eReefs modelling suggests *Trichodesmium* may be a major nitrogen source in the Great Barrier Reef

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ABSTRACT

Trichodesmium can fix nitrogen that is later released into the water column. This process may be a major source of 'new' nitrogen in the Great Barrier Reef (GBR), but to date this contribution is poorly resolved. We have estimated the seasonal, spatial and annual contributions of *Trichodesmium* to the annual nitrogen budget of the GBR using the eReefs marine models. Models were run for the interval December 2010 to November 2012. During this period La Niña conditions produced record rainfalls and widespread flooding of GBR catchments. Model outputs suggest nitrogen fixation by *Trichodesmium* in the GBR (which covers about 348,000 km^2) contributes approximately 0.5 MT/yr, exceeding the total average annual riverine nitrogen loads (0.05–0.08 MT/yr). Nitrogen fixation loads are exceeded by riverine loads only if the comparison is restricted to inshore waters and during the wet season. The river pollution is likely to have impacts in freshwater wetlands, mangroves, seagrasses and in-shore coral reefs; while *Trichodesmium* blooms are likely to be less intense but more widespread and affect offshore coral reefs and other oceanic ecosystems. Phosphorus and iron are suggested to be potential drivers of *Trichodesmium* growth and nitrogen fixation. This result is provisional but reinforces the need for more detailed assessment and reliable quantification of the annual nitrogen contribution from nitrogen fixation in the GBR and other coastal waters. Such advances will improve understandings of the role of terrestrial nitrogen loads in the GBR and of terrestrial phosphorus and iron loads which can modulate *Trichodesmium* abundance. These findings will help to broaden the focus of water quality management programmes and support management to improve GBR water quality.

1. Introduction

1.1. Trichodesmium *and surface blooms*

Trichodesmium is a non-heterocystous, nitrogen-fixing (i.e., diazotrophic) cyanobacterium that is common in the surface waters of tropical and subtropical oligotrophic oceans (Capone et al., 1997; Westberry and Siegel, 2006). *Trichodesmium* can form extensive blooms, especially when skies and seas are clear and calm (Capone et al., 1997). Surface blooms range in colour from yellow to red and have been observed in the eastern tropical Atlantic Ocean (Ramos et al., 2005), south-western Pacific Ocean (Dupouy et al., 2011; McKinna et al., 2011), eastern Pacific Ocean, Arabian Sea and southern Indian Ocean (Westberry and Siegel, 2006). Nitrogen fixed from atmospheric dinitrogen (N$_2$) by *Trichodesmium* may later be released into the water

column by remineralisation (Mulholland et al., 2006) and may enhance the growth of other phytoplankton species (Wang et al., 2019; Zehr and Capone, 2020) and cause eutrophication of oligotrophic waters (Higgins et al., 2018).

Trichodesmium cells aggregate and form single trichomes (colonies) or larger colonies (tufts or puffs) in the water column (Capone et al., 1997). *Trichodesmium* possess very strong intracellular gas vesicles that allow them to occur at up to 200 m depth but also enable buoyancy that can lead to surface blooms in calm conditions (Heimann and Cirés, 2015). *Trichodesmium* buoyancy allows the shading of other non-buoyant phytoplankton species in the water column thereby interrupting light influx (Huisman et al., 2018). Additionally, *Trichodesmium* gas vesicles provide a high backscatter cross-section (Borstad et al., 1992). *Trichodesmium* possess unique phycobilipigments, phycourobilin (PUB) and phycoerythrobilin (PEB). PUB has an absorption peak at

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495 nm and PEB has absorption peaks at 545 and 565 nm (Subramaniam et al., 1999). These distinctive bio-optical features allow surface blooms of *Trichodesmium* to be readily detected and differentiated from unicellular cyanobacteria by satellites (Subramaniam et al., 1999).

Surface blooms form when *Trichodesmium* grows rapidly in surface waters due to elevated concentrations of certain nutrients (especially phosphorus and iron (Rodier and Le Borgne, 2008, 2010; Rahav and Bar-Zeev, 2017)) and when sea surface temperatures are between 24 °C and 28 °C (Paerl, 1996; Rodier and Le Borgne, 2008, 2010). Environmental conditions that favour accumulation at the surface also promote bloom development (Paerl, 1996; Rodier and Le Borgne, 2008, 2010). For example, low wind speed (<4 m s^{-1}) limits vertical mixing and enhances the surface accumulation of *Trichodesmium* colonies. However, blooms have also reportedly formed during higher wind conditions (up to 7.3 m s^{-1}), when temperature is > 26 °C (Rodier and Le Borgne, 2008). Low light (<10 μmol quanta m^{-2} s^{-1}) (Bell and Fu, 2005; Breitbarth et al., 2008) and salinity conditions (<22 PSU) (Fu and Bell, 2003) constrain growth and thus may limit bloom development. High temperatures (>28 °C) also reduce *Trichodesmium* growth and nitrogen fixation (Boyd et al., 2013; Hutchins et al., 2019; Ani and Robson, 2021). During bloom events, reddish-pink discolourations due to the leaching of PEB have been observed as an early indicator of bloom decay (Padmakumar et al., 2010).

The unique bio-optical properties of *Trichodesmium* enable the detection and mapping of surface blooms on marine environments using ocean-colour satellites (Westberry and Siegel, 2006; McKinna, 2015; Rousset et al., 2018; Blondeau-Patissier et al., 2018; Bell, 2021). The capability of satellites to detect dispersed single trichomes at greater depths below the water surface is limited, and thus estimates of *Trichodesmium* abundance and associated fixed-nitrogen loads calculated from satellite observations typically only capture surface bloom events (often associated with *Trichodesmium* senescence rather than peak growth (Bell et al., 2005; Jyothibabu et al., 2017)).

1.2. The need for quantifying the nitrogen contributed by Trichodesmium to marine ecosystems

The contribution of *Trichodesmium* to marine nitrogen budgets must be considered to understand the potential impacts of blooms on water quality. However, such estimates are difficult to calculate and are often variable. For example, an early attempt demonstrated that approximately half of the "new" nitrogen (i.e., nitrogen that is not generated from remineralised organic matter) in the subtropical North Pacific Ocean was produced by *Trichodesmium* (Karl et al., 1997). In the same year, Capone et al. (1997) reported that *Trichodesmium* added around 80 MT N annually to the world's tropical oceans (which cover about 1.5×10^8 km^2) during non-bloom conditions. A decade later, Westberry and Siegel (2006) used satellite ocean-colour data to map *Trichodesmium* occurrence and estimate the nitrogen it contributes to the world's oceans. Using this approach, they calculated that ~ 42 MT N yr^{-1} were added during bloom conditions and ~ 20 MT N yr^{-1} during non-bloom conditions. More recently, Wang et al. (2019) used an inverse biogeochemical and a prognostic ocean model to calculate a global nitrogen fixation rate of 163 MT N yr^{-1}, these vastly different loads demonstrate the uncertainty associated with these estimates. We also note that *Trichodesmium* influence on coastal waters nitrogen budgets has received little attention. As eutrophication driven by nitrogen (and other nutrients) is a major management challenge in many coastal settings (Bell et al., 2014; Damar et al., 2019; Barcellos et al., 2019; Bonsdorff, 2021), quantifying the nitrogen contributed by *Trichodesmium* is a fundamental knowledge gap.

1.3. Great Barrier Reef and water quality management

One high value marine ecosystem under pressure from increased nutrient loads is the Great Barrier Reef (GBR) of north-eastern Australia (Brodie et al., 2011, 2012). The GBR is the world's largest coral reef system containing about 3,700 individual reefs and stretching over 2,300 km along the north Queensland coast. The GBR is approximately 330 km across at its widest point and extends over an area of 348,000 km^2. Enshrined as a World Heritage Area (UNESCO, 1981), the GBR supports an abundance of marine life, provides economic, social and recreational services, and is worth about \$56 billion (in uncorrected 2013 Australian dollars) to the Australian economy (Anon, 2017). However, landuse changes since European settlement in coastal catchments draining into the GBR have increased riverine nutrient and sediment loads three–fourfold, reducing GBR water quality (McCloskey et al., 2021a,b). Increased nutrient loads have been linked to increased phytoplankton growth (Bell et al., 2014) and macroalgal growth (Chen et al., 2019), changes in the coral community composition (Thompson et al., 2014), increased coral disease (Willis et al., 2004) and the enhanced growth of crown-of-thorns starfish (COTS) larvae whose adults prey on corals (Fabricius et al., 2010; Babcock et al., 2016).

