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Acropora tenuis energy acquisition along a natural turbidity gradient

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Predicted future increases in both local and global stressors are expected to lead to elevated turbidity levels and an expansion of the geographical range of turbid coral reefs. Corals typically respond to elevated turbidity by increasing their rates of heterotrophy as means of compensating for low energy levels from reduced light and photosynthesis. We analysed *Acropora tenuis* energy acquisition along a natural turbidity gradient over two time points in Exmouth Gulf, Western Australia, using *in-situ* environmental data with coral physiology attributes and stable isotopes to assess trophic strategy. Our hypothesis was that as turbidity levels increased, so too would heterotrophy rates. Both $\delta^{13}C$ and $\delta^{15}N$ values decreased from the clear-water to the turbid sites, which along with Bayesian analysis revealed that all *A. tenuis* communities along the turbidity gradient are on a mixotrophic-heterotrophic feeding strategy scale. We propose that the low $\delta^{15}N$ levels at the most turbid site may result from a combination of *Acropora* physiological limitations (e.g., reduced feeding capacity) and highly variable turbidity levels. In contrast, the higher $\delta^{15}N$ at the clear-water site likely results from increased nutrient availability from additional sources such as upwelling. Our findings suggest that increased heterotrophy by coral hosts in turbid coral reef areas is not a universal pattern. Importantly, the loss of carbon in the turbid sites is not supplemented by nitrogen intake, which might suggest that Exmouth Gulfs *Acropora* communities are more vulnerable to future climate stressors and bleaching.

KEYWORDS

turbidity, coral reef, physiology, stable isotopes, feeding strategy

1 Introduction

Turbid coral reefs are light-limited coral habitats characterized by elevated turbidity, high sedimentation, and variable nutrient concentrations (Larcombe and Woolfe, 1999; Zweifler et al., 2021). It is predicted that future increases in local and global stressors will elevate turbidity levels and expand the geographic range of turbid coral reefs (Oppenheimer et al., 2019; Cartwright et al., 2021). To date, turbid reefs have been under-studied due to the logistical difficulties associated with working in low visibility conditions both directly (*in-situ*) and indirectly using remote sensing technologies (Morgan et al., 2017), resulting in less data and collective knowledge on turbid reef systems (Zweifler et al., 2021). In addition, in turbid coral reefs, increased light attenuation with depth typically confine them to shallow inshore water settings (<10 m depth) (Morgan et al., 2016; Luo et al., 2022) where higher and more variable sea surface temperatures (SST's) are likely to elevate the frequency and severity of coral bleaching (Brown et al., 2019). Yet, over the last decade, field observations suggested that turbid coral reefs are potentially more resilient to bleaching than clear-water reefs (Morgan et al., 2017; Browne et al., 2019; Teixeira et al., 2019; Sully & van Woesik, 2020).

Reef-building corals obtain nutrition autotrophically through their symbiotic algae, Symbiodiniaceae, which utilize sunlight and carbon dioxide to produce organic carbon and oxygen (Muscatine and Porter, 1977; Page et al., 2019). Additionally, corals can acquire nutrition heterotrophically through particle capture (Houlbrèque and Ferrier-Pagès, 2009). It is has been observed that coral in turbid reefs exhibit high rate of mixotrophy and/or heterotrophy as a physiological adaptation (Fox et al., 2018; Travaglione et al., 2023). These feeding strategies can compensate for energy deficits caused by the reduced light and photosynthesis (Anthony et al., 2009; Houlbrèque and Ferrier-Pagès, 2009; Wooldridge, 2014). In turbid reefs, the combination of increased heterotrophic feeding (Anthony and Fabricius, 2000; Anthony et al., 2007; Piniak and Storlazzi, 2008) and reduced UV stress from accelerated light attenuation (Luo et al., 2022) may enhance coral survival during heat stress events which often lead to coral bleaching (Grottoli et al., 2006; Browne, 2012; Hughes and Grottoli, 2013). Coral bleaching is initiated by the synergistic effect of high SST with high UV irradiance, leading to the photoinhibition of the symbiotic algae (Iglesias-Prieto et al., 1992; Warner et al., 1999).

Many studies have shown that shifts from autotrophy to heterotrophy can occur within species across a wide range of water depths (Palardy et al., 2005), turbidity (Anthony and Fabricius, 2000), or availability of nutrition resources (Fox et al., 2019). However, not all corals have the same ability to switch between autotrophy and heterotrophy (Houlbrèque and Ferrier-Pagès, 2009). Corals (e.g., *Platygyra*, *Turbinaria*) that are able to effectively switch to heterotrophy may have larger polyps to capture larger particulates in the water column, have lower surface area to volume ratios and/or are able to produce mucus which traps particulates as they settle on the coral (Porter, 1976; Conti-Jerpe et al., 2020). Although a review of heterotrophy in corals by Houlbrèque & Ferrier-Pagès (2009) concluded that feeding rates (and success) were a result of increased feeding effort rather than polyp size or morphology. Regardless, corals that are less effective at trapping particulates may acclimate to low light levels through other mechanisms such as increased symbiont densities and/or chlorophyll concentrations (Titlyanov & Titlyanova, 2002; Cooper et al., 2008). This enables the coral to increase its light capturing efficiencies and therefore maintain photosynthesis. These types of acclimatory responses have been observed in corals on turbid reefs such as Singapore (Browne et al., 2015) and nearshore Great Barrier reef (Rocker et al., 2017).

The effect of turbidity on coral physiology and their potential adaptation mechanisms has been investigated under both natural (Ferrier-Pagès et al., 2011; Browne et al., 2015) and experimental (Bessell-browne, 2017; Luter et al., 2021) conditions, mostly through coral physiology measurements such as photosynthesis, respiration, growth and feeding rates (Jones et al., 2020; Roitman et al., 2020; Tisthammer et al., 2020; Bollati et al., 2021). These studies provide estimations of energy sources under varying turbidity regimes. For example, Anthony (2000), showed under experimental conditions using sediment labelled with ^{14}C that the rates of sediment ingestion are a linear function of sediment load, with an assimilation efficiency of 50-80% in the coral *Acropora millepora*. However, the feeding strategies of the coral host and its symbiont algae (i.e., autotrophy, mixotrophy or heterotrophy) may vary in accordance with local environmental conditions, including nutrient concentrations, light availability, and temperature (Baumann et al., 2014; Krueger et al., 2018), as well as nutritional conditions such as the isotopic values of the dissolved inorganic carbon and nitrogen (Hoegh-Guldberg et al., 2004; Nahon et al., 2013; Seemann et al., 2013; Price et al., 2021). Hence, assessing feeding strategies under experimental conditions may not represent the absolute incorporation of the various nutritional sources by the coral holobiont. This is also the case when relying solely on direct measurements of photosynthesis and feeding rates. However, by employing the assessment of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes natural abundance in both the coral host and symbiont algae, using Bayesian ellipses metrics (Jackson et al., 2011), one can effectively identify the coral trophic strategy and isotopic niche (Ferrier-Pagès et al., 2011; Fox et al., 2018; Radice et al., 2019a; Conti-Jerpe et al., 2020). Despite the potential benefits of Bayesian approach in stable isotopes analysis, they have not been widely used for this purpose in coral research (Price et al., 2021).

