

Research Article

Invasive red alga *Kappaphycus alvarezii* on the reefs of the Gulf of Mannar, India – a persistent threat to the coralsArasamuthu A.¹, Laju R.L.¹, Diraviya Raj K.¹, Ashok Kumar T.K.², Rob J. Leewis³ and Edward J.K. Patterson^{1,*}¹Suganthi Devadason Marine Research Institute, Tuticorin, 628001, India²Gulf of Mannar Marine National Park, Ramanathapuram, 623503, India³Warmond, The Netherlands

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Citation: Arasamuthu A, Laju RL, Diraviya Raj K, Ashok Kumar TK, Leewis RJ, Patterson EJK (2023) Invasive red alga *Kappaphycus alvarezii* on the reefs of the Gulf of Mannar, India – a persistent threat to the corals. *BioInvasions Records* 12(1): 151–166, <https://doi.org/10.3391/bir.2023.12.1.13>

Received: 9 May 2022**Accepted:** 6 November 2022**Published:** 23 January 2023**Handling editor:** Tatenda Dalu**Thematic editor:** Andrew Davinack**Copyright:** © Arasamuthu et al.

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Abstract

Habitat destruction by destroying the foundation species is one of the important damages caused by invasive species. The red alga *Kappaphycus alvarezii* is commercially important as a source of carrageenan and has been introduced in many countries for commercial cultivation. Due to its invasive potential, this red alga has been widely reported to be a big threat to coral reefs in many reef regions including the Gulf of Mannar (GoM) in India. Here we report the invasion of red alga *K. alvarezii* to new reef sites in Valai and Thalaiyari Islands within GoM and the coral mortality caused in the newly invaded sites from 2019 to 2021. We also discuss the geographical extension of *K. alvarezii* within GoM from its initial invasion point and its impact on corals from 2005 to 2021. During our regular reef monitoring surveys within GoM, we found *K. alvarezii* to be overgrowing live acroporan corals of Valai and Thalaiyari islands of GoM for the first time in May 2019 and we used standard underwater protocols to assess the impact of the alga on corals at different time periods between May 2019 and March 2021. Live coral cover in the invaded area decreased by 9.1% in Valai Island and by 3.9% in Thalaiyari Island due to the coral mortality caused by *K. alvarezii* during the study period. *K. alvarezii* was observed to overgrow live corals and kill them eventually at the affected sites. *Acropora* branching morphotype was found to be the most affected by *K. alvarezii*. Various measures including manual removal have been taken to keep the invasion under control. In spite of the efforts to eradicate *K. alvarezii* from the reefs of GoM, it remains a persistent threat to the survival of corals. We emphasize the importance of properly managing the already stressed and ecologically sensitive reef resources of GoM from the invasion of *K. alvarezii* in order to guarantee the long-term livelihood benefits of dependent fisher-folk.

Key words: Indian Ocean, coral reefs, bio-invasion, manual removal, macroalgae cultivation, coral mortality

Introduction

Invasive species are non-native species that cause harm to the habitats, biodiversity, and economy in the new environment. With more than 300 invasive species, marine macroalgae are a predominant category of invasive species around the world (Davidson et al. 2015). Whether native or invasive, macroalgae can affect the critical coral reef ecosystems directly

or indirectly by overgrowth, abrasion, shading, allelopathy, and microbial enhancement (Brown et al. 2020). The invasive macroalgae by virtue of their faster growth rates and higher propagation potential cause more extensive damage to corals (Chandrasekaran et al. 2008; Pérez-Estrada et al. 2013; Salimi et al. 2021). Coral reefs are one of the important tropical marine ecosystems that play crucial ecological roles (Brandl et al. 2019), which include sheltering a myriad of commercially and economically important marine species, protecting the shore from erosion, playing critical roles in nutrient recycling, assisting in carbon fixing and acting as hotspots for tourism. In spite of their ecological importance, coral reefs have suffered declines during the past few decades due to various climatic and non-climatic factors like coral bleaching events, disease outbreaks, ocean acidification, ocean deoxygenation, space competition, coral harvesting, destructive fishing practices, tourism, and pollution (Hoegh-Guldberg et al. 2017; Eddy et al. 2021). In addition to these threats, biological invasions have also caused significant damage to coral reefs globally (Coles and Eldredge 2002; Avila and Carballo 2009; Pérez-Estrada et al. 2013; Salimi et al. 2021).

Red alga *Kappaphycus alvarezii* (Doty) L.M. Liao, 1996, is a commercially important red macroalga that is widely cultivated around the world (Buschmann and Camus 2019). Being an essential source of commercially important carrageenan, *K. alvarezii* is ranked 5th among the world's most cultivated macroalgae (Rudke et al. 2020). A native to the Philippines, *K. alvarezii* has been introduced in more than 30 countries for commercial cultivation (Ask 2003). In many countries, *K. alvarezii* has been reported to invade areas outside the cultivation sites (Conklin and Smith 2005; Edward and Bhat 2012a, b; Sellers et al. 2015; Cabrera et al. 2019). It has been termed as “a destructive invasive species” and “a serious danger to coral reefs” by the Global Invasive Species Database (GISD) of the International Union for Conservation Network (GISD 2022). Due to its high plasticity, *K. alvarezii* is capable of rapid growth and quick biomass increase even after removal (Conklin and Smith 2005; Edward et al. 2012; Kamalakannan et al. 2014), and this is the main reason for its invasiveness (Smith et al. 2002). Under ideal conditions, *K. alvarezii* can double its biomass within 15 to 30 days or less (Azanza-Corrales et al. 1992). Reef areas of Kaneohe Bay in Hawaii and GoM in India are among the regions affected the most by the invasion of *K. alvarezii*.