Addressing the negative impacts of eutrophication is a priority for the management agency responsible for the GBR (GBRMPA, 2021). However, monitoring and management programmes implemented over many years to improve GBR water quality caused by increased riverine nutrient loads have had limited success (Kroon et al., 2016; Dale et al., 2018). The Reef Water Quality Protection Plan (RWQPP, 2013) focuses on improving water quality by reducing the inflow of sediments and dissolved inorganic nitrogen to the GBR via the adoption of improved land management practices. The management focus on riverine nutrient loads exported to the GBR is appropriate, but the dynamics of these loads and possible interactions with nutrient sources originating within the GBR may have been overlooked. The possibility that *Trichodesmium* is a significant source of nitrogen in the GBR and may, in some years and areas, be more significant than terrestrial sources has long been suggested (Bell et al., 1999; Furnas et al., 2011; Messer et al., 2017; Erler et al., 2020; Bell, 2021). These studies used various methods to estimate nitrogen fixation. Bell et al. (1999) measured concentrations of *Trichodesmium* and nitrogen fixation rates from available observations of *Trichodesmium* whereas Furnas et al. (2011) used weakly-constrained values for *Trichodesmium* nitrogen fixation rates and abundance to derive their estimate. Bell (2021) used satellite ocean-colour data to determine his estimate. None of these studies provide a detailed understanding of the drivers of *Trichodesmium* growth and nitrogen fixation, nor of its spatial and temporal occurrence in the GBR.

To date *in situ* measurements of nitrogen fixation in the GBR are limited because measurement of nitrogen fixation has not been done in the region. However, the measurement of nitrogen fixation has been reported to be challenging and expensive (Mohr et al., 2010; Großkopf et al., 2012; Luo et al., 2012; Zehr and Capone, 2020). Accurate measurement and reporting of *Trichodesmium* concentrations are also challenging. The ability of *Trichodesmium* to form surface aggregations during bloom events will make it difficult to meaningfully and consistently quantify its abundance. For example, water quality sampling in the GBR follows standard oceanic sampling techniques and hence typically takes samples 0.5 m below the sea surface (and approximately 1 m off the seafloor). This routine monitoring approach is likely to miss surface aggregations of *Trichodesmium*. Another reason for limited field observations is the uneven distribution of buoyant surface aggregations of *Trichodesmium* due to the influence of wind stress (Capone et al., 1997). The vertical movement of *Trichodesmium* due to buoyancy changes add further complexities to the effective monitoring and measurement of *Trichodesmium* quantities in the water column. This is because the occurrence of a surface bloom does not indicate *Trichodesmium* are abundant at depth and the lack of a surface bloom does not confirm low *Trichodesmium* concentrations below the surface.

Finally, even when population counts are available, it is unclear how they relate to the cellular abundance as *Trichodesmium* colonies range from individual trichomes to larger "puffs" and "tufts" (Heimann and Cirés, 2015). Clearly, the effective management of water quality on the GBR must also understand the drivers of *Trichodesmium* growth and nitrogen fixation, and correctly measure nitrogen fixation.

1.4. The contribution of Trichodesmium to the Great Barrier Reef nitrogen budget

Trichodesmium surface blooms have been detected and mapped on the GBR using ocean-colour satellites (Rousset et al., 2018; Blondeau-Patissier et al., 2018; Bell, 2021). As indicated above, these estimates generally omit *Trichodesmium* growing outside of bloom events, *Trichodesmium* located below the surface, and *Trichodesmium* located in cloud-covered areas. The accuracy of satellite-derived estimates of *Trichodesmium* fixed-nitrogen loads in the GBR may be substantially limited by these omissions (Bell, 2021).

Another approach to estimate the contribution of nitrogen fixation to GBR waters is to use a 3D coupled hydrodynamic-biogeochemical-sediment model that simulates nitrogen fixation as a function of environmental conditions and numerical representations of the key physical and biological processes involved. We adopted this approach and applied the eReefs marine modelling suite (Steven et al., 2019) to estimate the contribution of nitrogen fixation by *Trichodesmium* to the total annual nitrogen budget of the GBR. One key advantage of this approach over ocean-colour estimates is that the models allow a 3D calculation of *Trichodesmium* dynamics, which is important as *Trichodesmium* is often distributed vertically through the water column and not only as surface blooms detected by satellites (Rousset et al., 2018; Bell, 2021). Furthermore, the models can be used to dynamically calculate changing nitrogen fixation rates in response to the availability of dissolved inorganic nitrogen in the water, intracellular nitrogen, phosphorus and carbon stores, and light and temperature conditions. The capacity for such nuanced analysis is an important advance over coarse estimations. For example, *Trichodesmium* does not always fix nitrogen due to the energetic cost of nitrogen fixation relative to taking up available ammonium and nitrate (Oliver et al., 2012) and appropriate adjustments can be made with this modelling approach.

Here we use the eReefs marine models to provide more detail of spatial and temporal occurrences of *Trichodesmium* in the GBR, and of the contribution of *Trichodesmium* to the total GBR nitrogen budget. The eReefs models using the CSIRO-EMS (CSIRO Environmental Modelling Suite) suite of models (here-after, "EMS") were developed for prediction of ecosystem dynamics in the GBR at broad spatial (4 km and 1 km nominal grid resolutions) and temporal scales. EMS is a coupled 3D hydrodynamic, biogeochemical and sediment modelling system that simulates the physical state and water quality of the GBR (Steven et al., 2019). The eReefs EMS simulations have been used to study riverine nutrients exported from coastal catchments (Wolff et al., 2018; Baird et al., 2021), ocean acidification impacts on the GBR (Mongin et al., 2016, 2021), coral bleaching (Baird et al., 2018) and the redistribution of sediment loads delivered from terrestrial catchments (Margvelashvili et al., 2018). We use EMS simulations to quantify the annual nitrogen load produced by *Trichodesmium* in the GBR for under the conditions experienced in our model years. Although very few *in situ* measurements of nitrogen fixation in the GBR exist, our results support earlier claims (Bell et al., 1999; Furnas et al., 2011; Messer et al., 2017; Bell, 2021) that in many years *Trichodesmium* may contribute more to the annual nitrogen budget of the GBR than riverine runoff.

2. Methods

2.1. Model

The EMS code is available from https://github.com/csiro-coasts/EMS/ and the algorithms and scientific basis of its biogeochemical

model are fully described by Baird et al. (2020). Details of its application to the GBR are well described in many Refs. (Herzfeld, 2006; Margvelashvili et al., 2018; Baird et al., 2018, 2021; Mongin et al., 2016, 2021). A detailed skill assessment and model evaluation for the biogeochemical model are given by Skerratt et al. (2019) and Robson et al. (2020). The hydrodynamic model (SHOC — Sparse Hydrodynamic Ocean Code (Herzfeld, 2006)) uses a curvilinear orthogonal grid in the horizontal and fixed 'z' coordinates in the vertical. SHOC simulates the physical conditions of the GBR. The biogeochemical model simulates nutrient cycles, optical conditions, plankton (two size-based phytoplankton groups plus, *Trichodesmium* and two size-based zooplankton groups), benthic organisms (coral metabolism and symbionts, three seagrass groups, microalgae and macroalgae), detritus and sediment dynamics in the GBR. The sediment transport model simulates sinking, deposition and resuspension of suspended sediments and other particulate materials, and the vertical movements of *Trichodesmium* due to buoyancy changes.

In the version of EMS described by Baird et al. (2020), the temperature dependence of *Trichodesmium* physiological processes is assumed to increase exponentially with increasing temperature. However, the exponential parameterisation in the EMS is no longer suitable for the ongoing temperature increases in the GBR because high temperatures (>28 °C) reduce *Trichodesmium* growth and nitrogen fixation (Boyd et al., 2013; Ani and Robson, 2021). To accurately capture the effects of extreme temperatures occurring in the GBR, the temperature dependence of *Trichodesmium* physiological processes is optimally parameterised using the function developed by Norberg (2004):

$$\mu_{Tricho}^{max} = \left(1 - \left(\frac{T - T_{opt}}{0.5w}\right)^2\right)0.059e^{0.0633T}. \tag{1}$$

μ_{Tricho}^{max} is a fraction reduction from the maximum physiological rate at temperature T, T_{opt} is the optimum temperature at which μ_{Tricho}^{max} is maximal (μ_{Tricho}^{max} decreases when $T > T_{opt}$) and w is the width of the thermal niche of *Trichodesmium*. The values of w and T_{opt} used in the model are 18 °C and 26 °C, respectively.