The north-west coast of Western Australia (WA) provides a key location to explore the differences in coral energy acquisition between clear and turbid water reefs. This region is home to both Ningaloo Marine Park (NMP), a clear water nearshore coral reef situated on the western flank of Cape Range, and Exmouth Gulf, which hosts turbid water inshore reefs. Importantly, the area's remoteness limits local anthropogenic impacts, resulting in a naturally occurring east – west turbidity gradient along the same latitude (Dee et al., 2020; Cartwright et al., 2021). The NMP also experiences less frequent and more localised coral bleaching events compared to the Great Barrier Reef (Great Barrier Reef Marine Park Authority, 2019), with the last major heat-wave event recorded in 2011-2013 (Gilmour et al., 2019). This event caused several coral reefs to bleach along the WA coast, including Bundegi reef situated on the border between Ningaloo and Exmouth Gulf (Depczynski

et al., 2013; Gilmour et al., 2019). Unfortunately, no data was found in the literature on coral bleaching within the eastern to southern turbid reefs of Exmouth Gulf.

In this study we chose to work on the coral *Acropora tenuis*, from four sites along a natural turbidity gradient in Exmouth Gulf, WA and across two time points. *Acropora* is an important reef building coral genus characterized by high growth rate, complex structure that serves as habitat for various organisms, and widespread distribution across diverse habitats, reefs and regions (Lewis, 1984; Wallace and Willis, 1994). *Acropora tenuis* is common on both clear-water reefs where corals are exposed to comparatively high light levels, as well as on inshore turbid reefs where colonies are typically exposed to high levels of suspended particulate matter and nutrients (Anthony & Connolly, 2004; Anthony, 2006), suggesting high acclimation potential to variable environmental conditions (Conlan et al., 2017; Rocker et al., 2017; Strahl et al., 2019, 2019). To better quantify sources of energy and strategies for resource acquisition under different turbidity regimes, we combined (1) *in-situ* environmental data (e.g., turbidity, temperature) with (2) physiology attributes (e.g., chlorophyll *a* and symbiont density) and (3) stable isotope data for trophic strategy assessments (heterotrophy, mixotrophy or autotrophy). By combining analysis of coral physiological and trophic strategies, we provide a detailed evaluation of the coral holobiont energy sourcing, thereby increasing our broader understanding of physiological trade-offs in a naturally turbid versus clear-water setting (Mydlarz et al., 2010; Rocker et al., 2017). This knowledge is fundamental to improving our understanding of coral health and resilience status, which heavily influences the vulnerability of Acropora corals to extreme environmental changes. In addition, understanding of the variability in heterotrophic capacity relative to environmental conditions is important when determining which coral communities are more likely to survive future climate change events. Therefore, this information should be incorporated in coral reef management and conservation efforts.

2 Materials and methods

2.1 Regional geography

Exmouth Gulf is a shallow (mean depth 11.9 m) and large (~3000 km2 area), subtropical inverse estuarine embayment influenced by a strong tidal cycle (Figure 1) (Twiggs and Collins, 2010). Throughout the Gulf, coral reefs are predominantly found as small shallow fringing reefs that typically surround small reef islands (Bonesso et al., 2022). Turbidity conditions are caused by: (1) runoff due to high rainfall from the rivers (e.g. Ashburton River) flowing north to the Gulf that deliver a pulse of sediments and nutrients into the nearshore environment (Cartwright et al., 2021), (2) bottom sediment resuspension and transport by wind waves and strong tidal currents (Dee et al., 2020), (3) cyclones (90 km-h), which occur on average five times per year (Australian Bureau of Meteorology, 2022) delivering an influx of red siliciclastic sediment from the hinterland, and (4) commercial prawn trawling that causes a sediment disturbance (Lough, 1998; Orpin et al., 1999). The fringing Ningaloo Reef is a UNESCO World Heritage Site that extends for 300 km along the western side of Cape Range national park (Collins et al., 2003). The Ningaloo reef flat is separated from shore by a wide, ~2 to 4 m deep lagoon where surface waves drive a cross-reef flow with water driven into the lagoon and returning to the ocean through reef channels all year round (Wyatt et al., 2010). During summer it is dominated by the Ningaloo Current along with wind-driven equatorial surface current on the continental shelf that drives upwelling on the shelf slope (Hanson et al., 2005). Upwelling of deep water generates fluxes of inorganic nutrients that increase the particulate resources across the reef and are important source for the coral primary productivity and growth (Stuhldreier et al., 2015; Radice et al., 2019b). In contrast, Exmouth Gulf, located on the Pilbara continental shelf is highly dominated by the Leeuwin Current, an oligotrophic eastern boundary current that flows strongest during autumn–winter and La Nina years (Feng et al.,

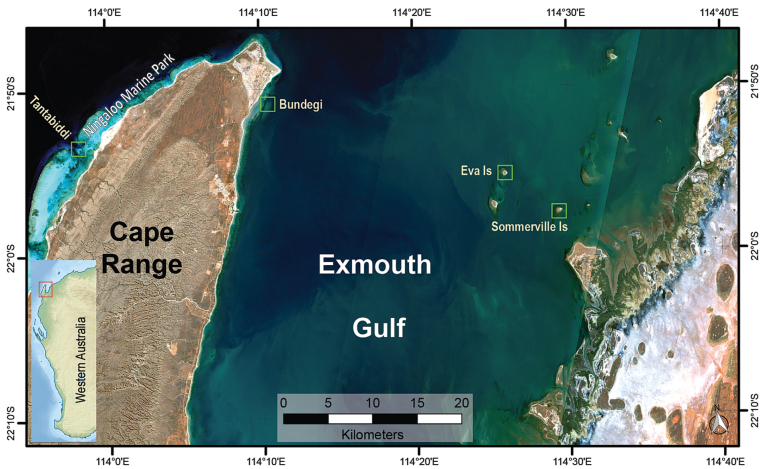

FIGURE 1
Map of the study sites at Exmouth Gulf and the Ningaloo Marine Park (green rectangles). Exmouth Gulf location on Western Australian coast (red rectangle in the small map, left hand side).