Gulf of Mannar (GoM) in southeast India is known for its 21 uninhabited islands surrounded by coral reefs and associated biodiversity, including the biologically important Krusadai Island. The shallow-water eco-sensitive zone encompassing all the islands was declared as the Gulf of Mannar Marine National Park (GOMMNP) in 1986 (Edward et al. 2018). *Kappaphycus alvarezii* was introduced in GoM in the 1990s with the intention of commercial cultivation. At the time of introduction, the possible damages to corals were not realized (Eswaran et al. 2002). The possible effects and

damages of *K. alvarezii* to coral reefs in GoM were first reported (Pereira and Verlecar 2005) in 2005 and the Government of Tamil Nadu issued an order to disallow the cultivation of *K. alvarezii* near the eco-sensitive zones of GoM and Palk Bay. In spite of this order, *K. alvarezii* continues to be cultivated in south Palk Bay, which is closer to GOMMNP (e.g. Abhilash et al. 2019). Since the first report of the *K. alvarezii* invasion (Pereira and Verlecar 2005), there have been many studies revealing the severity of the invasion and the damages caused to the corals of GoM by the alga (Chandrasekaran et al. 2008; Kamalakannan et al. 2010, 2014; Edward and Bhatt 2012a, b; Edward et al. 2012, 2015; Joshi and Marimuthu 2015; Bast et al. 2016; NCSCM Interim Report 2014; MoEF&CC Project Report 2018). Fragments of *K. alvarezii* from the cultivation sites of Palk Bay reached the reef areas of GoM through water currents and colonized the reefs (Chandrasekaran et al. 2008; Edward and Bhatt 2012a, b). *Acropora robusta*, *Acropora muricata*, *Acropora intermedia*, *Acropora cytherea*, *Montipora digitata*, *Montipora divaricata*, *Porites solida*, and *Turbinaria* sp. are the coral species reported to have been invaded by *K. alvarezii* in GoM (Chandrasekaran et al. 2008; Kamalakannan et al. 2010; MoEF&CC Project Report 2018).

Of the 21 islands of GoM, Shingle, Krusadai, and Poomarichan of Mandapam region (Edward and Bhatt 2012a, b) and Mulli of the Keelakarai region (Edward et al. 2015) have been reported to be invaded by *K. alvarezii*. The continuous effort of the Tamil Nadu Forest Department from 2010 onwards to manually remove the alga has reduced the extent of *K. alvarezii* in GoM (MoEF&CC Project Report 2018; Kamalakannan et al. 2014). The present study reports and documents the invasion of *K. alvarezii* to new reef sites within GoM and assesses the temporal trend of the *K. alvarezii* cover and the corresponding trend of live coral cover to understand the impact of the alga on corals at newly invaded sites. The study also discusses the geographical extension of *K. alvarezii* within GoM between 2005 and 2021 since its first report and its impact on corals. We hypothesize that the invasion of *K. alvarezii* is a persistent threat to the corals of GoM.

Materials and methods

The present study was carried out from May 2019 to March 2021 to assess the impact of *K. alvarezii* on corals of Valai (09°11'14.78"N; 78°56'23.99"E) and Thalaiyari Islands (09°11'06.28"N; 78°55'57.98"E) of the Keelakarai region of GoM. The observation of the invasion of *K. alvarezii* in these islands was random during our regular reef monitoring surveys in May 2019 as *K. alvarezii* has not been reported from these islands before. *Kappaphycus alvarezii* was identified underwater by its tough, fleshy, and firm thalli with a yellowish-green to brown colour. Valai and Thalaiyari are continuous islands (Figure 1) occurring at about 4.5 km from Mulli Island (Figure 1), where the invasion of *K. alvarezii* has already been reported.

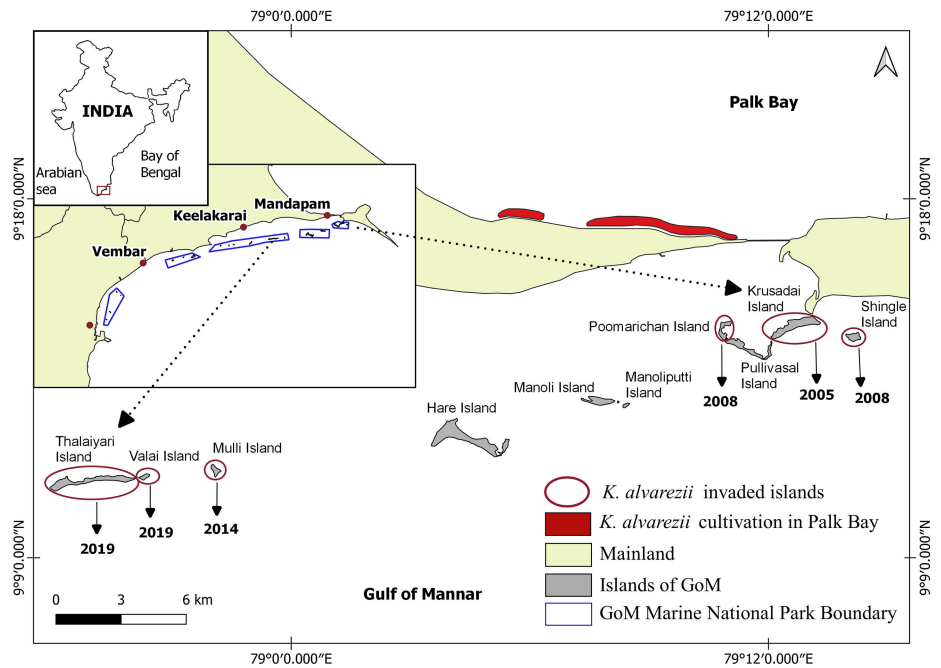


Figure 2. Map showing the islands of Gulf of Mannar, the boundary of Gulf of Mannar Marine National Park, islands invaded by *K. alvarezii*, and the year of invasion reported.