From Baird et al. (2020), *Trichodesmium* growth rate is defined in the EMS as

$$\frac{\partial Tricho}{\partial t} = \mu_{Tricho}^{max}P^*N^*C^*. \tag{2}$$

See Tables 1 and 2 for variable and parameter descriptions. Nitrogen fixation by *Trichodesmium* occurs when dissolved inorganic nitrogen (DIN) is less than a critical threshold DIN_{crit}. In the EMS, it is assumed that DIN = $NO_3 + NH_4$. As a result, nitrogen fixation rate (N_{fix}) per cell is defined as:

$$N_{fix} = max \left(4\pi r D_{NO_3} DIN_{crit}C^*P^*\left(1 - N^*\right) \right.$$
$$\left. - 4\pi r D_{NO_3}\left[NO_3 + NH_4\right]\left(1 - N^*\right), 0 \right). \tag{3}$$

The energetic cost of nitrogen fixation is given as a fixed proportion of fixed carbon ($f_{N_{fix}}$) equivalent to a reduction in quantum efficiency, and as a proportion, $f_{nitrogenase}$, of fixed nitrogen:

$$\frac{\partial C_R}{\partial t} = -\left(1 - f_{N_{fix}}\right)\left(1 - f_{nitrogenase}\right)k_I. \tag{4}$$

The buoyancy adjustment of *Trichodesmium* in the water column is represented as the density difference between the cell (ρ_c) and the water (ρ_w). By Stoke's law approximation,

$$\frac{\partial Tricho}{\partial t} = -\frac{2gr_{col}^2\left(\rho_c - \rho_w\right)}{9\mu}\frac{\partial Tricho}{\partial z}, \tag{5}$$

where

$$\rho_c = \rho_{min} + C^*\left(\rho_{max} - \rho_{min}\right), \tag{6}$$

z is the distance in the vertical and μ is the dynamic viscosity of water. Detailed descriptions of the EMS *Trichodesmium* growth model are available in Robson et al. (2013) and Baird et al. (2020).

Table 1
State and derived variables for the *Trichodesmium* growth model.

Variable	Symbol	Units
Structural *Trichodesmium* biomass	$Tricho$	mg N m^{-3}
Nitrogen reserves	N_R	mg N cell^{-1}
Carbon reserves	C_R	mg C cell^{-1}
Phosphorus reserves	P_R	mg P cell^{-1}
Maximum nitrogen reserves	N_R^{max}	mg N cell^{-1}
Maximum carbon reserves	C_R^{max}	mg C cell^{-1}
Maximum phosphorus reserves	P_R^{max}	mg P cell^{-1}
Normalised nitrogen reserves	$N^* = N_R/N_R^{max}$	–
Normalised carbon reserves	$C^* = C_R/C_R^{max}$	–
Normalised phosphorus reserves	$P^* = P_R/P_R^{max}$	–
Molecular diffusivity of NO_3	D_{NO_3}	m^2 s^{-1}
Photon absorption rate	k_I	mol photon cell^{-1} s^{-1}

Table 2
Constants and parameters for the *Trichodesmium* growth model.

Variable	Symbol	Units	Reference
Acceleration due to gravity	g	9.81 m s^{-2}	–
Trichodesmium cell radius	r	5 μm	Robson et al. (2013)
Trichodesmium colony radius	r_{col}	5 μm	Robson et al. (2013)
Minimum cell density	ρ_{min}	900 kg m^{-3}	Calculated from observed sinking rates in Villareal and Carpenter (2003)
Maximum cell density	ρ_{max}	1050 kg m^{-3}	Calculated from observed sinking rates in Villareal and Carpenter (2003)
Critical threshold for N fixation	DIN_{crit}	10 mg N m^{-3}	Robson et al. (2013)
Fraction of energy used for nitrogenase	$f_{nitrogenase}$	0.07	Robson et al. (2013)
Fraction of energy used for N fixation	$f_{N_{fix}}$	0.33	Robson et al. (2013)

2.2. Model forcing

The regional hydrodynamic model was forced with outputs from a global circulation model, the 10 km Ocean Modelling Analysis and Prediction System (OceanMAPS — https://researchdata.edu.au/ocean maps-analysis/1440629), meteorological data obtained from the 12 km Australian Community Climate and Earth-System Simulator (ACCESS-R — http://www.bom.gov.au/nwp/doc/access/NWPData.shtml) and observations of 22 river flows. Simulated physical conditions used to drive the biogeochemical model included: (a) wave data (wave amplitude, direction and period from the Bureau of Meteorology (BoM) regional wave model AUSWAVE-R (which is a 0.1° regional configuration of WAVEWATCH III)); and (b) P2R GBR Dynamic SedNet with 2019 catchment conditions of nutrient and sediment loads (McCloskey et al., 2017, 2021a,b).

The EMS hydrodynamic model configured at 4 km resolutions (GBR4 grid) with the modified temperature response function described above was used in this study. The GBR4 grid extends from 7.518°S to 28.679°S (Fig. 1) and has 600 × 180 grid cells in the horizontal, with 47 vertical layers. The 4 km resolution EMS has been thoroughly validated for the GBR region by Skerratt et al. (2019) and Robson et al. (2020), but the *Trichodesmium* growth model has not been evaluated against field observations due to a scarcity of relevant observational data. The model was run for two years from December 1, 2010 to November 30, 2012 because during this period, La Niña conditions were established and peaked between late 2010 and early 2011. Northern and eastern Australia, including the GBR catchments experienced severe storms and record high rainfall causing widespread flooding. As a result, most rivers discharging into the GBR lagoon experienced large flood flows, particularly in the southern half of the GBR causing increased riverine nutrient and sediment loads. The storms damaged 15% of the total coral reef area within the GBR, with approximately 4% experiencing structural damage (Beeden et al., 2015). Likewise, about 16% of mangroves in Hinchinbrook Island experienced severe windthrow (Asbridge et al., 2018) and seagrass habitats declined (Mckenzie and Unsworth, 2011; McKenna et al., 2015).

2.3. Quantification of nitrogen load from nitrogen fixation

R software version 4.0.5 (R Core Team, 2021) was used for simulated data extraction, analysis and visualisation. The depth-integrated cumulative moving mean of the *Trichodesmium* nitrogen fixation rate ($Nfix_{rate}$ — mg N m^{-3} s^{-1}) of *Trichodesmium* was extracted from simulated data using the eReefs R package (Robson, 2018). The fixed-nitrogen load was calculated for the area of the Great Barrier Reef Marine Park (GBRMP) rather than the whole 4 km EMS domain (Fig. 1). Modelled nitrogen fixation was calculated daily and integrated over the 3D volume of the GBRMP, obtained from https://www.gbrmpa.gov.au/about-us/resources-and-publications/spatial-data-information-services.

To estimate the total annual fixed-nitrogen loads in the GBR cross-shelf waterbodies, $Nfix_{rate}$ was extracted from simulated data using the three cross-shelf waterbodies defined by Belperio (1983). The waterbodies distinguished by Belperio (1983) include: the inner-shelf between 0–20 m deep dominated by terrigenous sedimentation; mid-shelf between 20–40 m deep characterised by palimpsest sedimentary zone; and the outer-shelf between 40–80 m deep where reefal sediments dominate. Fig. 2 shows the cross-shelf waterbodies in the GBR based on our extracted simulated datasets. As the size of cross-shelf waterbodies varies significantly (inner-shelf ∼ 25,390 km^2; mid-shelf ∼ 64,180 km^2; outer-shelf ∼ 92,360 km^2) the total annual fixed-nitrogen load is estimated in both kg m^{-2} and tonnes.

