

3.2 | Spatial and seasonal trends in *Trichodesmium*

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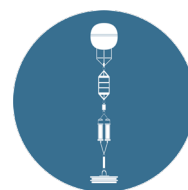
Summary

Trichodesmium is an important nitrogen fixer especially in oligotrophic areas of the oceans and a major component of primary production. Monitoring the changes in abundances and seasonal variations in *Trichodesmium* around Australia help us to understand which environmental variables are driving abundance and distribution. It appears that sea surface temperature and phosphate availability are the major drivers for increased abundances in the GBR. The increased abundances we are seeing over time at the Yongala National Reference Station may be a response to climate change and will have implications for nutrient cycling in the region.

Key Data Streams



Ships of Opportunity



National Reference
Stations

Rationale

Trichodesmium is a large filamentous marine cyanobacterium (**Figure 1**), notable for its ability to fix atmospheric nitrogen. It forms extensive, high biomass surface blooms visible from space. These blooms are known in Australia as “sea sawdust” and were noted by Captain James Cook sailing down the Great Barrier Reef in 1770. *Trichodesmium* blooms can be a major contributor to primary production in tropical systems. By fixing atmospheric nitrogen, *Trichodesmium* introduces “new” nitrogen into the low-nutrient waters (Blondeau-Patissier et al., 2018), supplementing the limited regenerated nitrogen. *Trichodesmium* is important in the global nitrogen cycle and is the only genus resolved in the eReefs biogeochemical model of the Great Barrier Reef (Skerratt et al., 2019).

When present in high densities, *Trichodesmium* can provide food and habitat for a diverse range of organisms including zooplankton (O’Neil, 1998) (**Figure 1**). *Trichodesmium*

produces potent neurotoxins, causing respiratory distress and contact dermatitis in humans (Schock et al., 2011). *Trichodesmium* thus has potential for significant environmental and economic impacts. Large blooms or surface expressions of *Trichodesmium* typically indicate cells and filaments no longer actively growing, and have ceased their characteristic vertical migration in the water column they use to search for optimal nutrient conditions (Villareal and Carpenter, 1990).

Whilst strongly associated with the tropics due to its preference for warm waters (the mean Species Temperature Index is 26.1°C from IMOS records), the genus is widely observed in the IMOS Continuous Plankton Recorder and National Reference Station samples (typically at low concentrations but occasionally in blooms) around Australia. A variety of morphological forms are observed, but true species diversity is poorly understood, and is currently the focus of genetic studies.



Figure 1. *Trichodesmium* morphology from the east coast of Australia. Straight filamentous forms from Yongala viewed under a) a light microscope (scale bar 100 μ m) and b) a scanning electron microscope (scale bar 10 μ m). c) A “Tuft” form from Yongala (scale bar 100 μ m) and d) a “puff” form from Port Hacking (scale bar 100 μ m). e) A composite collection of various forms of filamentous cyanobacteria from Port Hacking (scale bar 500 μ m). Images a) Ruth Eriksen CSIRO, b) Gustaaf Hallegraeff IMAS, c-e) Julian Uribe Palomino CSIRO (see Robson et al. in prep.). f) The marine copepod *Macrosetella gracilis*, which uses *Trichodesmium* as a food source and physical substrate for all aspects of its life-cycle (image: A. Slotwinski CSIRO).

Methods

Time-series observations of *Trichodesmium* around Australia were compiled from counts at the IMOS National Reference Stations (Eriksen et al. (2019) and the Australian Continuous Plankton Recorder survey. At the IMOS National Reference Stations, we used counts from zooplankton net samples rather than abundance estimates from phytoplankton bottles as is more typical. This was because zooplankton net samples (volume of water sampled = 10s of m³ water sampled) had far fewer absences of *Trichodesmium* than phytoplankton bottle samples (several litres) because of the larger volume sampled. We used additional observations of *Trichodesmium* from the Australian Phytoplankton Database available on the AODN (Davies et al., 2016). All data were sourced from the AODN (<https://portal.aodn.org.au/>; see the datasets “IMOS National Reference Station (NRS) - Zooplankton Abundance”, “IMOS - AusCPR: Phytoplankton Abundance”, and “The Australian Phytoplankton Database (1844 - ongoing) - abundance and biovolume”).