2003). By generating large-scale downwelling, it transports tropical water poleward and carries warm, low salinity, low-nutrient water to the Exmouth Gulf, thus, limiting productivity and species distribution (Smith et al., 1991; Hanson et al., 2005; Twiggs & Collins, 2010).

2.2 Study sites

This study took place at four shallow (2-4 m) sites across a turbidity gradient from Exmouth Gulf to the adjacent Ningaloo Marine Park (NMP) (Figure 1). Somerville (21°57'27.9"S 114° 29'35.3"E) and Eva (21°55'02.1"S 114°25'56.9"E) Islands, located on the eastern side of the Gulf, have similar fringing reef morphology and are naturally fluctuating turbid reefs that experience episodic (daily to monthly) severe turbidity (>150 NTU or approximately >50 mg L–1) events interspersed by periods of low turbidity (<15 NTU or approximately <5 mg L–1) or clear water (<2 NTU or approximately <0.5 mg L-1) (Dee et al., 2020; Zweifler et al., 2021). Bundegi Reef (21°50'07.7"S 114° 10'40.8"E), located at the north-western tip of the Gulf, is at the boundary of the NMP, and is a low turbidity patchy fringing reef (Speed et al., 2013; Doropoulos et al., 2022). In contrast, Tantabiddi (21°52'50.8"S 113°58'52.3"E) is part of the fringing reef of the NMP on the western side of Cape Range characterised by clear waters (Collins et al., 2003).

2.3 Environmental conditions

Turbidity and temperature data were logged *in-situ* at each site using data loggers (NTU-LPT, *In-Situ* Marine Optics, Bibra Lake, WA) that recorded the average of ten measurements every thirty minutes. Loggers were deployed horizontally at 30 cm above the seabed on a metal frame from May 2020 to October 2021. Turbidity, measured in nephelometric turbidity units (NTU), is the incident light scattered at right angles from suspended particles in the water column. Logger optics were cleaned every hour to avoid organic growth using an integrated wiper. Batteries were recharged, and data downloaded every 3-4 months. Raw data underwent a cleaning process to remove anomalously high values that exceeded the trend observed at a single time point prior to calculating the daily (24hr) average and plotting (Figure 2). We also obtained one day composite data of diffuse attenuation (Kd490; MODIS) used as a proxy for turbidity, and multi-scale ultra-high resolution (MUR) of sea surface temperatures (SST). These remote data sources provided

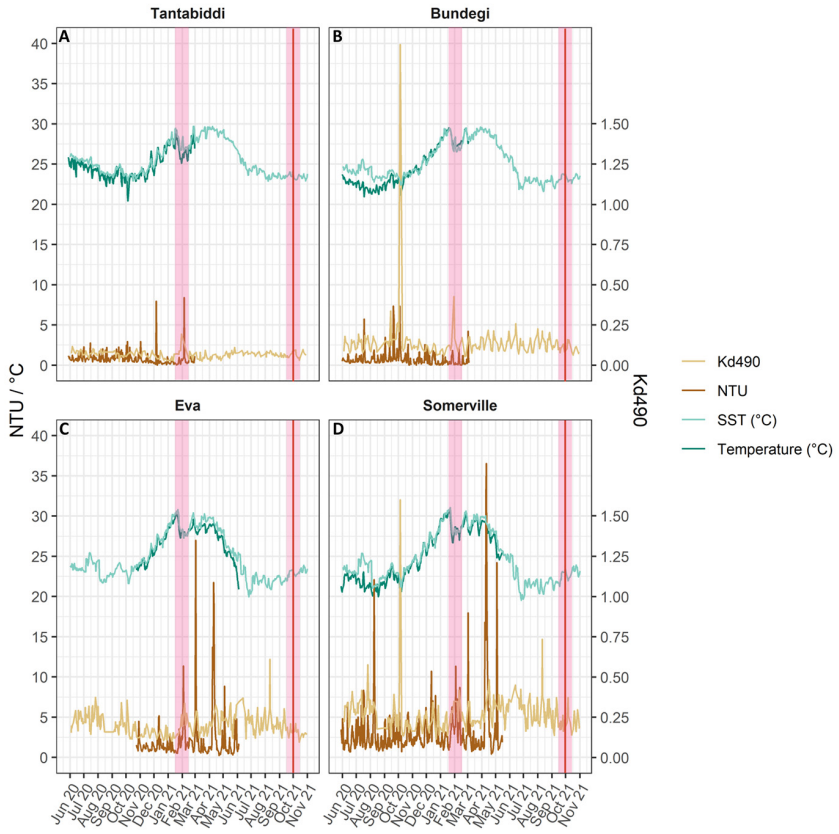

FIGURE 2
Left Y axis: Daily mean of NTU (brown), *in-situ* temperature °C (NTU data loggers; dark green) and SST °C (MUR; light green). Right Y axis: Daily Kd490 (Aqua MODIS; light brown). **(A)** Tantabiddi, **(B)** Bundegi, **(C)** Eva and **(D)** Somerville. Pink vertical lines highlight coral sampling times, red line indicate water sampling time.

an alternative when the *in-situ* data loggers failed (June-October 2021), allowing us to verify spatial differences in turbidity and temperature (Australian Bureau of Meteorology, 2022b).

2.4 Sample collection

Coral samples were collected to measure physiological attributes (chlorophyll *a* and symbiont density) and for stable isotope analysis. Between six to eight *Acropora tenuis* colonies (> 20 cm in diameter) within a ~15 m radius were tagged at each site. Each coral colony was sampled (3-5 fragments of ~5cm long) in February 2021 (end of summer) and October 2021 (end of winter) by SCUBA. Samples were placed in tagged bags with seawater and transferred to shore, where each individual sample was wrapped with aluminum foil before being snap frozen in liquid nitrogen (Grottoli et al., 2021). Samples were transferred in a dry shipper to a -80 freezer in the Indian Ocean Marine Research Centre (IOMRC) at the University of Western Australia until further analysis.

In October 2021, water samples were collected for the analysis of zooplankton (>167 µm) and phytoplankton (>67 µm) stable isotopes to identify potential carbon and nitrogen sources. A single sample, of approximately 1000 L of seawater from each site, was acquired using a bilge pump and preserved at -20°C prior to filtration. In the laboratory, duplicates from the defrosted samples were filtered using a pre-combusted (550°C for 4hr) 0.7 micron 47 mm glass fiber filters. Filters were than dried in an oven at 60°C for 48 hr and stored in a Ziplock bag with desiccant dehumidifier beads until further analysis. Due to technical issues no water samples were taken in February 2021.