2.4. Statistical models

Generalised additive models (GAMs) were used to relate simulated *Trichodesmium* concentrations and nitrogen fixation rates to environmental factors. While EMS provides a complex mechanistic model to predict *Trichodesmium*, statistical analysis of the results can provide a simpler predictive model and shed light on environmental drivers of *Trichodesmium* growth. GAMs were used to identify the emergent properties/patterns of simulated results.
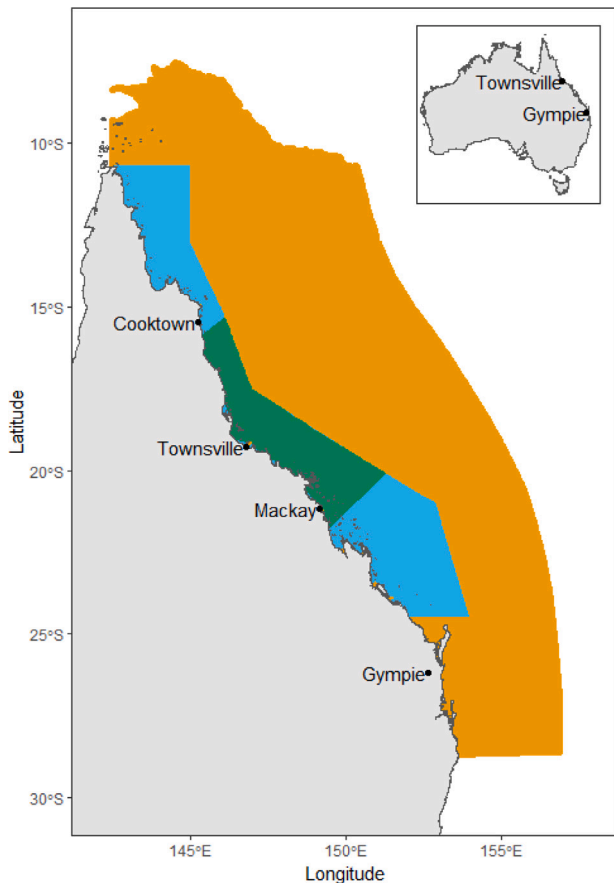
Fig. 1. Map showing the GBR4 domain (orange), the Great Barrier Reef Marine Park (GBRMP) Boundary (soft blue and green) and Central GBR (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
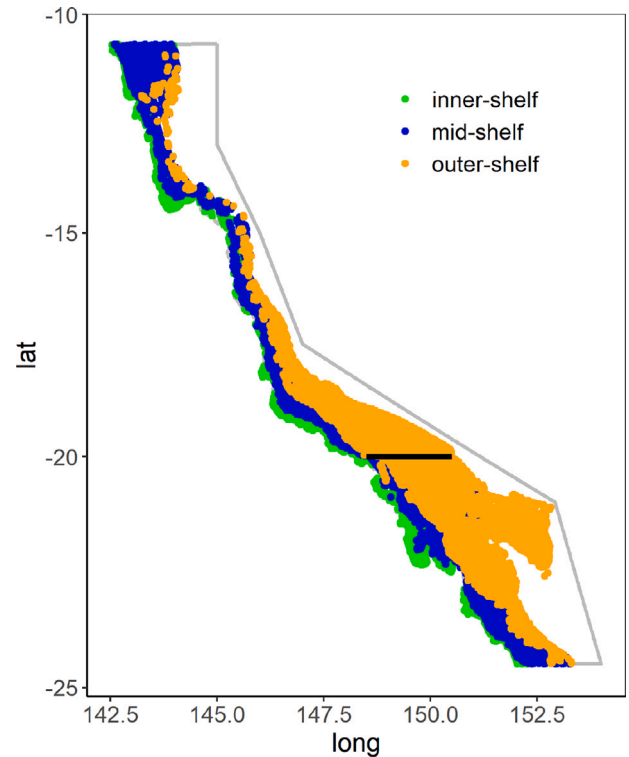

Fig. 2. Map showing the cross-shelf waterbodies in the Great Barrier Reef Marine Park (GBRMP) boundary (grey). Inner-shelf is 0–20 m deep, mid-shelf is 20–40 m deep and outer-shelf is 40–80 m deep (Belperio, 1983). The black line represents a transect on the cross-shelf waters that starts from the geolocation (20°S, 148.5°E) and ends at (20°S, 150.5°E). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Emergent properties are relationships or patterns observed in nature that occur as ecosystem functions and are key indicators to assess that models correctly capture important biogeochemical processes. To create simulated datasets of *Trichodesmium* concentrations and nitrogen fixation rates that are used for GAM analyses, 15,000 depth-integrated data points were randomly selected from GBRMP grid coordinates. The GAMs implemented in R (R Core Team, 2021) using the splines package are defined as:

$$lm(\text{Trichodesmium N} \sim ns(\text{DIN}, df = 5) + ns(\text{SST}, df = 5) + ns(\text{day}, df = 3)$$
$$+ \ ns(\text{salinity}, df = 4) + ns(\text{depth}, df = 4) \quad (7)$$
$$+ \ ns(\text{DIP}, df = 4) + ns(\text{PAR}, df = 5))$$

and

$$lm(\text{N-fixation rate} \sim ns(\text{DIN}, df = 2) + ns(\text{SST}, df = 5) + ns(\text{day}, df = 1)$$
$$+ \ ns(\text{salinity}, df = 4) + ns(\text{DIP}, df = 5) + \quad (8)$$
$$+ \ ns(\text{PAR}, df = 5)),$$

where df values represent the degrees of freedom of variables that are statistically significant (p-value ≤ 0.05) and best fit the data. Depth variable was not included in (8) because it was non-significant. *Trichodesmium* N is the structural *Trichodesmium* nitrogen indicating *Trichodesmium* abundance (biomass), day is day of the year (1 to 365) and SST is simulated sea surface temperature. DIN is the simulated concentration of dissolved inorganic nitrogen, DIP is the simulated concentration of dissolved inorganic phosphorus, depth is depth of the seafloor at the corresponding latitude/longitude geolocation and PAR is simulated photosynthetic active radiation at midday.

3. Results

3.1. Estimated total annual fixed nitrogen for the Great Barrier Reef and for cross-shelf waters

The annual load of nitrogen fixed by *Trichodesmium* in the GBRMP estimated using the eReefs marine models is approximately 0.5 MT/yr; ~ 0.2 MT/yr is estimated for the Central GBR region alone (Fig. 3). The highest nitrogen load was fixed during spring (126 KT) and the lowest during summer (118 KT), however seasonal variations were small. In all seasons less nitrogen was fixed in the inner-shelf waters of the GBR and the highest nitrogen loads were fixed on the outer-shelf (Table 3). The total annual nitrogen load fixed in the inner-shelf is 5.6×10^{-4} kg m^{-2} or 14 KT, mid-shelf is 1.3×10^{-3} kg m^{-2} or 83 KT, and outer-shelf is 1.9×10^{-3} kg m^{-2} or 171 KT. Together these sum to 268 KT or approximately 0.3 MT/yr, noting that this yield is produced in shelf waters shallower than 80 m and thus does not include the entire GBRMP (see Fig. 2), which when included gives the total fixed nitrogen of 0.5 MT/yr. The total annual nitrogen produced per unit area in the GBR is 1.4×10^{-3} kg N m^{-2} yr^{-1}.

3.2. Seasonality of nitrogen fixation and environmental drivers

During summer and spring *Trichodesmium* is abundant (>0.8 mg N m^{-3}) in coastal (inner-shelf) areas especially in the Central and Southern GBR (Figs. 4 and 5). Fixed-nitrogen loads are also highest in the inner-shelf during summer and spring (Table 3). Mean SSTs range

Table 3

EMS estimates of the seasonal differences in annual total (tonnes (T)) and per unit surface area (kg m^{-2}) *Trichodesmium* nitrogen fixation contributions to the nitrogen budget within inner-, mid- and outer-shelf waters of the Great Barrier Reef from December 1, 2010 to November 30, 2011. The total N load (T) values consider area and depth (volume) differences between the different water bodies. Inner-shelf is 0–20 m deep, mid-shelf is 20–40 m deep and outer-shelf is 40–80 m deep. Seasons are defined as summer (from December 2 to March 1), autumn (from March 2 to June 1), winter (from June 2 to September 1) and spring (from September 2 to December 1).

Waterbody	Season	Total N yield (KT)	N production per unit area (kg m^{-2})
Inner-shelf	Summer	3.7	1.5×10^{-4}
	Autumn	3.3	1.3×10^{-4}
	Winter	3.1	1.2×10^{-4}
	Spring	4.0	1.6×10^{-4}
Mid-shelf	Summer	21.0	3.3×10^{-4}
	Autumn	21.1	3.3×10^{-4}
	Winter	19.1	3.0×10^{-4}
	Spring	22.2	3.5×10^{-4}
Outer-shelf	Summer	36.3	3.9×10^{-4}
	Autumn	45.5	4.9×10^{-4}
	Winter	44.4	4.8×10^{-4}
	Spring	45.2	4.9×10^{-4}
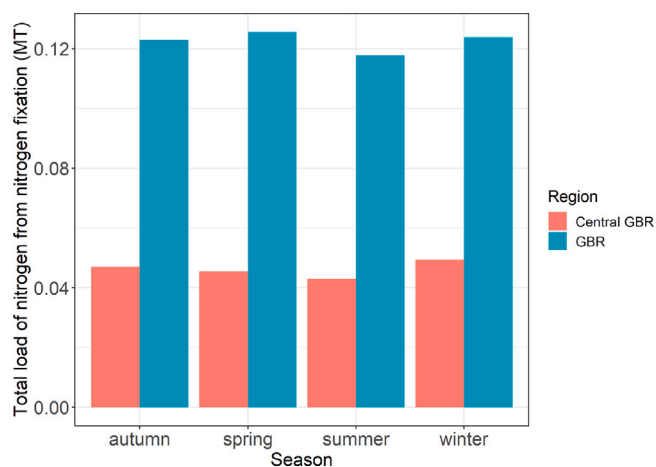
Fig. 3. EMS estimates of seasonal contribution of *Trichodesmium* nitrogen fixation to the nitrogen budget of the Great Barrier Reef and Central Great Barrier Reef from December 1, 2010 to November 30, 2011. Seasons are defined as summer (from December 2 to March 1), autumn (from March 2 to June 1), winter (from June 2 to September 1) and spring (from September 2 to December 1).

from 28 °C to 31 °C in summer (Fig. 4) and between 24 °C and 28 °C in spring (Fig. 5) in the regions where modelling indicates abundant *Trichodesmium*.