Only one site at each island was observed to be invaded by *K. alvarezii*. After observing the invasion, an underwater assessment on the impact of *K. alvarezii* was initiated in May 2019 and subsequent assessments were carried out in October 2019, April 2020, October 2020, and March 2021 in the affected sites of Valai and Thalaiyari islands. Figure 1 provides the names of the Islands invaded by *K. alvarezii* within GoM and the year of the observation. Figure 2 shows the incidences of *K. alvarezii* invasion on corals of GoM and removal measures before the present observation.

For the underwater assessment, line intercept transect method (English et al. 1997) was followed using an underwater measuring tape. Three 20-m line intercept transects were laid on the affected sites perpendicular to the island shore with an interval of five meters between them. The starting point of each transect was always set such that the entire transect fell within the *K. alvarezii* invaded area and the transects did not overlap. Using this method, the covers of live corals, *K. alvarezii*, octocorals, sponges, sand, dead corals, algae (other than *K. alvarezii*), crustose coralline algae (CCA) were assessed by calculating the fraction of the length of the underwater line that is intercepted by that particular life form. The covers of coral morphotypes in these transects were also assessed as per the codes given in English et al. (1997). For example, *Acropora* branching corals are represented by the code ACB and *Acropora* table corals by the code ACT (English et al. 1997). The same three 20-m transects were used as belt transects (20 × 2 m) to assess the prevalence of coral colonies invaded by *K. alvarezii* (English et al. 1997). Live coral colonies within one meter on either side of the transect were counted, and thus each transect covered



Figure 2. Representative figures of earlier reports of *K. alvarezii* in Gulf of Mannar; a, *Acropora* corals overgrown by *K. alvarezii* at Krusadai Island; b, *Montipora* corals overgrown by *K. alvarezii* at Mulli Island; c and d, Manual removal efforts carried out by the Tamil Nadu Forest Department; e, Attachment of *K. alvarezii* fragments on corals after removal; f, *K. alvarezii* on bleached corals in 2016.

a 40 sq m area. Corals were identified following Corals of the World online (<http://www.coralsoftheworld.org/>) and the World Register of Marine Species (WORMS; <http://www.marinespecies.org/>). Coral colonies invaded by *K. alvarezii* along each transect were counted separately. In September 2019, manual removal of *K. alvarezii* was carried out by the Tamil Nadu Forest Department in the invaded areas of both islands by skin diving, and

the removed algal mass was taken carefully to the shore and destroyed. During every assessment, the area of impact was measured with an underwater measuring tape by using Simpson's 1/3 rule. The first baseline was fixed along the longest direction, then at equal intervals offset distance above and below the line was measured (Punmia et al. 2016). The invasion of *K. alvarezii* was documented with underwater cameras including Nikon Coolpix W300 and Olympus TG-6.

Statistical analyses

Pearson correlation coefficient (r) was performed using SPSS version 16.0 to determine the relationship of *K. alvarezii* cover with live coral cover and the coral morphotype ACB. *Kappaphycus alvarezii* was taken as the explanatory variable and the live coral cover and ACB cover were taken as response variables. The relationship between the density of invaded and healthy *Acropora* colonies was also analysed with the same test. Since the alga had severely affected live coral cover, coral morphotype ACB and the genus *Acropora*, these parameters were selected for statistical analyses. To test the level of significance of the correlation coefficient, the results are interpreted according to Bakus (2007). One-way ANOVA was performed to identify deviations between the covers of *K. alvarezii* in the Valai and Thalaiyari islands.

Results

This is the first time the invasion of *K. alvarezii* was observed in Valai and Thalaiyari islands of GoM, and with these two islands the number of islands invaded by the alga increased to six (Figure 1). The depth of the affected site at Valai Island ranged from 1 to 4 m and at Thalaiyari Island from 1 to 2 m. The coral morphotypes observed at the affected sites during the study period are *Acropora* branching (ACB), *Acropora* table (ACT), *Acropora* digitate (ACD), *Acropora* foliose (ACF), *Acropora* encrusting (ACE), Coral massive (CM), Coral foliose (CF), and Coral encrusting (CE).

During the initial assessment in May 2019 at Valai Island, the percentage cover of *K. alvarezii* was $11.9 \pm 1.9\%$ SE and the live coral cover was $57.7 \pm 2.7\%$ SE. Removal of *K. alvarezii* carried out by the Tamil Nadu Forest Department in September 2019 reduced the cover of *K. alvarezii* in October 2019, but it increased gradually since then (Figure 3a). Correspondingly, live coral cover was found to have gone down to $48.6 \pm 2.8\%$ SE in March 2021. By March 2021, the cover of *K. alvarezii* was as high as $18.0 \pm 1.0\%$ SE. Invasion of *K. alvarezii* killed the host corals by overgrowing and thus increased the dead coral cover from $5.5 \pm 0.1\%$ SE in May 2019 to $11.9 \pm 1\%$ SE in March 2021. After killing the invaded coral, *K. alvarezii* was found to invade adjacent fresh live coral colonies or get detached from the dead corals to be drifted away by water currents. Among the coral morphotypes,