As *Trichodesmium* is most abundant at the Yongala National Reference Station, we explored its environmental drivers there. We used a linear model to investigate how abundance is related to a suite of environmental drivers including sea surface temperature, phosphate concentration, mixed layer depth, and month at this site. We used a harmonic term – a mix of sine and cosine waves – to model the seasonal cycle. SST data were sourced from GHRSSST (http://rs-data1-mel.csiro.au/thredds/catalog.sstL3Syts.html?dataset=l3s_sst_day_1dts) and Chl-a data from MODIS (<http://rs-data1-mel.csiro.au/thredds/dodsC/imos-srs/oc/aqua/>). Phosphate concentration and mixed layer depth were from concurrent measurements at Yongala (<https://portal.aodn.org.au/>; see the dataset “IMOS National Reference Station (NRS) - Salinity, Carbon, Alkalinity, Oxygen and Nutrients (Silicate, Ammonium, Nitrite/Nitrate, Phosphate)”). Predictors were retained in the model based on AIC (Akaike's Information Criterion).

To investigate the spatial distribution of *Trichodesmium* around Australia and how it varies seasonally, we developed a species distribution model using a generalised linear model using a suite of environmental predictors, including sea surface temperature, phosphate concentration, water column depth (bathymetry) and month. We used a negative binomial error structure, which can better model count data with a preponderance of zeros than a more typical Poisson distribution.

Results and Interpretation

Trichodesmium has been observed at almost all locations sampled around the Australian coastline, although it is rare outside tropical waters. Its presence in more southerly and seasonally cooler waters is often the result of prevailing winds and currents. In tropical waters of Yongala, *Trichodesmium*

has been observed in all but one of the monthly net samples collected since 2009 ($n = 120$), and an increase in abundance has been observed over the monitoring period (**Figure 2**). Abundances at Darwin, Rottnest Island, North Stradbroke Island and Port Hacking are generally lower, and vary more seasonally than at Yongala (**Figure 2**). Overall, abundances have declined significantly at North Stradbroke Island over the past decade. *Trichodesmium* is rarely observed in southern Australia, with one occurrence at Kangaroo Island and it has never been seen at Maria Island.

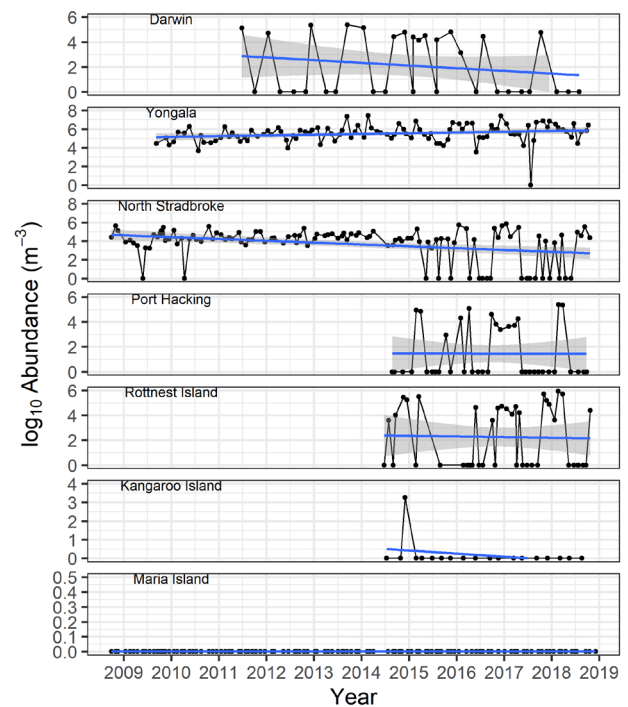


Figure 2. *Trichodesmium* abundance at the IMOS National Reference Stations, based on counts of monthly zooplankton net samples.