Simulated DIP is ≤ 25 mg P m^{-3} (0.807 mol L^{-1}) in regions of high *Trichodesmium* concentrations (>0.8 mg N m^{-3}) during summer in the GBR (Fig. 4). In contrast, during spring, simulated concentrations of DIP in most parts of the northern inner-shelf areas are ≤ 4 mg P m^{-3} (0.129 mol L^{-1}) (Fig. 5).

Trichodesmium concentrations decreased with depth across the cross-shelf waterbodies (Fig. 6). This is supported by the emergent patterns of the simulated data in Fig. 7 as *Trichodesmium* concentrations (biomass) decreased with depth (i.e., 0–200 m deep). Fig. 7 also shows that DIP predicts *Trichodesmium* concentrations in the GBR and that *Trichodesmium* concentrations slightly peak at 26 °C and increased in 34 ppt sea water salinity. The emergent relationships in Fig. 8 show that *Trichodesmium* nitrogen fixation rate increased with DIP, PAR, in 32 ppt seawater salinity and at temperatures between 20 and 30 °C whereas elevated DIN concentrations inhibit nitrogen fixation rates (Fig. 8).

4. Discussion

4.1. Comparison of the contribution of Trichodesmium *and river-derived nutrients to the annual nitrogen budget of the Great Barrier Reef*

The annual nitrogen load produced by *Trichodesmium* nitrogen fixation within the GBRMP calculated using our method was ~ 0.5 MT, with a smaller load of ~ 0.3 MT estimated for the restricted area included in the cross-shelf waterbodies which do not include the outer shelf waters exceeding 80 m depth. Importantly, both estimates are markedly larger than the 2010–2011 annual total nitrogen load of ~ 0.1 MT exported to the GBR from its catchments (Turner et al., 2013). Similarly, the annual nitrogen load contributed to the GBR by nitrogen fixation of 0.5 MT is well above published estimates of mean-annual riverine nitrogen load to the GBR of 0.08 MT estimated by Kroon et al. (2012) and 0.05 MT modelled by McCloskey et al. (2017, 2021a,b). Kroon et al.'s (2012) estimate is at the higher end compared to McCloskey et al.'s (2017, 2021a, 2021b) because the particulate nitrogen loads they used relied on an earlier and less accurate soil database. Although our model-derived fixed nitrogen loads for the entire GBR significantly exceed earlier estimates of mean-annual riverine loads of nitrogen, the fixed load added by *Trichodesmium* in inner-shelf areas (~14 KT) is less than the catchment-derived nitrogen load. It is, nonetheless, "new" nitrogen which to date has not been reliably quantified, and in dry years with limited runoff may comprise the major nitrogen source.

Our eReefs model-derived annual estimate of 200 KT/yr of *Trichodesmium* fixed nitrogen within the Central GBR also markedly exceeds the 14 KT estimated by Bell (2021) using ocean-colour satellite estimates of surface *Trichodesmium* distribution. Bell (2021) assumed a concentration of 20 mg m^{-3} over a 1 m surface mixed layer where surface blooms were observed, and that most nitrogen contained within *Trichodesmium* is derived from nitrogen fixation. Although Bell's (2021) estimate is comparable to earlier average fixed-nitrogen load estimates (Bell et al. (1999) ~ 3.3 KT/yr; Erler et al. (2020) ~ 6.7 KT/yr), he acknowledged his approach did not include variations in *Trichodesmium* concentrations with depth which would significantly influence load outputs. The eReefs model simulations applied here capture vertical distributions of *Trichodesmium* in GBR waters (Fig. 6). This important difference accounts for the much higher nitrogen yields calculated in this study compared to those derived from surface observations only.
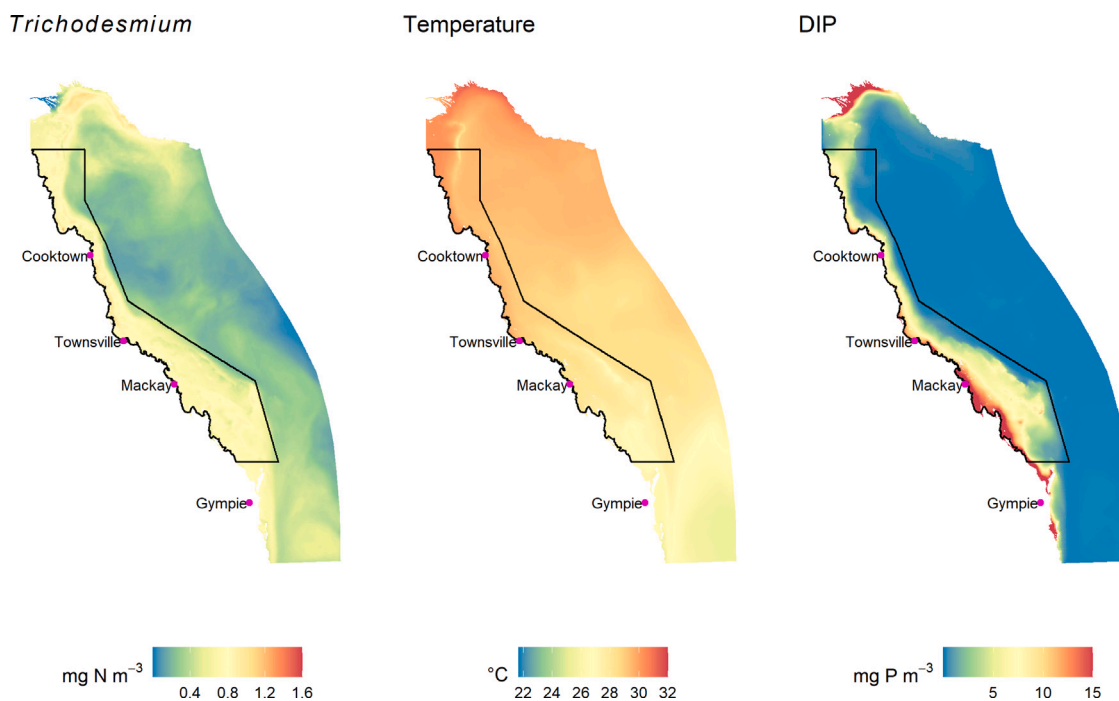
Fig. 4. Spatially-resolved simulated mean *Trichodesmium* concentrations, sea surface temperature and Dissolved Inorganic Phosphorus (DIP) during summer (from 2 December 2010 to 1 March 2011) in the Great Barrier Reef.
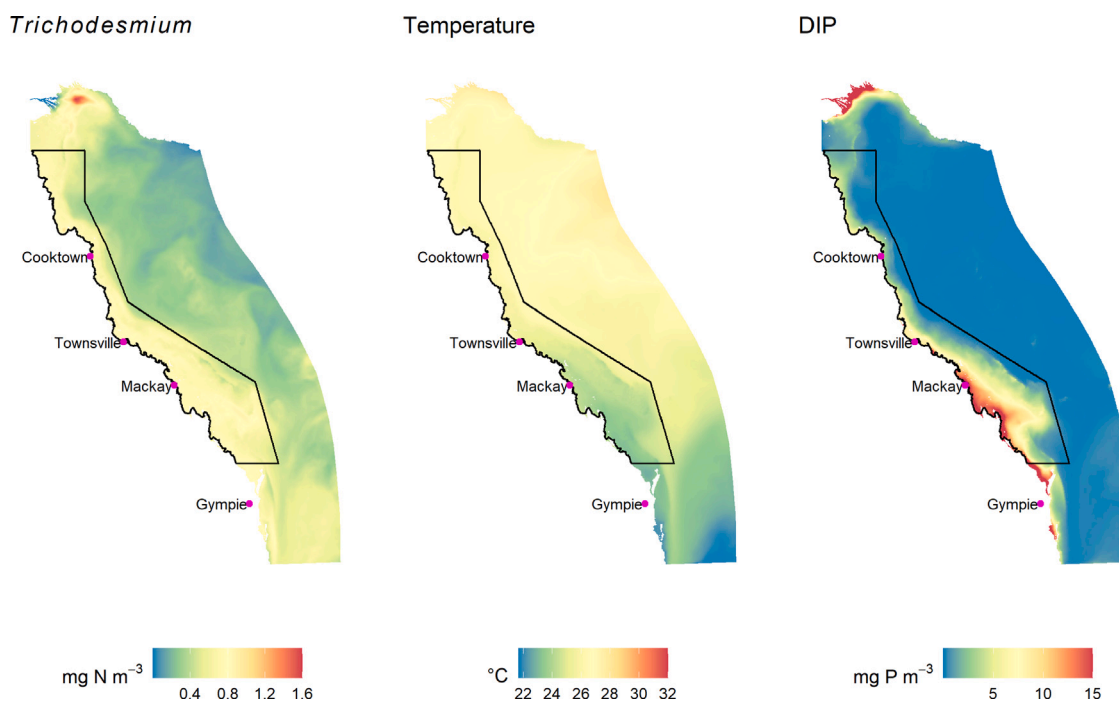