2.5 Coral physiology

Two coral fragments from each tagged colony were processed to assess coral symbiont density and chlorophyll *a* (Chl *a*) concentration. Coral tissue was removed from the frozen coral fragments using an airbrush and filtered (0.22 uM) seawater (FSW) producing 15 ml tissue slurry. Skeletons were dried and kept for surface area measurement using the wax dipping technique (Stimson and Kinzie, 1991). Coral tissue slurry was homogenized for 2 minutes using an electrical tissue homogenizer (TissueRuptor, QIAGEN) and centrifuged at 3,000 g for 5 minutes to separate host and symbiont fractions. Additional centrifugation at 3,000 g for 5 minutes and washing with FSW was performed to isolate the symbiont for cell count and photosynthetic pigment extraction for Chlorophyll *a* concentration. Symbiont cells were counted in replicates of six using a Neubauer haemocytometer under a microscope and normalized to the coral surface area (cell cm^{-2}). Pigments were extracted for 24 h in 90% acetone at 4°C in the dark and Chl *a* concentration was measured at 630, 664, and 750 nm with a spectrophotometer (UV/VIS SP8001, Metertech Inc, Taiwan). Chl *a* concentration was determined using the equations offered by (Jeffrey and Humphrey, 1975) and normalized to surface area (µg cm^{-2}).

2.6 Stable isotopes

Stable isotope ($\delta^{15}N$ and $\delta^{13}C$) analysis was conducted separately for coral host tissue and symbiont in duplicates from five of the eight tagged colonies at each site. Samples were prepared for analysis following Rosenberg et al. (2022). Coral tissue was removed, and the homogenate was centrifuged to separate the algae from the host tissue at 3,000 g for 5 minutes at 4°C. Supernatant containing host tissue was transferred to a 50 ml falcon tube. The remaining pellet containing the algae was re-suspended in 1 ml of FSW and transferred to a 1.5 ml Eppendorf tube. To eliminate all other remaining cells, symbiont samples were centrifuged at 4,000 g for 5 minutes and host tissue at 13,500 g for 10 minutes, both at 4°C. The remaining supernatant was discarded, and the pellet was re-suspended in 1 ml of deionized water (DIW). 0.1 ml of 1N HCL was added to all samples (host and symbiont), which were then left with cap off for 10 minutes at room temperature. Symbiont and host samples were then centrifuged at 4,000 and 13,500 g, respectively, for 5 minutes at 4°C. Supernatant was discarded and pellets were re-suspended in 1 ml DIW. This process was repeated two more times before a final centrifugation (5 min at 4°C) at 5,000 g for symbiont samples and 15,000 g for host samples. Once the supernatant was discarded, samples were dried in a freeze-dryer for 48 hours.

Signatures of $\delta^{15}N$ and $\delta^{13}C$ for all samples (symbiont, host and water) were analysed using a continuous flow system consisting of a Delta V Plus mass spectrometer connected with a Thermo Flush 1112 via Conflo IV (Thermo-Finnigan, Germany) at the West Australian Biogeochemistry Centre (WABC), School of Biological Sciences, University of Western Australia. All $\delta^{13}C$ and $\delta^{15}N$ values are given in per mil [‰, Vienne Pee Dee Beleminte] and [‰, Air], respectively (Skrzypek, 2013). Multi-points normalization was used on the raw isotopic data and compared to the international reference scale (Skrzypek, 2013). Normalization was done based on international standards provided by the International Atomic Energy Agency (IAEA) ($\delta^{13}C$ - NBS22, USGS24, IAEA600, USGS40; and $\delta^{15}N$ - N1, N2, USGS40, USGS32) and laboratory standards. The external error of analysis (1σsd) was $\delta^{13}C$ = 0.10 ‰, $\delta^{15}N$ = 0.10 ‰, and C/N=0.1.

2.7 Statistical analysis

All statistical analysis and plotting of the data were conducted in R software version 4.1.1 (R Core Team, 2021). Means were produced by first averaging the two duplicates of each colony and then calculating colony mean per site. Data were tested for normality using the Shapiro–Wilk test with QQ-plots and homogeneity of variance with Levene's test. When the statistical test assumptions were not met, a Log_{10} transformation was performed on symbiont density and Square root transformation on Chl *a* data. The environmental data (i.e., NTU, temperature, SST, Kd490) monthly mean, site and site by time interaction were analysed using Two-way ANOVA with a Tukey's *post-hoc* test to identify differences among the sites and between sampling times at each site. A Pearson's correlation (Wei et al., 2021) test was also

used to detect if there were similar trends between the *in-situ* (NTU and temperature) and the remotely sensed (Kd490 and SST) environmental data. A linear mixed effects model was used with the package *nlme* (Pinheiro et al., 2022) to assess potential differences in coral physiology parameters (symbiont density, Chl *a*) and coral host and symbiont algae stable isotopes ($\delta^{13}C$, $\delta^{15}N$) between sites, time and the site by time interaction, with individual coral colonies treated as a random effect. Where appropriate, a pairwise Tukey's *post-hoc* comparisons of marginal estimated means was performed using the package *emmeans* (Lenth et al., 2022). We recognize the limitations associated with temporal pseudoreplication in this analysis, as colony replicates between sampling times lack statistical independence. The average of the duplicated water samples from each site was used to assess the potential contribution by phytoplankton and zooplankton to the coral holobiont diet at each site. Typically, these sources have lower $\delta^{13}C$ values compared to Symbiodiniaceae by at least 4-6 ‰ (Alamaru et al., 2009). Consequently, increased heterotrophic nutrition may result in reduction in coral host $\delta^{13}C$ (Fox et al., 2018). Therefore, the relative difference between host and symbiont ($\Delta^{13}C = \delta^{13}C_{host\text{-}symbiont}$) can be used to provide an assessment of the relative effects of the photosynthetic fractionation and incorporation of heterotrophic carbon. Further, it can also indicate if there are deviations from a fully autotrophic diet and track gradients in resource availability (Fox et al., 2018). Differences between host and symbiont $\delta^{15}N$ values ($\Delta^{15}N = \delta^{15}N_{host\text{-}symbiont}$) were calculated to evaluate the autotrophy to heterotrophy spectrum, where higher $\Delta^{15}N$ values indicate increased heterotrophy (Ferrier-Pagès et al., 2011; Conti-Jerpe et al., 2020; Price et al., 2021). Further, the stable isotopic signature shift between each coral host and its associated symbiont algae along with the phytoplankton and zooplankton isotope values per site were used to determine sources of energy (autotrophic, heterotrophic, mixed).