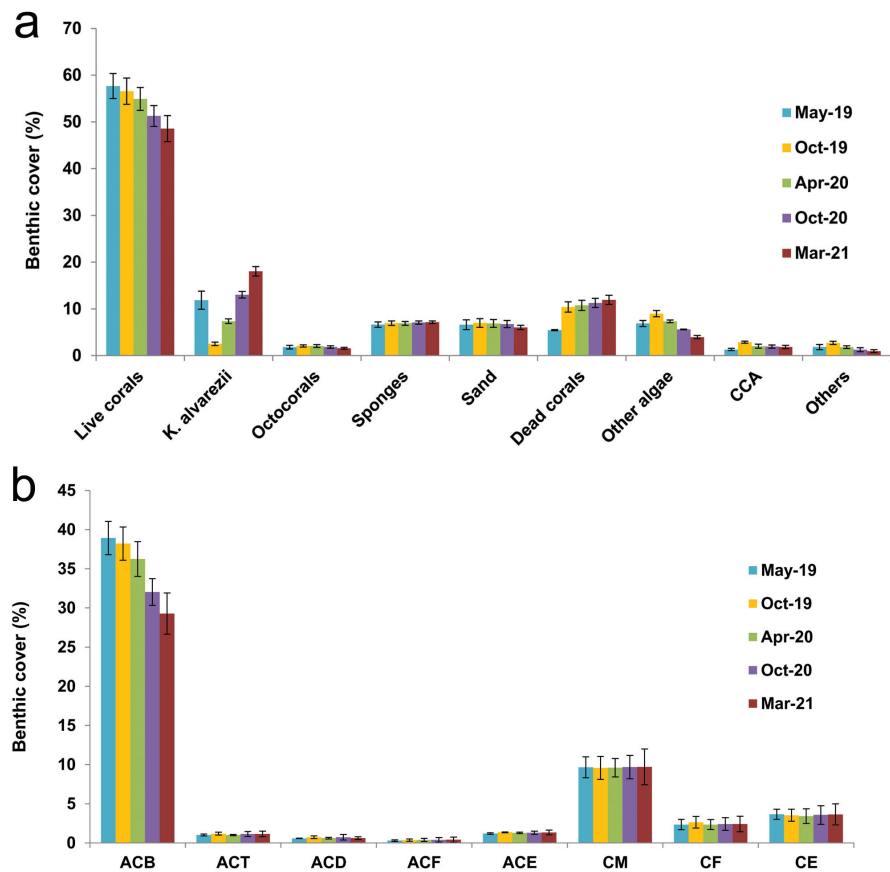


Figure 3. a. Benthic community structure in Valai Island during the study period between May 2019 and March 2021; b. Benthic cover of each coral morphotype in Valai Island. CCA = Crustose coralline algae, ACB = *Acropora* branching, ACT = *Acropora* table; ACD = *Acropora* digitate, ACF = *Acropora* foliose, ACE = *Acropora* encrusting, CM = Coral massive, CF = Coral foliose, CE = Coral encrusting.

ACB was the most abundant category with $38.9 \pm 2.1\%$ SE (out of 57.7%) in May 2019, which decreased to $29.3 \pm 2.6\%$ SE (out of 48.6%) in March 2021 (Figure 3b) due to the mortality caused by *K. alvarezii*. *Acropora* was by far the most abundant coral genus in the affected area with its contribution ranging between 83.7 and 90.6% during the study period (Supplementary material Table S1). Other coral genera observed in the affected site of Valai Island include *Montipora*, *Porites*, *Dipsastraea*, *Favites*, *Goniopora*, *Platygyra*, *Hydnophora*, *Turbinaria*, *Symphyllia*, and *Echinopora*. Among the acroporans, $15.4 \pm 2.6\%$ SE ($n = 124$) were found covered by *K. alvarezii* in May 2019 and the prevalence of affected acroporans increased to $33.4 \pm 9.1\%$ SE ($n = 184$) in March 2021. About 200 sq m area was found to be invaded by *K. alvarezii* in March 2021, which was 110 sq m in May 2019.

The trend of invasion by *K. alvarezii* and the corresponding loss of live coral cover in Thalaiyari Island (Figure 1) are as in the Valai Island. The manual removal of the alga was carried out during the same period in both islands and hence the decrease of *K. alvarezii* cover after the removal in October 2019 and gradual increase since then was similar to Valai Island