Fig. 5. Spatially-resolved simulated mean *Trichodesmium* concentrations, sea surface temperature and Dissolved Inorganic Phosphorus (DIP) during spring (from 2 September 2011 to 1 December 2011) in the Great Barrier Reef.

4.2. Comparison of EMS simulations and satellite-derived and field observations of Trichodesmium *bloom dynamics in the Great Barrier Reef*

Our EMS simulated results are consistent with satellite and field observations of *Trichodesmium* bloom dynamics in the GBR. Satellite observations from Blondeau-Patissier et al. (2018) showed increases in bloom sizes from the northern to southern GBR and specifically more frequent surface blooms of *Trichodesmium* during July–August

in the northern GBR and during November–December in the southern GBR. They also showed that the largest and most frequent surface blooms occurred in the southern GBR at temperatures > 24 °C and suggested that the increased bloom frequency observed in 2009–2011 could be attributed to the strong La Niña phases in 2010–2011 when temperatures were relatively high. Although Blondeau-Patissier et al. (2018) reported a clear seasonal pattern in *Trichodesmium* surface blooms in the GBR, our model suggests little seasonal variability. This
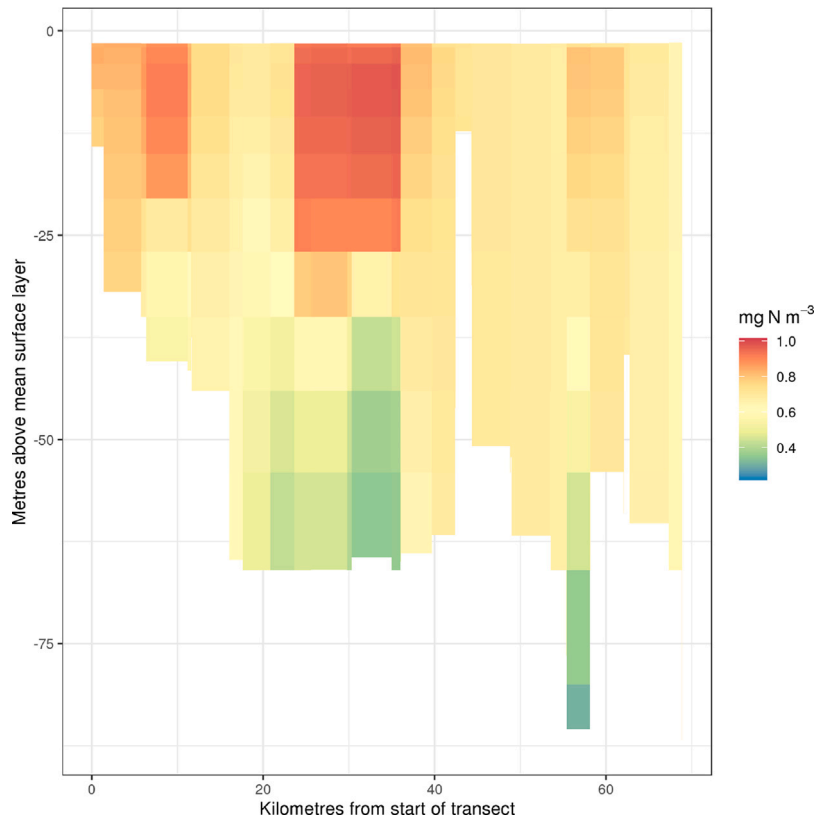
Fig. 6. The vertical distribution of simulated *Trichodesmium* concentrations observed along a transect on the cross-shelf waters of the Great Barrier Reef (see Fig. 2) on 10-08-2011. The transect starts from the geolocation (20°S, 148.5°E) and ends at (20°S, 150.5°E).
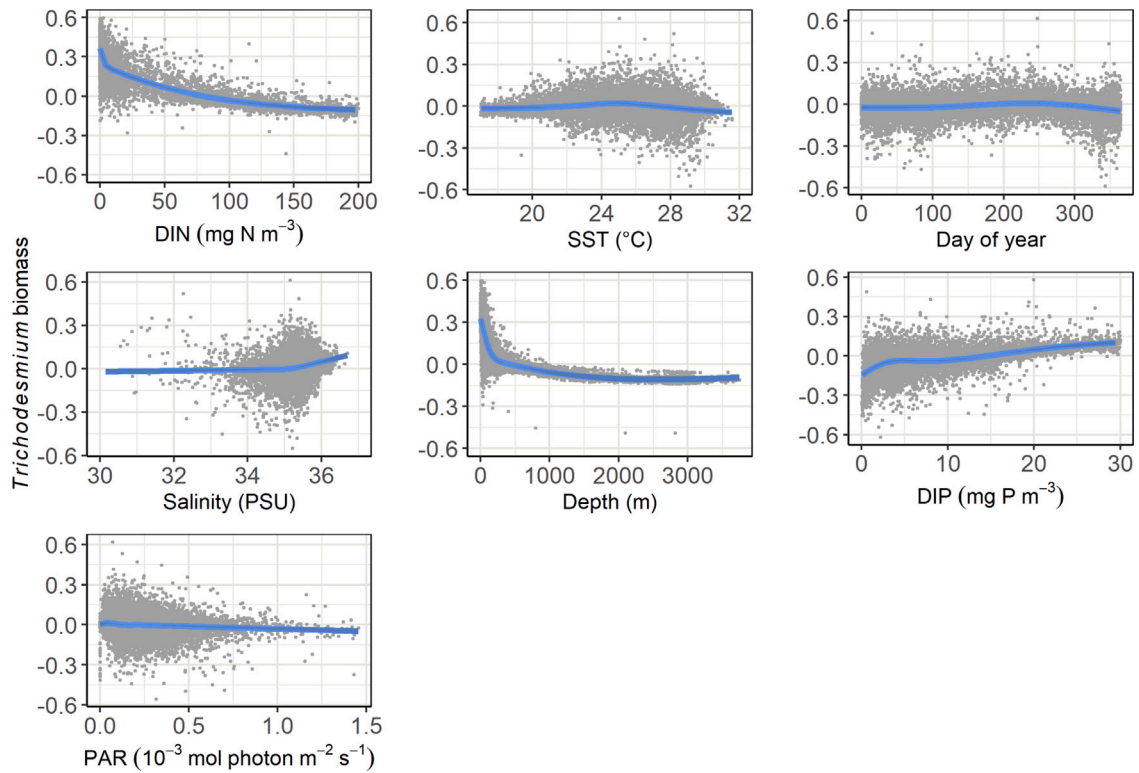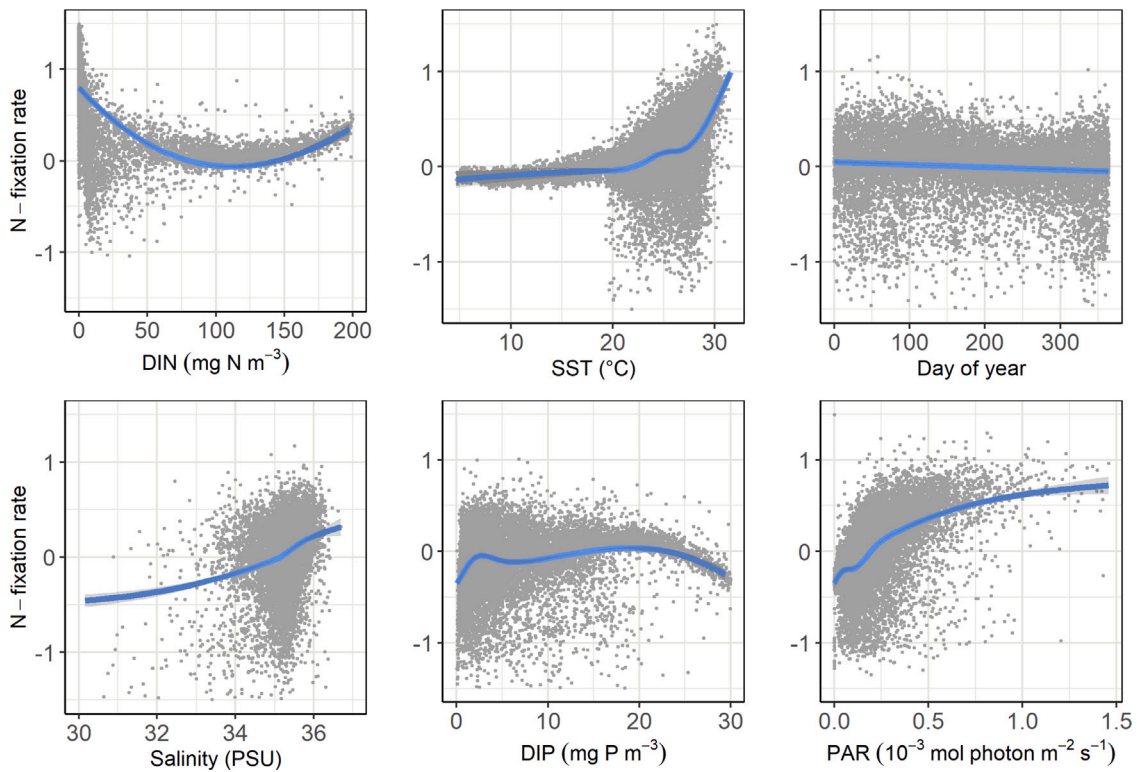