To explore differences in isotopic niches, for each site and time, host and symbiont fractions were fitted with 40% and 95% variation ellipses to their $\delta^{13}C$ and $\delta^{15}N$ values and plotted on an isotope biplot. The standard ellipse area (‰^{2}) of their distribution was also estimated correcting for sample size (SEA_C, a proxy for isotopic niche) using the Stable Isotope Bayesian Ellipses in R (SIBER) (Jackson et al., 2011; Jackson & Parnell, 2021). A method that enables direct comparison of isotopic niches across communities. Applying both ellipse sizes (0.4 and 0.95) provide a means to determine whether the coral holobiont is autotrophic (with the 40% ellipse), or heterotrophic (with the 95% ellipse). To determine whether the relative placements of the host and symbiont niche differed, the Euclidean distance between the centroids (means) of the two was calculated with p.interval = 0.95. A residual permutation procedure and Hotelling T^2 test were also used to evaluate significance, with $p < 0.05$ indicating that niches occupy significantly different isotopic space, an indication for heterotrophic feeding strategy (Turner et al., 2010). The ellipse overlap (p.interval = 0.95) of coral host and symbiont cut-off was eventually used to determine trophic strategy where ≥70% overlap indicates autotrophy, ≤10% indicates heterotrophy and overlap between >10% and < 70% indicates mixotrophy (Conti-Jerpe et al., 2020).

3 Results

3.1 Environmental monitoring

NTU data show a distinct turbidity gradient across the four study sites (ANOVA, F=49, p<0.001) from the most turbid site, Somerville, with monthly (May 2020-May 2021) levels of 3.2 ± 3 NTU (mean ± sd), to the clearest site, Tantabiddi, with 0.8 ± 0.6 NTU (monthly, May 2020-March 2021, mean ± sd) at the western side of Cape Range (Figure 2; Supplementary Table S1, Figure S1). Fluctuating high turbidity events at Somerville and Eva occurred all year round with a daily average max of 36.5 NTU at Somerville (11/04/2021) and 27 NTU at Eva (02/03/2021). In contrast, turbidity at Tantabiddi (monthly, May 2020-March 2021) and Bundegi (monthly, May 2020-March 2021) is less variable, typically ranging from 0 to 2.5 NTU with occasional peaks of 4 to 8 NTU (Figure 2). Although Turbidity (NTU) and Kd490 satellite derived data were not significantly correlated (Pearson's correlation, r <0.5, p>0.05; Supplementary Figure S2A, Table S2), Kd490 was still used separately as an estimate of in-water turbidity conditions during the three months (June – November 2021) when the loggers failed to record data. Temporal differences in NTU mean values were significant at all sites (ANOVA, F=10.15, p<0.0001), while Kd490 mean values presented significant interaction between site and time (ANOVA, F=2.24, p<0.0001). Temperature recorded by our *in-situ* data loggers was strongly positively correlated with remote sensed SST (Pearson's correlation, r>0.85, p<0.0001; Supplementary Table S2, Figure S2B) and both parameters produced significant differences at each site between times (ANOVA, p<0.0001; Supplementary Table S1). The highest SST monthly mean ± sd was recorded in Somerville (29.3 ± 1.3 °C) during January 2021 with a max of 30.5 °C while Tantabiddi recorded 27.4 ± 1.1°C with a max of 29 °C (Figure 2). The lowest temperatures recorded were also at Somerville (20.9 ± 0.7 °C) during August 2021 while Tantabiddi monthly mean ± sd at that time was 23.3 ± 0.6 °C. Somerville SST (°C) varied significantly (ANOVA, p<0.0001) by 12 °C between the warmest (31 °C, January 2021) and the coldest (19.5 °C, June 2021) months, compared to Tantabiddi where temperature range was 7°C degrees between 29.6 °C (February 2021) to 22.8 °C (August 2021) (ANOVA, T=397, P<0.0001).

3.2 Coral physiology

Across all sites and sampling times, mean symbiont density was 46 ± 22.8 (10^5 cell cm^{-2}) with the highest mean found at Tantabiddi (53.7 ± 22, 10^5 cell cm^{-2}; Figure 3A; Supplementary Table S3). Symbiont densities were greater at Tantabiddi and lower at Eva in both times, however, the only significant difference observed was between Tantabiddi and Bundegi and between Tantabiddi and Eva (Tukey's HSD, p=0.006 and p=0.003, respectively; Supplementary Table S4, S5) in October 2021. No significant temporal differences in symbiont density within a site were observed, despite an increase at Tantabiddi, from 52.1 ± 19 in February 2021 to 79.8 ± 22.5 (10^5 cell cm^{-2}) in October 2021.

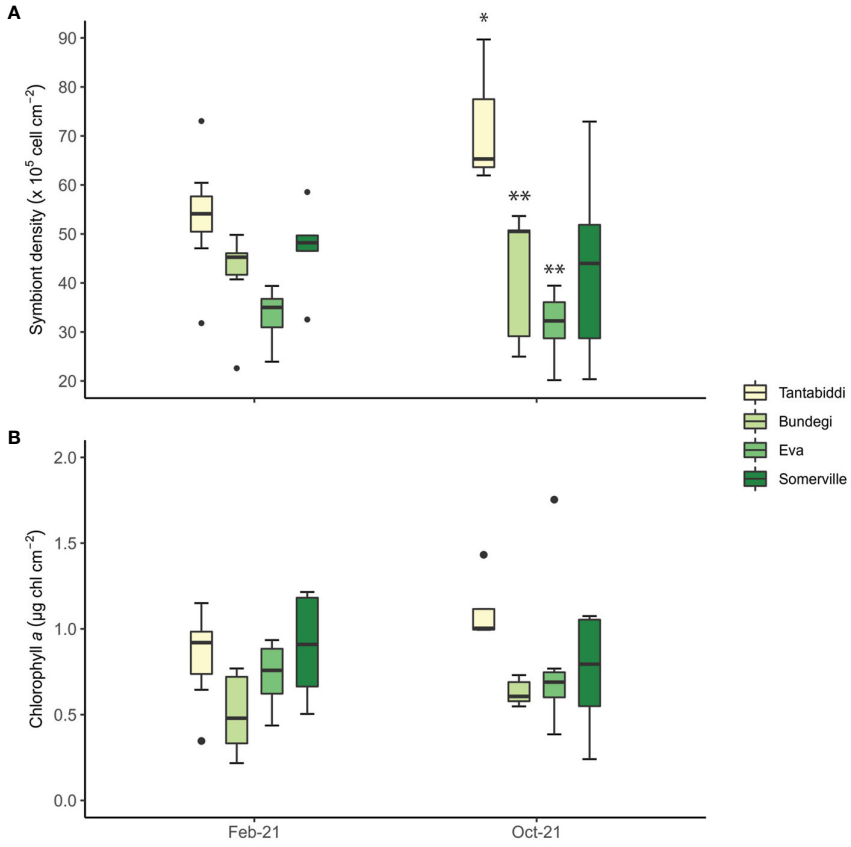

FIGURE 3
(A) Symbiont density (10^5 cell cm^{-2}) and **(B)** chlorophyll *a* (µg Chl cm^{-2}) collected at each site during two sampling times. Whiskers represent minimum and maximum values, of the lower and upper quartile, respectively; dots represent outliers. n=6-8 colonies, two duplicate samples from each colony were analysed (Supplementary Table S3). Asterisks (*) indicate statistical differences between the sites.