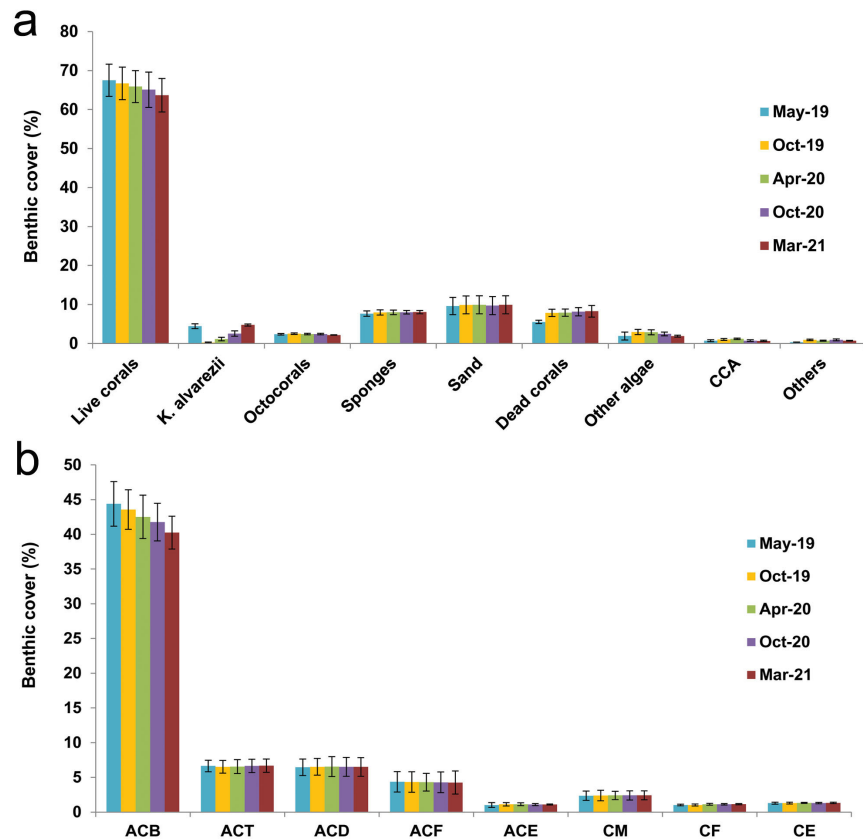


Figure 4. a. Benthic community structure in Thalaiyari Island during the study period between May 2019 and March 2021; b. Benthic cover of each coral morphotype in Thalaiyari Island. CCA = Crustose coralline algae, ACB = *Acropora* branching, ACT = *Acropora* table; ACD = *Acropora* digitate, ACF = *Acropora* foliose, ACE = *Acropora* encrusting, CM = Coral massive, CF = Coral foliose, CE = Coral encrusting.

(Figure 4a). The cover of *K. alvarezii* was comparatively lower at Thalaiyari Island than Valai Island as it was only 4.7 ± 0.3 SE by March 2021. ACB was again the affected coral morphotype in this island (Figure 4b) and *Acropora* was the only affected genus. *Acropora* was the most abundant coral genus in the affected area of Thalaiyari Island during the study period (Table S1) and the other observed genera include *Montipora*, *Porites*, *Dipsastraea*, *Favites*, and *Platygyra*. Among the acroporans, $6.1 \pm 1.2\%$ SE ($n = 41$) were found to be covered by *K. alvarezii* in May 2019 and it was only $0.3 \pm 0.1\%$ SE ($n = 2$) in October 2019 after the removal and it started increasing again (Figure 5). About 65 sq m area was found to be covered by *K. alvarezii* in Thalaiyari Island by March 2021. Figure 6 shows the photos of *K. alvarezii* invasion in Valai and Thalaiyari Islands during the study period.

According to Pearson correlation coefficient, a negative correlation was found between the cover of *K. alvarezii* and the cover of live corals in Valai ($R = -0.633$, $P = 0.011$) and Thalaiyari islands ($R = -0.824$, $P = 0.00$). The decrease in coral cover was corresponding to the increase in *K. alvarezii* cover. Similarly, the cover of the coral morphotype ACB also showed a negative correlation with *K. alvarezii* cover in Valai ($R = -0.613$, $P = 0.015$)

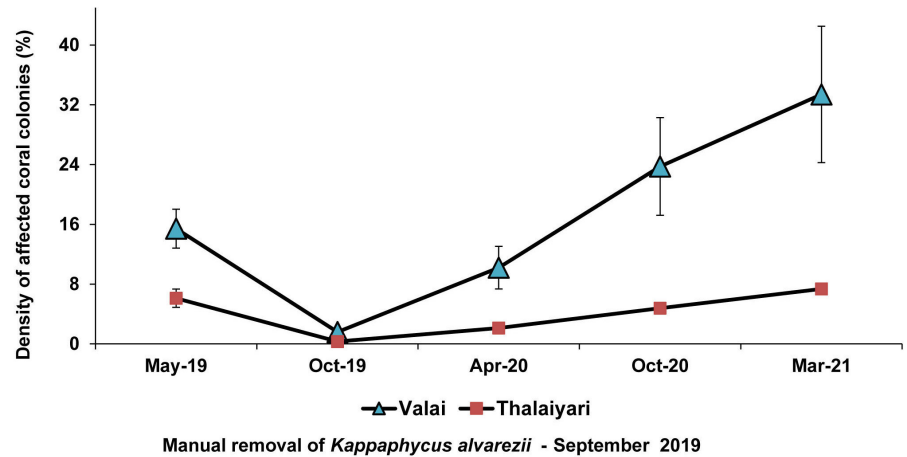


Figure 5. Prevalence of *K. alvarezii* invaded coral colonies in Valai and Thalaiyari Islands between May 2019 and March 2021.