Fig. 7. Additive effects plots from the generalised additive model (GAM) of simulated depth-integrated environmental variables relative to simulated *Trichodesmium* biomass (concentrations — mg N m^{-3}) (Adjusted R^2 = 0.94). DIN is dissolved inorganic nitrogen, DIP is dissolved inorganic phosphorus, PAR is photosynthetic active irradiance, SST is sea surface temperature, depth is depth of the bathymetry at the corresponding geolocation and R^2 is coefficient of determination. To avoid fitting to outliers the *x*-axis of DIP and DIN were limited to a maximum of 30 mg P m^{-3} and 200 mg N m^{-3}, which correspond to about 95% of the simulated data.

Fig. 8. Additive effects plots from the generalised additive model (GAM) of simulated depth-integrated environmental variables relative to simulated *Trichodesmium* nitrogen fixation rate (10^{-6} mg N m^{-3} s^{-1}) (Adjusted R^2 = 0.8). DIN is dissolved inorganic nitrogen, DIP is dissolved inorganic phosphorus, PAR is photosynthetic active irradiance, SST is sea surface temperature and R^2 is coefficient of determination. To avoid fitting to outliers the *x*-axis of DIP and DIN were limited to a maximum of 30 mg P m^{-3} and 200 mg N m^{-3}, which correspond to about 95% of the simulated data.

may be because *Trichodesmium* are less concentrated at the surface and more evenly distributed with depth outside these months, or it may indicate an important missing environmental driver of bloom variability in the model. Our results agree with the latitudinal patterns reported by Blondeau-Patissier et al. (2018), which showed an increase in bloom sizes from the northern to southern GBR and the occurrence of the largest blooms at temperatures > 24 °C. Davies et al. (2020) showed that the two tropical Integrated Marine Observing System (IMOS) National Reference Stations (NRS), Yongala and North Stradbroke Island, experienced higher *Trichodesmium* abundance relative to NRS in Australian coastal locations outside the GBR. High *Trichodesmium* abundance was observed at Yongala during September–November and March–May, and lowest abundance during June–July. A decadal decline in *Trichodesmium* abundance was observed at North Stradbroke Island. Although Davies et al. (2020) showed decreased *Trichodesmium* abundance from the northern to southern GBR, they showed maximum *Trichodesmium* abundance at temperatures > 24 °C.

4.3. Environmental factors that influence Trichodesmium *abundance and nitrogen fixation in the Great Barrier Reef*

Our results suggest seasonal, spatial and emergent patterns of *Trichodesmium* abundance and nitrogen fixation in the GBR. The emergent relationships suggested by the GAM analyses indicate that the observed spatial and temporal patterns of *Trichodesmium* abundance and nitrogen fixation reflect a range of environmental factors. Simulated *Trichodesmium* concentrations and distribution are greatest during spring when mean temperatures range from 24 °C to 28 °C and the emergent patterns show peak *Trichodesmium* concentrations at 26 °C and increased nitrogen fixation at temperatures between 20 °C and 30 °C. Field observations in the GBR by Davies et al. (2020) note abundant *Trichodesmium* at temperatures between 24 °C and 26 °C and Blondeau-Patissier et al. (2018) established that larger *Trichodesmium* blooms

were more probable as sea temperatures warm. *Trichodesmium* abundance may be increasing globally with climate change. Global warming has been projected to increase ocean stratification and reduce the mixed layer depth (Capotondi et al., 2012). These factors have been associated with surface blooms of *Trichodesmium* and may increase the frequency of future blooms (Bergman et al., 2013). Increased temperatures (up to a threshold) will likely result in more frequent surface blooms and increased fixed-nitrogen loads in the GBR. This will have implications for nutrient cycling and other ecosystem processes such as phytoplankton growth.

In the GBR *Trichodesmium* grows best when DIP concentrations are between 0.08 and 0.12 μmol L^{-1} (Furnas, 1997) and fixes nitrogen at increased rates in conditions of elevated DIP concentrations (Erler et al., 2020). Our simulations indicate that the spatial distribution and timing of *Trichodesmium* abundance coincide with the seasons and regions (i.e., inner-shelf) of higher DIP concentrations (mostly > 0.12 μmol L^{-1}) (Figs. 4 and 5). This is supported by the emergent patterns in Figs. 7 and 8 that indicate DIP is a predictor of *Trichodesmium* concentrations and nitrogen fixation. Summer has the second highest contribution of fixed nitrogen on the inner-shelf regions (Table 3). This trend is likely driven by the higher DIP loads supplied from rivers during the summer wet season months which may reduce the inhibiting effect of high temperatures on *Trichodesmium* growth and nitrogen fixation (Mulholland and Bernhardt, 2005). Elevated DIP concentrations during summer in our models are likely due to increased and widespread river flows associated with Tropical Cyclone Tasha (December–January 2010/2011), Tropical Cyclone Anthony (January 2011) and severe Tropical Cyclone Yasi (February 2011) in northern Queensland. Frequent *Trichodesmium* blooms in the GBR have been attributed to the interacting effects of optimal temperature range and DIP availability (Davies et al., 2020). Therefore, the abundance of

Trichodesmium in conditions of high temperatures and DIP concentrations suggest that temperature or the availability of DIP alone does not control *Trichodesmium* blooms. There are complex interactions, and more favourable conditions in one environmental variable may offset less optimal conditions in others so that predicting *Trichodesmium* bloom occurrence using single factors can be problematic.

Dust storms and atmospheric input of nutrients via rainfall also deliver nutrients to the world's oceans (Herut and Krom, 1996). In particular, aeolian additions of iron and phosphorus are known to influence*Trichodesmium* growth and distribution. For example, high iron concentrations in the North Atlantic Ocean and Arabian Sea have been linked to *Trichodesmium* abundance (Sohm et al., 2011) and phytoplankton community composition has been shown to shift from small to large phytoplankton groups (e.g., *Trichodesmium* and diatoms) following episodes of dust influx (Shaw et al., 2008). In waters with low nitrogen concentrations but rich in iron and phosphorus *Trichodesmium* have a competitive advantage over other phytoplankton (Huisman et al., 2018). The dynamics of iron and phosphorus in the GBR are thus likely to influence *Trichodesmium* and associated fixed nitrogen loads. However, at present they remain poorly known and cannot yet be included in our model or estimates of nitrogen fixation.

