mumbai, and Andaman waters, though their aggregations are not yet known (Ramesh *et al.* 2021). Jellyfish toxins have been known to cause skin erythema, dermal inflammation with blisters, and burning sensation. Sometimes, the stings can trigger necrosis of the skin along with cardiovascular and neurotoxic effects (Mariottini *et al.* 2008). Every year, jellyfish stings have been reported during post monsoon season in Mumbai coast threatening tourism (Purushottama *et al.* 2013). Beach stranding of jellyfish are regularly noticed along famous tourist beaches of Puri, Gopalpur, Kochi, Chennai, Rameswaram, Goa and Mumbai (Sahu & Panigrahy 2013; Baliarsingh *et al.* 2020) which is impacting the tourism sector in the country, severely.

Aside from all the fatal effects of jellyfish swarms on the economy, it has been positively utilized by Indian fishermen who have now started harvesting edible jellyfish (up to 800 tonnes per season) due to their huge demands from China and Southeast Asian markets (CMFRI 2010b). Edible jellyfish like *Crambionella annandalei, Catostylus mosaicus*, *Cephea cephea*, *C. orsini*, *Rhopilema esculentum,* and *Stomolophus meleagris* are being harvested and exported to Southeast Asian countries and China to earn foreign exchange (Behera *et al.* 2020; Ramesh *et al.* 2021; Sreeram *et al.* 2021).

Future directions

This study markedly advances our knowledge about the autecology of swarm forming jellyfish, and discusses the factors that promote jellyfish swarm such as hydrographical, hydrodynamic and meteorological changes in the ocean along with increased anthropogenic activities. The present review emphasizes the impact of jellyfish swarm on the aquatic community, human health, and economy of India. The four-decade data on jellyfish aggregation from Indian waters confirmed that there has been a rise in jellyfish swarming in Indian coastal and estuarine waters. There are prominent evidences for the geospatial spread of swarm incidence along with an increase in the number of swarm events along the coastal waters of India. The diversity of swarm-forming jellyfish has also surged in the recent decade. Moreover, our research points out that oceanographic conditions during the summer monsoon, fall, and early winter create a conducive environment facilitating jellyfish to swarm in Indian waters.

Variability in hydrographical features influences marine organisms in an interconnected way. Jellyfish can be an excellent indicator of climate change and eutrophication-related detrimental impacts on the marine ecosystem (Hay 2006). Furthermore, marine organisms are a useful source of biologically active substances (BAS) that show antimicrobial, antioxidative, mitogenic, and membrane protective activities. Pathogenetic therapy of some disease require high biological activity. BAS can be used for the preparation of liposomal structures for drug delivery for the treatment of cancer, infectious diseases, diabetes, skin lesions, and also in cosmetology industries (Chzhu *et al.* 2020). BAS extract studies from jellyfish are very meagre from Indian waters and they should be assessed in the future for their pharmacological roles.

From the literature study, it is comprehensible that vast areas of coastal India are still unexplored with respect to jellyfish diversity and ecology. Limited information is available on jellyfish distribution and abundance from the Indian waters, mainly attributable to constraints faced during sampling and preserving delicate gelatinous organisms. The impact of mesoscale processes and environmental shifts on the life history, growth, and reproduction of jellyfish from Indian waters is lacking. Therefore, future work on the impact of hydrography and meteorology on the swarming of jellyfish should be carried out. Attention should given to the identification of swarm forming jellyfish, their impact on the economy, and studies related to jellyfish toxicology. A coastal database on the distribution and systematics of jellyfish from India should be constructed to understand the geospatial spread of jellyfish species. Targeted monitoring programmes should be launched to record the hydrographical and biological changes in regions that showed jellyfish swarms earlier. It will also be pertinent to formulate effective management strategies to deal with devastating swarms.

Aznar *et al.* (2017) proposed using UAVs (unmanned aerial vehicles) or swarm robotics to detect the swarming of jellyfish. Jellyfish swarms have been monitored through the field, aerial surveys, acoustics, and video profiling across the world's oceans (Nickell *et al.* 2010; Kim *et al.* 2015), but such methods have not been deployed effectively in Indian waters. Predictive models can be developed and tested from remote sensing data and provide warnings to humans and coastal industries of the approaching swarm. It will also facilitate site selection for the setting up of new industries and farms. Real-time observation of swarming behaviour will be helpful for the smooth running of power plants. Moreover, investment in public information systems should be carried out to protect the marine environment and periodic evaluation of economic losses caused due to such biological impacts.

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DATA AVAILABILITY STATEMENT

All relevant data are included in the paper or its Supplementary Information.

CONFLICT OF INTEREST

The authors declare there is no conflict.

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