At Yongala, the strongest predictor of *Trichodesmium* abundance was the seasonal cycle, with abundance increasing in spring, dipping slightly in summer, before increasing again in autumn and declining in winter (**Figure 3**). The next most important predictor was Year, exhibiting a strong increasing trend in *Trichodesmium* abundance. We also found that more phosphate and deeper mixed layers corresponded to higher *Trichodesmium* abundances. SST, chlorophyll-a and iron concentration were not significant.

The generalised linear model of *Trichodesmium* around Australia showed that the more tropical National Reference Stations (Yongala and North Stradbroke Island) had higher *Trichodesmium* abundance compared with other areas (**Figure 4**). The decline in abundance from northern to southern areas is evident. There was also a marked seasonal cycle, very similar to that observed at Yongala. There were high abundances in spring and autumn, with a slight dip in summer, and a large dip in winter. There is evidence for vertical migration, with higher *Trichodesmium* abundances at night (note that we could not test for this at Yongala because

all samples were collected during the day). In terms of bathymetry, the *Trichodesmium* abundance declines strongly offshore. *Trichodesmium* is rare in water <20°C, peaks in water of ~23°C, then the abundance declines gently to 31°C. This is similar to other studies that have found a preferred temperature niche of 24–29°C (Bergman et al., 2013).

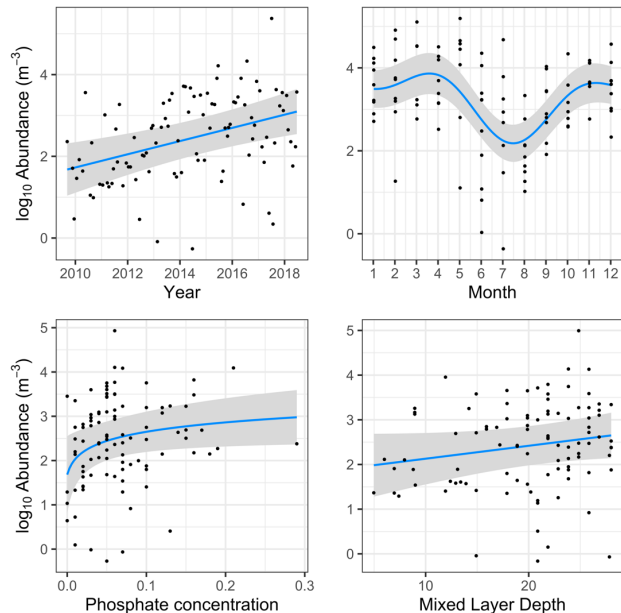


Figure 3. Effect plots for the linear model at the Yongala NRS, showing the influence of key parameters on *Trichodesmium* abundance.

Counterintuitively, *Trichodesmium* was inversely related to phosphate concentration, in contrast to the model from Yongala alone. *Trichodesmium* abundance increases with iron concentration, similar to the model for Yongala. *Trichodesmium* abundance increased with chlorophyll-a concentration, whereas chlorophyll-a was found not to be important at Yongala.

The map of the distribution of *Trichodesmium* based on the generalised linear model shows a tropical inshore distribution (Figure 5). Temperature was the most significant driver, and bathymetry was also important in determining *Trichodesmium* abundance (Figure 4). The model provides an integrated picture of the seasonal distribution of *Trichodesmium*, as well as expected abundance in areas that have not been sampled, or only sampled infrequently such as the North West Coast (Figure 5). It is clear that *Trichodesmium* extends further south during summer.

Implications for people and ecosystems

We found a significant increase in *Trichodesmium* abundance at Yongala. This increase will enhance the capture of new nitrogen into the oligotrophic waters of the region and will undoubtedly have implications for nutrient cycling. The increase is consistent with hypothesised impacts of climate change on phytoplankton communities in nutrient-poor regions.