Mean Chl *a* values in the *Acropora tenuis* colonies across all sites and sampling times were 0.7 ± 0.3 (µg chl cm^{-2}; Figure 3B; Supplementary Table S3). Chl *a* content was significantly different between sampling times with lower values in February 2021 (ANOVA, p<0.05; Supplementary Table S4). Highest Chl *a* values were observed at Tantabiddi 0.77 ± 0.35 (µg chl cm^{-2}) and lowest values were recorded at Bundegi 0.58 ± 0.21 (µg chl cm^{-2}). Still, we found no significant differences in Chl *a* values between sites.

3.3 $\delta^{13}C$ and $\delta^{15}N$ variability along the turbidity gradient

$\delta^{13}C$ signatures differed significantly between the host and its symbiont only at Somerville in February 2021 (Tukey's HSD, p=0.003; Supplementary Table S7, S8) with lower values in the host (-15.78 ± 1.24) compared to the symbiont (-14.94 ± 1.71). In contrast, $\delta^{15}N$ values were significantly higher in the host compared to the its symbiont across all sites in both sampling times (Tukey's HSD, P ≤ 0.0001; Supplementary Table S7, S8).

Between the sites, coral host tissue $\delta^{13}C$ signatures (Figure 4A; Supplementary Table S6) show a significant trend from higher values at the clear water sites, Tantabiddi and Bundegi, (Tukey's HSD, P ≤ 0.0001) compared to lower values at the turbid Eva and Somerville sites. Coral host tissue $\delta^{13}C$ signatures were also significantly lower in October 2021 across all sites (Tukey's HSD, p ≤ 0.001; Supplementary Table S10, S11). Similarly, symbiont $\delta^{13}C$ signatures at the clear-water sites were significantly higher than at the turbid water sites (Tukey's HSD, p<0.0001). However, a significant difference between sampling times (Tukey's HSD, p=0.005; Supplementary Table S10, S11) was only present at Somerville with lower symbiont $\delta^{13}C$ signature in October 2021 (-17.69 ± 1.22) compared to February 2021 (-14.94 ± 1.71). As with $\delta^{13}C$ values, coral host tissue $\delta^{15}N$ levels show a significant decreasing trend from the clear-water Tantabiddi and Bundegi to the turbid Eva and Somerville (Tukey's HSD, p ≤ 0.0001) across the two sampling times. However, unlike $\delta^{13}C$ values, coral host $\delta^{15}N$ did not vary significantly between sampling times at each site. These spatial and temporal patterns were also observed in the symbiont $\delta^{15}N$ values (Figure 4B; Supplementary Table S10, S11).

Interestingly, spatial differences in zooplankton and phytoplankton $\delta^{13}C$ and $\delta^{15}N$ values from the sites water samples, did not always reflect the spatial differences in the coral host and symbiont $\delta^{13}C$ and $\delta^{15}N$ values (Supplementary Figure S2, Table S9). $\delta^{13}C$ in the zooplankton and phytoplankton were higher at the clear-water sites where $\delta^{13}C$ was also higher in the coral tissue and symbiont. However, zooplankton and phytoplankton $\delta^{15}N$ levels were typically higher at the turbid water sites whose coral and symbiont had relatively lower $\delta^{15}N$ than at the clearwater sites.

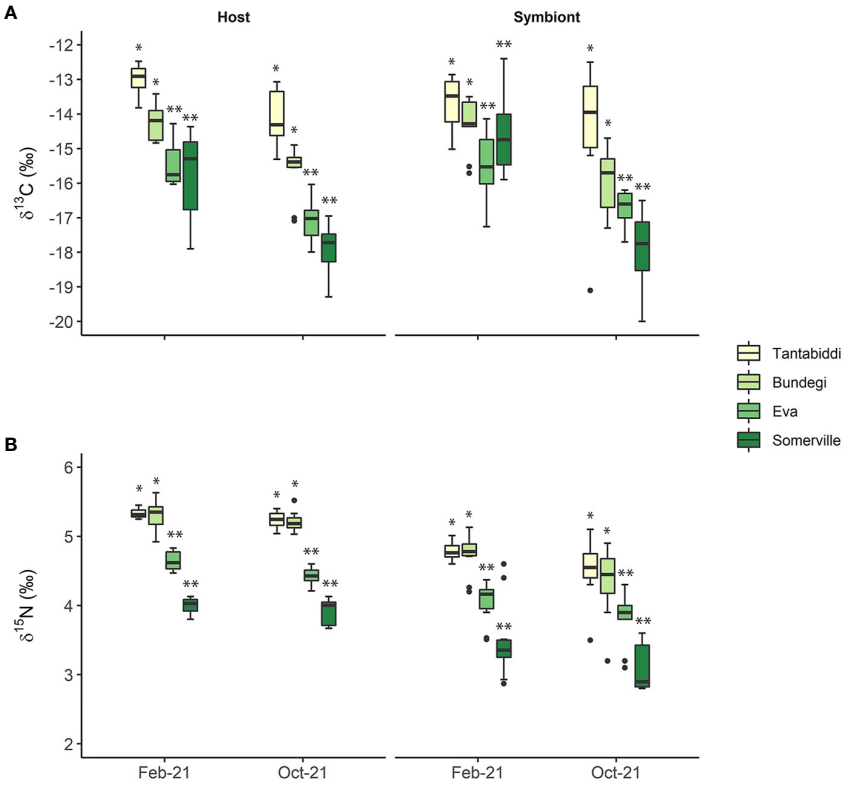

FIGURE 4
(A) $\delta^{13}C$ and **(B)** $\delta^{15}N$ signature values of the coral host tissue and the symbiont algae in the four study sites over two sampling times. Whiskers represent minimum and maximum values, of the lower and upper quartile, respectively; dots represent outliers. n=5 colonies, two duplicate samples from each colony were analysed. Asterisks (*) indicate statistical differences between the sites.