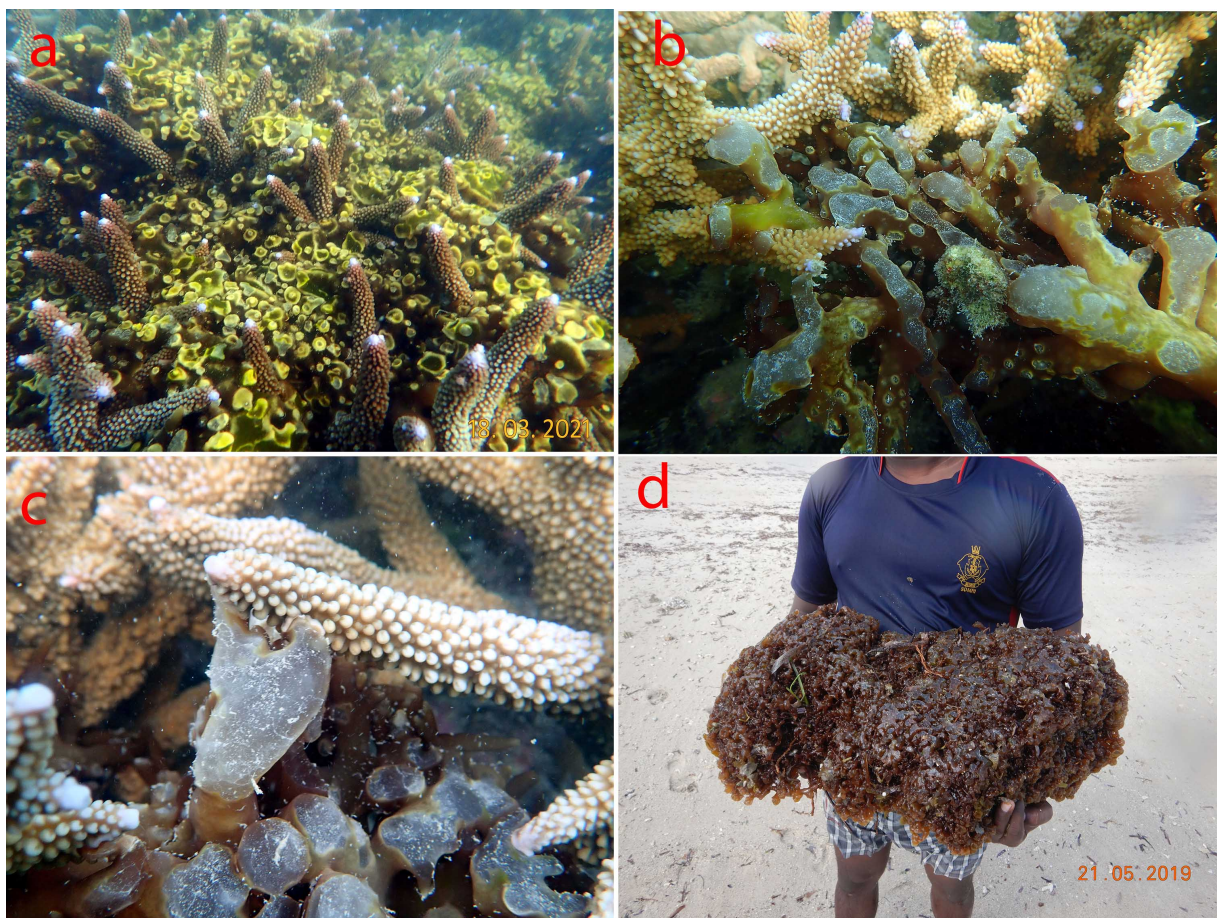


Figure 6. Invasion of *K. alvarezii* on the reefs of Valai and Thalaiyari islands in Gulf of Mannar; a, *K. alvarezii* forming thick mats over live coral colonies in Valai Island (09°11'14.78"N; 78°56'23.99"E); b and c, Point of contact and the attachment of *K. alvarezii* on live corals; d, Washed ashore mat of *K. alvarezii* in Thalaiyari Island (Lat. 9°10'59.71"N; Long. 78°56'5.08"E).

and Thalaiyari islands ($R = -0.824$, $P = 0.00$) indicating the impact of *K. alvarezii* on the morphotype ACB. The correlation between the density of healthy and affected coral colonies was also negative on Valai ($R = -0.633$, $P = 0.011$) and Thalaiyari islands ($R = -0.824$, $P = 0.208$). One-way ANOVA showed a significant deviation between the covers of *K. alvarezii* in Valai and Thalaiyari islands ($F = 26.341$, $P = 0.00$).

Discussion

Destruction of habitat by means of destruction of the foundation species is one of the important damages caused by invasive organisms (Salimi et al. 2021). Thus the mortality of reef-building corals would directly affect the fragile coral reef habitat. In the present study, the area cover of *K. alvarezii* was observed to be inversely related to the area cover of live corals. There was a decrease of 9.1% of live corals on Valai Island between May 2019 and March 2021, and a decrease of 3.9% on Thalaiyari Island in response to the increasing *K. alvarezii* cover. The loss of corals of this magnitude within a short duration, if not addressed, will have a huge impact on the coral reef habitat. The affected acroporans eventually died due to the smothering effect caused by the overgrowth of *K. alvarezii*, which led to an increase in the dead coral cover at the affected sites. Among the two islands, Valai was the most affected by the *K. alvarezii* invasion as evidenced by the loss of a greater amount of coral biomass. Significant coral mortalities by the bio-invasion of *K. alvarezii* have been reported in GoM by the present study and many other previous studies (Chandrasekaran et al. 2008; Edward and Bhatt 2012a, b; Kamalakannan et al. 2014). Earlier, a total reef area of 2,076 sq m from the Krusadai, Shingle, and Mulli islands was reported to be affected by *K. alvarezii* (MoEF&CC Project Report 2018) (Figure 2a, b; Figure S1). The decline of coral cover due to *K. alvarezii* invasion has been reported to be as high as 45.6% in GoM by Kamalakannan et al. (2014). Considering the damages caused by the invasive *K. alvarezii* on the coral ecosystem of GoM, the alga can be aptly termed as a “destructive invasive species” and a “serious danger to coral reefs” as coined by the Global Invasive Species Database (GISD) of International Union for Conservation Network (GISD 2022).

Once *K. alvarezii* overgrew, it smothered and killed the live coral colonies as reported by many other studies (Chandrasekaran et al. 2008; Edward et al. 2012a, b). It is also to be noted that there was no significant bleaching, disease outbreak, or any other natural or human-induced factors observed during the study period in the study sites at Valai and Thalaiyari islands. The decreased live coral cover at the affected sites is directly due to the invasion of *K. alvarezii* as there is a negative correlation between them. A relative decrease of 21% in coral cover and an increase of 30% in algal cover were reported for Valai Island between 2005 and 2017 (Raj et al. 2021). This benthic change was brought about by the multiple bleaching events encountered by corals (Edward et al. 2018; Raj et al. 2021). But the algae involved were native and *K. alvarezii* was never observed on this island before 2019. The present observation of the *K. alvarezii* invasion would further deteriorate the scenario on this island. A significant increase in dead coral cover was witnessed after the removal of *K. alvarezii* due to the exposure of dead skeletons of corals after the removal of the alga.