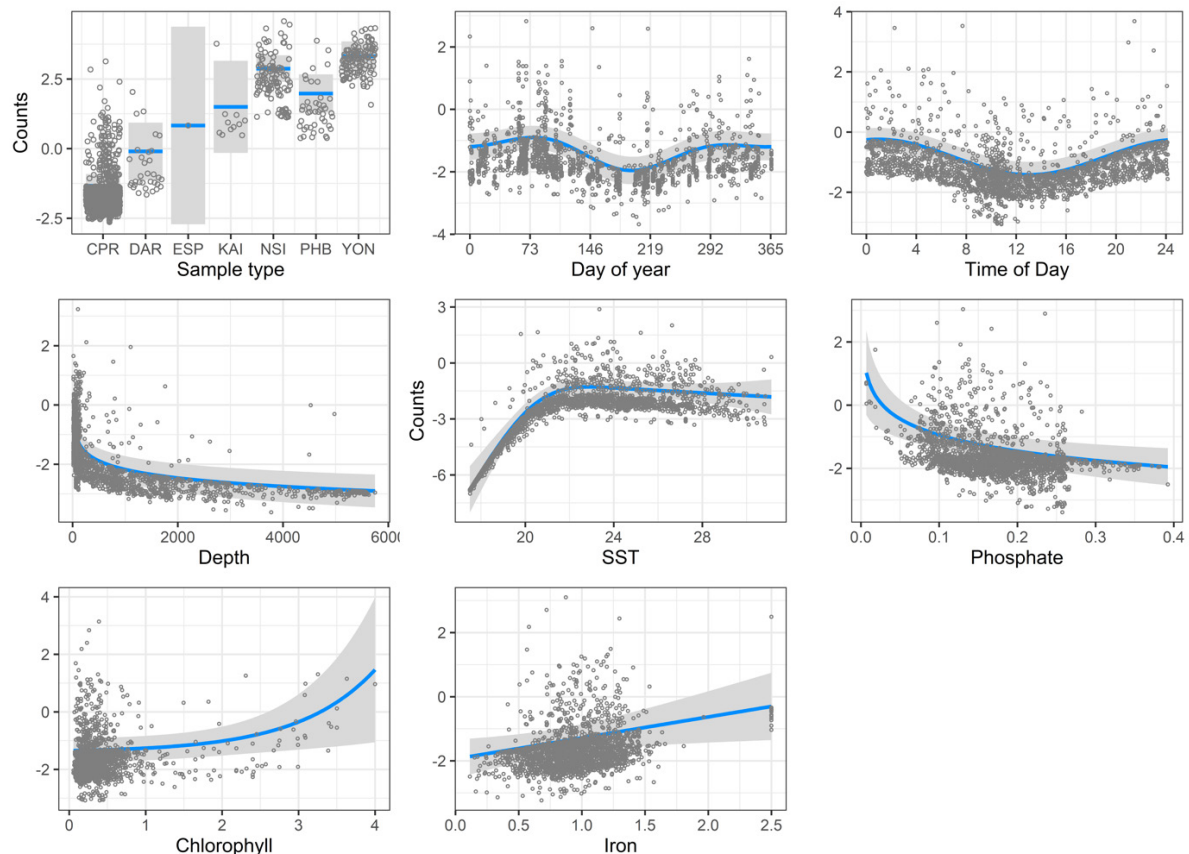


Figure 4. Negative binomial model output for distribution and abundance of *Trichodesmium* around Australia.

Because of enhanced stratification and the subsequent decline in surface nutrient conditions with climate change, nitrogen fixers such as *Trichodesmium* are expected to benefit (Beardall and Stojkovic, 2006).