3.4 $\Delta^{13}C(= \delta^{13}C_{host\text{-}symbiont})$ and $\Delta^{15}N$ (= $\delta^{15}N_{host\text{-}symbiont}$) along the turbidity gradient

$\Delta^{13}C$ values were low ranging between -0.96 ± 2 (mean ± sd) at Eva and 0.09 ± 1.64 (mean ± sd) at Tantabiddi, both in October 2021 (Figure 5A). Despite these observations, there were no significant differences in $\Delta^{13}C$ over space and time. Nevertheless, Somerville is found with the greatest range of $\Delta^{13}C$ from -0.84 ± 0.87 in February 2021 to -0.21 ± 0.56 in October 2021. Similarly, $\Delta^{15}N$ values did not differ significantly between sites and sampling times, although $\Delta^{15}N$ values at Somerville were consistently higher at 0.70 ± 0.18 and 0.81 ± 0.22 in February 2021 and October 2021, respectively (Figure 5B). Lowest $\Delta^{15}N$ values were recorded in February 2021 at Bundegi (0.43 ± 0.19) and Eva (0.45 ± 0.14). Across all sites there was a non-significant increase in $\Delta^{15}N$ levels from February 2021 to October 2021 (Supplementary Table S12).

3.5 SIBER analysis

Plotting both the 40% (*p*.interval) and 95% (*p*.interval) SEA_C ellipses for the coral host and symbionts revealed 0% overlap at the 40% (*p*.interval) SEA_C across all sites and sampling times (Figure 6). A broader investigation of the 95% (*p*.interval) SEA_C overlap found the *Acropora tenuis* coral community at Tantabiddi with 0% overlap between coral host and symbiont in February 2021 (summer) and 11% in October 2021 (winter) (Figures 6A, B; Supplementary Table S13, S14). In contrast, Bundegi corals displayed the greatest level of overlap (39% and 52%, in February 2021 and October 2021, respectively; Figures 6C, D). Similarly, at Eva, overlap between host and symbiont was 22% and 19% in February 2021 and October 2021, respectively (Figure 6E, F). At Somerville, the *A.tenuis* coral community displayed 23% overlap in February 2021 and 0% overlap in October 2021 (Figures 6G, H; Supplementary Table S13, S14).

4 Discussion

The main aim of this study was to identify *Acropora tenuis* physiological attributes and energy acquisition strategies in response to varying turbidity levels at four sites and two sampling times (February and October). We expected to find increased heterotrophy rates to compensate for lower levels of light with increasing turbidity levels. In addition, coral physiology parameters were expected to vary significantly among sites, with higher amounts of Symbiodiniaceae and Chl *a* at the turbid sites, while the clear-water site were expected to have increased autotrophic feeding. The results of this study contradict our hypothesis and

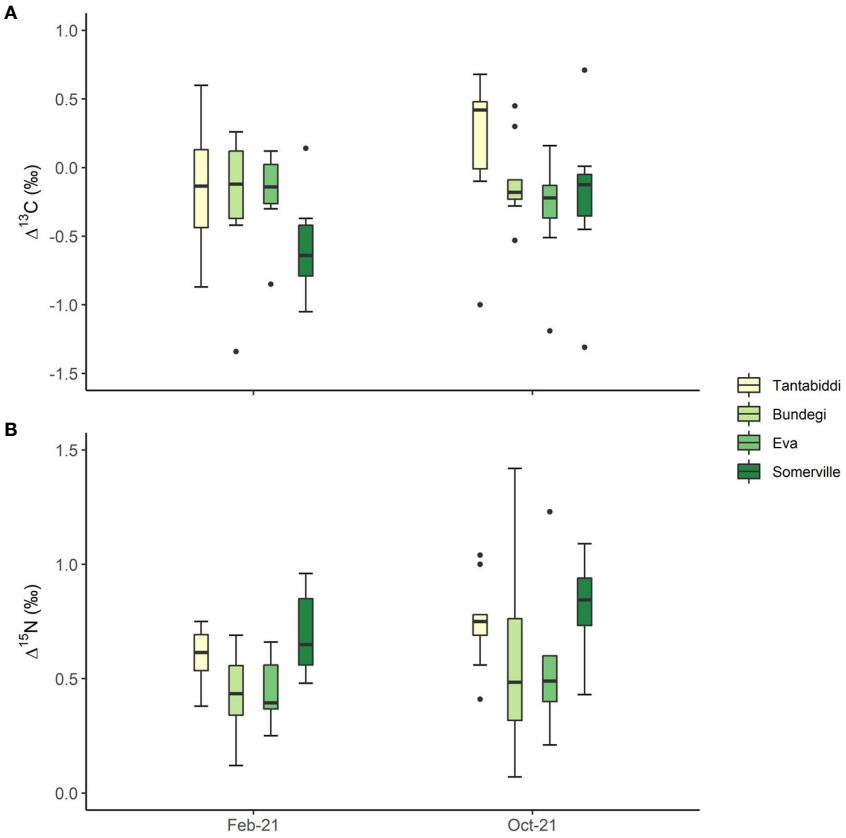

FIGURE 5
(A) $\Delta^{13}C$ ($\delta^{13}C_{host\text{-}symbiont}$) and **(B)** $\Delta^{15}N$ ($\delta^{15}N_{host\text{-}symbiont}$) in the four study sites from two sampling times. Whiskers represent minimum and maximum values, of the lower and upper quartile, respectively; dots represent outliers. n=5 colonies, two duplicate samples from each colony were analysed.

instead suggest that the physiological behavior of *Acropora tenuis* does not directly correlate to turbidity but may be influenced by a wider range of environmental conditions that are unique to each site.

4.1 Coral physiology

Symbiont densities and Chl *a* showed no significant trend across the turbidity gradient. However, we did see a decline in these parameters from the low turbidity site Tantabiddi to the mid-turbid site Eva before they increased at the most turbid site Somerville. Typically, symbiont density and Chl *a* concentrations increase with increasing turbidity levels, most likely to compensate for decreasing light levels. For example, in the Burdekin region in the GBR, *Acropora tenuis* sampled from a turbid nearshore reef site was found to have a symbiont density of ~15 (10^5 cell cm^{-2}), which was three times higher compared to the most offshore remote reef site (Rocker et al., 2017). Similarly, Strahl et al. (2019) found that total chlorophyll of *Acropora tenuis* (7 µg chl cm^{-2}) was also higher at turbid sites with levels decreasing as water quality increased. Jacquemont et al. (2022) reported values of ~12 Chl *a* (µg chl cm^{-2}) and symbiont density of ~ 30 (10^5 cell cm^{-2}) in *Acropora tenuis* from the Bouraké in New-Caladonia, a reef site noted for its marginal environmental conditions, including high turbidity (Maggioni et al., 2021). The atypical trend observed in this study could be due to additional environmental drivers (e.g., nutrients) influencing symbiont densities (and Chl *a*). For example, in a study of *A.tenuis* health with water quality on the GBR, dissolved organic carbon (DOC) was also positively correlated with symbiont densities (Rocker et al., 2017). Overall, symbiont densities were well within optimum ranges (10 to 30 x 10^5 cells per cm^2) suggested by Woolridge (2020) under non-ideal environmental conditions. However, Chl *a* levels were comparatively low (0.5 to 1 µg chl cm^{-2}), indicating low Chl *a* concentration per symbiont. These trends partially explain the pattern observed in $\delta^{13}C$ values (explained below).