Our results suggest that the highest fixed-nitrogen loads on the GBR occur in spring, when usually winds are relatively light and seawater salinities are normal. High loads of fixed nitrogen in the mid- and outer-shelf during spring (Table 3) suggest shelf-edge upwelling as a possible source of the phosphorus and iron needed for *Trichodesmium* nitrogen fixation. Upwelling is known to occur on the shelf adjacent to the Central GBR (Berkelmans et al., 2010) and may contribute to the high fixed nitrogen loads indicated for this region by our modelling. The emergent patterns show that in the model normal seawater salinity favours *Trichodesmium* growth and nitrogen fixation. Our results also indicate that the lowest nitrogen load from *Trichodesmium* occurs during the summer (wet season) months (Fig. 3). It is possible that the stronger winds (>6 m s^{-1}) and low light and salinity conditions (≪ 33 PSU due to flood events) that often accompany wet season storms contribute to this outcome; Blondeau-Patissier et al. (2018) noted such conditions are suboptimal for *Trichodesmium* bloom formation.

4.4. Comparison of the spatial and temporal variation of river-derived and Trichodesmium-derived nitrogen in the Great Barrier Reef

We note that while our estimate of the annual nitrogen contributed by *Trichodesmium* to the GBR is around fivefold greater than that delivered by rivers from the adjacent catchments, there are spatial and temporal (and possibly bioavailability) differences that warrant further appreciation. Firstly, much of the terrestrial nitrogen load is generally delivered to the GBR over a short period (typically weeks) over the summer wet season (December to April) (Brodie et al., 2011). Hence the ~ 100 KT of nitrogen contributed by terrestrial inputs in the 2010–2011 year (Turner et al., 2013) is comparable to the nitrogen contribution of 120 KT from *Trichodesmium* during the summer months. Secondly, the riverine flood plumes, which disperse the terrestrial nitrogen loads, cover a much smaller spatial area of the GBR. Because of these localised areas (particularly the nearshore areas) the inner-shelf (Table 3) may be exposed to more terrestrially derived nitrogen than *Trichodesmium* during the summer months (~3.7 KT), although the annual loads are comparable. Thirdly, the period of assimilation of nitrogen in the GBR from the terrestrial and *Trichodesmium* sources may be different, although *Trichodesmium* is very bioavailable. For example, the DIN component of terrestrial runoff is immediately bioavailable and triggers widespread algal growth (Brodie et al., 2011) that can be observed as green colouring in satellite images of flood plumes (Devlin and Schaffelke, 2009; Brodie et al., 2010). These features only persist while the plumes remain intact, but our modelling indicates nitrogen from *Trichodesmium* clearly dominates the nitrogen loadings from external

sources over the remaining seasons and is an essential component of nitrogen cycling in the GBR.

The much higher river-derived nitrogen concentrations in nearshore areas of the GBR will have more direct impacts on nearshore reefs. Since the vast majority of fixed nitrogen occurs in the mid- and outer-shelf waters, the potential increase in *Trichodesmium*-derived nitrogen loads due to increased bloom frequency could be important for the long-term health of offshore reefs in the GBR. However, high DIN concentrations have been reported to enhance coral heterotrophy and reduce bleaching (Ezzat et al., 2019). About 80%–90% of nitrogen fixed by *Trichodesmium* is released as DIN in seawater during the exponential growth and surface accumulation phases (Mulholland and Bernhardt, 2005). The concentration of DIN may not always be high within and around areas where surface blooms occur if the released DIN is rapidly taken up by other nearby phytoplankton. During and after surface bloom demise, *Trichodesmium* mortality produces large dissolved or particulate organic matter that is most likely buried in sediments (Furnas et al., 2011) or remineralised by bacteria (Furnas et al., 2005; Lønborg et al., 2018) both with potential oxygen-demand implications. Furthermore, nutrients stored in sediments may be released and transported to the water column to again promote *Trichodesmium* bloom formation and the growth of other phytoplankton species (Garzon-Garcia et al., 2021). Thus, the river pollution is likely to have impacts in freshwater wetlands, mangroves, seagrasses and in-shore coral reefs; while *Trichodesmium* blooms are likely to be less intense but more widespread and affect offshore coral reefs and other oceanic ecosystems.

4.5. Limitations of the EMS Trichodesmium growth model

The EMS allows the calculation of the vertical distribution of *Trichodesmium* dynamics and the rate of change of nitrogen fixation in response to changing environmental conditions. These are key advantages over satellite image informed estimates of *Trichodesmium* contributions to the annual nitrogen budget of the GBR. However, there are several areas where the model could be improved, most particularly by including physiological features not yet considered by the EMS *Trichodesmium* growth model. The physiological features include but are not limited to:

- Salinity effects on *Trichodesmium* growth, nitrogen fixation and pigmentation (Fu and Bell, 2003).
- Variations of phycobilipigments and their influence on light absorption and photoprotection (Subramaniam et al., 1999).
- Iron as a limiting nutrient for growth and nitrogen fixation (Sohm et al., 2011).
- Wind effects on the occurrence of surface aggregates of *Trichodesmium* (Capone et al., 1997).
- CO_2 effects on *Trichodesmium* nitrogen and carbon fixations (Hutchins et al., 2007).

We acknowledge that the EMS *Trichodesmium* growth model has not been evaluated against field observations in the GBR because very few *in situ* observations of *Trichodesmium* concentrations or nitrogen fixation rates are available. Despite these limitations, EMS simulated results are in accord with satellite-derived and field observations of *Trichodesmium* bloom dynamics in the GBR as indicated in Section 4.2. Our total-annual-production-per-unit-area estimate of 1.4×10^{-3} kg N m^{-2} yr^{-1} is also comparable to global fixed nitrogen estimates. These global estimates include Capone et al.'s (1997) estimate of 0.53×10^{-3} kg N m^{-2} yr^{-1} in the world's tropical oceans and Wang et al.'s (2019) 0.61×10^{-3} kg N m^{-2} yr^{-1} and 0.45×10^{-3} kg N m^{-2} yr^{-1} estimates in the Pacific Ocean and global oceans, respectively. Thus although validation of the model must be a priority, we are nonetheless confident that the outputs discussed here are reasonable.

5. Conclusions and implications for GBR management

This study provides a new line of evidence supporting the conjectured role of *Trichodesmium* as a major contributor to the nitrogen budget of the GBR. We quantified the annual nitrogen budget from *Trichodesmium* nitrogen fixation using the 3D EMS and showed that the total annual fixed-nitrogen load is much greater than the riverine nitrogen input. It is not yet possible to validate the *Trichodesmium* model and resulting nitrogen budget with currently available data, but our results highlight the need for further monitoring and measurement of *Trichodesmium* and nitrogen fixation in the GBR. We also identified key environmental factors that predict *Trichodesmium* growth and nitrogen fixation in the GBR (e.g., phosphorus). Our model results, which support estimates based on satellite observations suggest iron and phosphorus in catchment runoff may be more important drivers of nitrogen fixation in the GBR than previously understood. Validation of these results will enable managers to better target activities to reduce the influence of these nutrients and excess nitrogen loads.

Understanding the drivers of *Trichodesmium* growth and nitrogen fixation is essential for GBR water quality management. The modelling approach used in this study provides a valuable perspective on spatial and temporal variability critical for targeted monitoring and management — from assessing exposure and risks to developing adaptive management approaches. Targeted monitoring will help provide field observations for the evaluation of the accuracy of EMS and satellite-derived estimates of fixed nitrogen, measurements of iron riverine loads and will help commence iron studies in the GBR. Adaptive management plans and catchment regulations may need to change by incorporating the management of terrestrial phosphorus and iron loads if our findings of phosphorus and iron as important drivers of *Trichodesmium* growth and nitrogen fixation prove to be correct.

These recommendations will help inform management to better detect, monitor, and manage the occurrence and impacts of *Trichodesmium* blooms in the GBR. Our findings will enable a more holistic understanding of nitrogen budgets and cycling in the GBR and recognise the importance of *Trichodesmium* growth and nitrogen fixation as well as other nutrient sources such as dust storms and upwelling. Our findings will help broaden the focus of water quality management programmes in providing more information on improving GBR water quality. We recommend that future modelling studies on the contribution of nitrogen fixation by *Trichodesmium* should focus on understanding the spatial and inter-annual variability of *Trichodesmium* nitrogen and other nutrient sources, their impacts across the GBR and the drivers of *Trichodesmium* growth and nitrogen fixation.

CRediT authorship contribution statement

Chinenye J. Ani: Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **Scott G. Smithers:** Writing – review & editing, Supervision. **Stephen Lewis:** Writing – review & editing, Supervision. **Mark Baird:** Writing – review & editing, Methodology. **Barbara Robson:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Chinenye J. Ani reports financial support was provided by Australian Institute of Marine Science. Chinenye J. Ani reports financial support was provided by Queensland Water Modelling Network. Chinenye J. Ani reports financial support was provided by James Cook University.

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