Although surface expressions of *Trichodesmium* may extend for many hundreds of kilometres (Blondeau-Patissier et al., 2018) it is currently unknown whether the increase in *Trichodesmium* at Yongala is indicative of a broader phenomenon across the Great Barrier Reef. We also noted an overall decline in *Trichodesmium* abundance at North Stradbroke Island, although causes of this change are unclear. Although changes in *Trichodesmium* abundance can have large effects on nutrient cycling, the degree to which *Trichodesmium* is used directly by higher trophic levels is also a subject of debate. There is a small but obligate community that lives on it, which includes the harpacticoid copepod, *Macrosetella gracilis* (Figure 1f). This species uses the filaments as a food source and as a protective substrate when young (O'Neil 1998).

Our observations confirm that *Trichodesmium* is a tropical species, with high abundances at warmer temperatures and in warmer months (although slightly lower in the middle of summer). We see the distribution of *Trichodesmium* extending further south during summer and receding north during winter. The southerly extent of *Trichodesmium* could be a good indicator of climate change. We will be monitoring whether it is making more frequent and deeper incursions into southerly areas. This is similar to the red tide species *Noctiluca*, which we have seen increase its range further south.

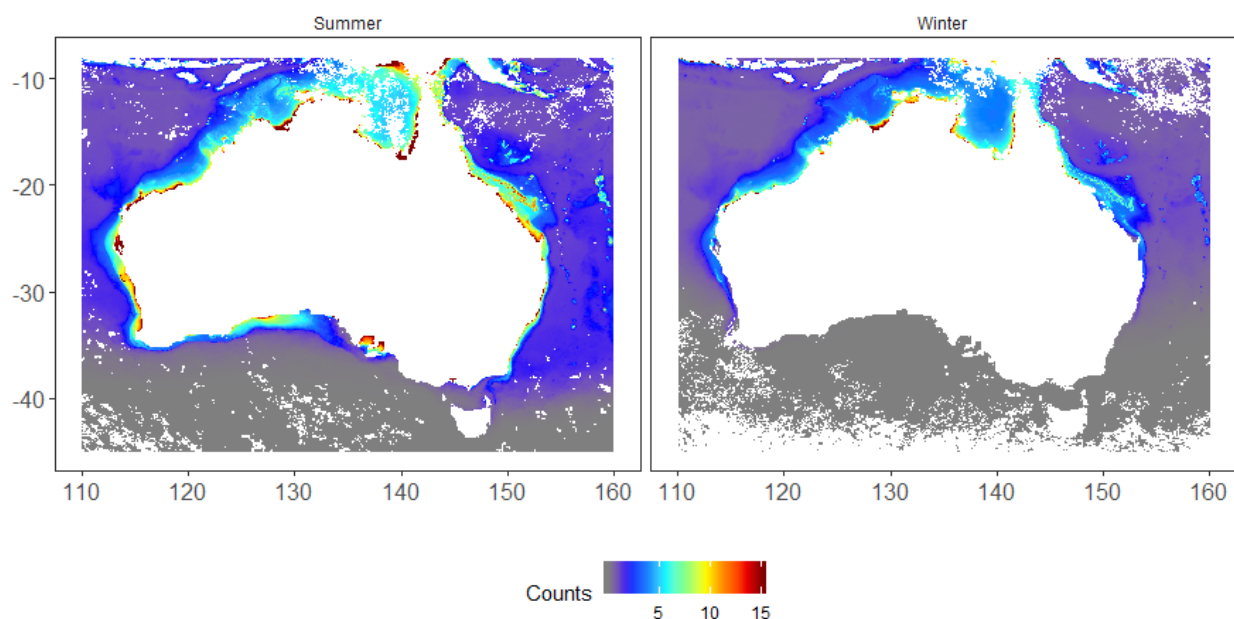


Figure 5. Seasonal distribution maps of *Trichodesmium* abundance, based on a negative binomial error structure with a suite of environmental predictors.

Acknowledgements

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Data Sources

IMOS National Reference Stations.

<http://imos.org.au/facilities/nationalmooringnetwork/nrs/>

IMOS Ships of Opportunity.

<http://imos.org.au/facilities/shipssofarportunity/>

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