Kappaphycus alvarezii uses live corals as substrates and this capacity makes the invader comparatively more dangerous than the native macroalgae. *Kappaphycus alvarezii* has also been reported to affect the native macroalgae (Kamalakaran et al. 2014), and it is obvious from the study that the cover of other algae from the genera *Halimeda*, *Lobophora*, *Caulerpa* and, *Padina* decreased gradually as the cover of *K. alvarezii* increased. Even though it is not assessed in this study, fish abundance in the affected sites is probably reduced due to the decreased covers of corals and native algae. Decrease in the abundance of reef fish has been previously reported to be caused by increased biomass of *K. alvarezii* in GoM (Edward et al. 2012).

The present report on the invasion of *K. alvarezii* in the reef areas of Valai and Thalaiyari Islands extends the geographical range of this invasive alga within GoM. The distance from the first of the 21 islands (Shingle) to the tenth (Thalaiyari) is about 45 km (Figure 1). After the first report of invasion in 2005 (Pereira and Verlecar 2005), *K. alvarezii* has spread to a distance of 40 km through vegetative propagation in the past 16 years as reported from many other studies (Woo 2000; Conklin and Smith 2005; Chandrasekaran et al. 2008; Edward and Bhatt 2012a, b; Kamalakaran et al. 2014; Sellers et al. 2015; Cabrera et al. 2019). This is facilitated by the transportation of fragmented branches from the cultivation sites in Palk Bay to GoM by the water movement (Chandrasekaran et al. 2008; Edward and Bhatt 2012a, b). A recent study by Cabrera et al. (2019) reported the transport of a fragment of *K. alvarezii* to Costa Rica from Panama by water currents. In the present study, the distance between the cultivation sites (in south Palk Bay) and Krusadai Island where the invasion was first reported is less than 4 km. There is regular water movement between Palk Bay and GoM via Pamban Pass, especially during the northeast monsoon (Jagadeesan et al. 2013; Krishnan et al. 2021). Since fishermen continue to cultivate *K. alvarezii* in Palk Bay, transportation of *K. alvarezii* fragments to GoM via currents is always a probability. Fragments and mats of *K. alvarezii* being washed ashore are observed frequently along the shores of GoM islands (Figure S2). Mandal et al. (2017) reported the observation of fragments of *K. alvarezii* from different islands in the Mandapam and Keelakarai regions.

Though drifting fragments of *K. alvarezii* are observed frequently in GoM and Palk Bay, colonization of these fragments requires proper substrates (MoEF&CC Project Report 2018). In certain islands of GoM, branching acroporans (ACB) grow tightly next to one another with branches interlocking. Such continuous stretches of interlocking branching acroporans have been reported to be the preferred substrates of *K. alvarezii* in GoM (MoEF&CC Project Report 2018). Krishnan et al. (2021) reported that 90.96% of *K. alvarezii* invasion in GoM was on branching corals. The present study observed that branching acroporans were the most abundant coral morphotype at the study sites in both Valai and Thalaiyari islands, which presumably enabled the fragments of *K. alvarezii* to colonize. The

drifting algal fragments get lodged among the branches of *Acropora* colonies, eventually entangling the whole coral colony and forming green mats over the top and lateral sides. Smith et al. (2002) reported that the cluster of apical cells present in the tip of each detached fragment was able to regenerate the whole thallus. Hence, the corals of the family Acroporidae (*Acropora* and *Montipora*) growing in tightly interlocking branching form are prone to *K. alvarezii* invasion in GoM. Such entanglement and colonization are possible in GoM considering the availability of such tightly interlocking branching acroporans. The corals in Palk Bay have not been reported to be significantly affected by *K. alvarezii* in spite of their proximity to the cultivation sites due to the fact that boulder corals dominate the reefs of Palk Bay and there is no continuous stretch of interlocking branching acroporans (Edward et al. 2015).

There was a severe coral mortality in 2016 in GoM due to bleaching caused by elevated sea surface temperature, when the cover of ACB decreased significantly (Edward et al. 2018; Raj et al. 2021) and also the cover of *K. alvarezii* due to the lack of preferred substrates (MoEF&CC Project Report 2018) (Figure 2f; Figure S3). After the bleaching episode in 2016, corals in GoM started to recover and increased in area cover especially branching acroporans (Edward et al. 2018; Raj et al. 2021). The present establishment of *K. alvarezii* in Valai and Thalairyari islands can be attributed to the recovery of branching acroporans in continuous stretches. There is a clear distributional movement of *K. alvarezii* from the north to south of GoM (Figure 1). It is also to be noted that islands situated towards the south of GoM have a higher coral cover (Raj et al. 2021) with continuous stretches of branching acroporans. Hence, it is highly likely that fragments of *K. alvarezii* can establish in more southerly islands where continuous stretches of branching acroporans are available.

From 2011 to 2019, manual removal of *K. alvarezii* was carried out in GoM in a total area of 4,162 sq m (GOMMNP 2019) (Figure 2c, d; Figure S4). The present study emphasizes the positive impact of manual removal from Valai and Krusadai Islands in September 2019. This removal reduced the *K. alvarezii* cover in both the islands. However, the problem with *K. alvarezii* is that it has the capacity to grow back from minute fragments (Woo 2000) to establish as before (Figure S5). According to Conklin and Smith (2005), tiny bits of residual tissue were able to regrow with 61% recovery within two months after the removal. This capacity of *K. alvarezii* for faster recovery is obvious from this study as well as other previous studies in GoM (Kamalakaran et al. 2014; MoEF&CC Project Report 2018). Kamalakannan et al. (2014) reported that the increase in biomass of *K. alvarezii* after removal was as high as 182% in GoM. A biomass increase of *K. alvarezii* from 300 g to 734 g was observed within four months on Krusadai Island (Edward et al. 2012). Nevertheless, the unscientific removal of *K. alvarezii* by self-help group members also resulted in the fragmentation

of the alga and the drifting of algal fragments (Kamalakaran et al. 2014; Krishnan et al. 2021).

A combination of manual removal and biological control with the sea urchin *Tripneustes gratilla* resulted in an 85% reduction in invasive algae cover in Kane'ohē Bay of Hawaii (Neilson et al. 2018). Such research on the biological control of *K. alvarezii* in GoM should be carried out while continuing the manual removal as it is the only currently available control measure. A total of 600 households from the state of Tamil Nadu have been reported to be involved in *K. alvarezii* cultivation (Rameshkumar and Rajaram 2019) and these families earn a maximum of Rs. 10,000 per month after spending Rs. 63,000 on farming infrastructure (Rameshkumar and Rajaram 2019). In comparison, the estimated value of a 1.0 sq km coral reef area in the Gulf of Kachchh (west coast of India) is around Rs. 7.95 million per year (Dixit et al. 2010). Thus, the number of beneficiaries and their earnings are too small when compared with the economic benefits in the form of associated fishery and other ecological services to over 100,000 small-scale fisher-folk of the GoM coast. Moreover, the removal of *K. alvarezii* from the reef areas of GoM has cost Rs. 38.75 lakh (USD 52,651) during the period between 2011 and 2019 (GOMMNP 2019).

Macroalga cultivation in general is a good alternate livelihood option (Hurtado et al. 2014), which can reduce the fishing pressure. However, the cultivation of invasive *K. alvarezii* in the vicinity of coral reefs would directly disturb the ecological balance and impact the livelihood of thousands of low-income fisher-folk. In this context, cultivation of other native macroalgae such as *Hypnea musciformis* and *Sarconema filiforme* would be a good idea as these algae are also capable of yielding carrageenan (Ganesan et al. 2019). To keep their livelihood intact, the fishermen who depend on *K. alvarezii* culture can be trained in the culture of native macroalgae which are already available (Ganesan et al. 2019). Development of commercially viable large-scale culture technologies for other commercially important native macroalgae such as *Gelidiella acerosa* and *Gracilaria edulis* would also serve the intended purpose of alternate livelihood for fishermen without compromising the health of corals. Corals of GoM have suffered significantly from the invasion of *K. alvarezii* during the past two decades. Hence, in order to take quick remedial and management measures, the reef areas of GoM should be regularly monitored to record the status of invasion in areas already affected and the expansion of invasion to new areas. The damages caused by *K. alvarezii* to the corals of GoM should be a lesson to reef managers when introducing any exotic species near the reef areas in the future. Hence, to serve the purpose of the creation of GOMMNP, Government should not permit further cultivation of *K. alvarezii* near the reef areas of GoM, for only such stoppage will ensure complete protection of the already stressed and ecologically sensitive reef resources and guarantee the long-term livelihood benefits of dependent fisher-folk.

Acknowledgements

The authors express their thanks to the Ministry of Environment, Forest and Climate Change, Government of India (GOI), Science and Engineering Research Board, GOI and Gulf of Mannar Biosphere Reserve Trust, Government of Tamil Nadu for funding support; to Chief Wildlife Warden, Tamil Nadu Forest Department and Wildlife Warden, Gulf of Mannar Marine National Park for permissions; and to Suganthi Devadason Marine Research Institute for facilities. The authors extend their thanks to the reviewers who helped in enhancing the quality of the manuscript.

Funding declaration

Funding agency – Ministry of Environment, Forest and Climate Change, GOI. Specific grant numbers – 22-32/2010-CS.I (author received award – JKP). Funding agency – Science and Engineering Research Board, Department of Science and Technology, GOI. Specific grant numbers – EMR/2017/002510 (author received award – KDR).

Authors' contribution

JKP, TKA, RL – Research conceptualization; AA, RLL, KDR, JKP – Sample design and methodology; AA, RLL, KDR – Investigation and data collection; AA, RLL, KDR – data analysis and interpretation; JKP, RL, KDR – roles/writing – original draft; JKP, TKA, RL – writing – review and editing.

Ethics and permits

Permission to carry out research inside the Gulf of Mannar Marine National Park was obtained from Tamil Nadu Forest Department. Following are the permit numbers WL (5A)/35876/2013 and WL (A)/8996/2019.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Density of coral genera at the affected sites in Valai and Thalaiyari Islands.

Figure S1. The earlier invasion of *K. alvarezii* in Krusadai and Mulli Islands (Before the 2016 bleaching event).

Figure S2. Transportation of detached *K. alvarezii* fragments and mats by currents in Gulf of Mannar.

Figure S3. Coral bleaching in *K. alvarezii* invaded reef areas of Gulf of Mannar during 2016.

Figure S4. Manual removal of invasive *K. alvarezii* from the reef areas of Gulf of Mannar.

Figure S5. Regrowth of *K. alvarezii* after manual removal in Gulf of Mannar (Krusadai Island).

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