4.2 Coral trophic strategy

The coral energy acquisition strategy was assessed by analysing the stable isotope values of the coral host and its symbiont algae, and the overlap between their fractions (SIBER). Here we found that the variations in turbidity levels among sites had a stronger impact on trophic strategy than temporal differences within a site. As expected, $\delta^{13}C$ values, a product of the photosynthesis process (Anthony and Fabricius, 2000), significantly decreased with

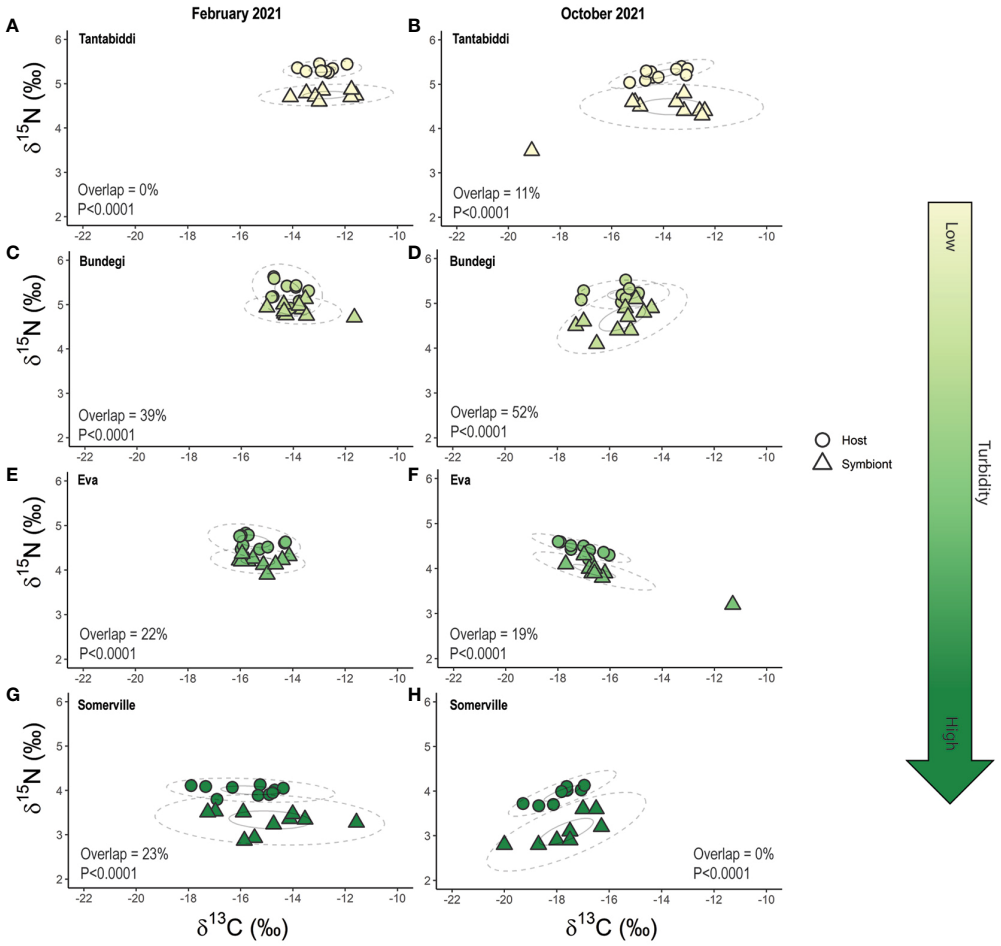

FIGURE 6
Isotope biplot of paired coral host and its algal symbiont $\delta^{13}C$ and $\delta^{15}N$ stable isotope measured in February 2021 (left column) and October 2021 (right column) at Tantabiddi **(A,B)**, Bundegi **(C, D)**, Eva **(E, F)** and Somerville **(G, H)**. Dotted (p.interval = 0.95) and solid (p.interval = 0.4) lines represent Standard Ellipse Areas corrected for sample size (SEA_C), analysed using SIBER r package. Overlap = 0.95 p.interval ellipse overlap between host and symbiont. p<0.05 is an indication of heterotrophic feeding strategy. n=5 colonies, two duplicate samples from each colony were analysed.

increasing turbidity (Anthony and Fabricius, 2000). A similar trend in $\delta^{13}C$ values with turbidity was also observed by Nahon et al. (2013) who found coral host tissue in *A. hyacinthus* from Moorea Island, French Polynesia, to be the most $\delta^{13}C$ depleted at the site with the highest levels of suspended particulate matter. Yet, $\delta^{13}C$ values in two other *Acropora* species sampled in their study (*A. cytherea* and *A. pulchra*) were similar across sites and seasons, regardless of differences in environmental conditions including suspended particulate matter. In contrast, *Porites* spp. (*P. rus, P. verrucose, P. cactus*) $\delta^{13}C$ values were found to vary with environmental change demonstrating large plasticity in their physiology. This suggests that there is a variation in physiological adaptation within and between coral genera, and that some species, including *A. tenuis* are more adaptable to varying turbidity and light levels. Counterintuitively, $\delta^{15}N$ values were also found to be highest at the clear-water site and lowest at the most turbid site. Ingestion of organic matter may represent an important source of nitrogen for corals living in shallow inshore waters (Houlbrèque and Ferrier-Pagès, 2009). As heterotrophic contribution rises, the $\delta^{15}N$ values of corals are expected to align with those of the nitrogen contributors and potentially reach levels of 2.5-3.5 ‰ higher than their food source when engaged in fully heterotrophic feeding (Muscatine and Kaplan, 1994; Reynaud et al., 2002). Thus, typically, $\delta^{15}N$ values will increase with increasing turbidity as the trophic strategy shifts from autotrophy to heterotrophy (Anthony and Fabricius, 2000; Nahon et al., 2013).

The outcomes of the SIBER analysis and the difference between coral host and symbiont, identified the *A. tenuis* communities in this study to be mixotrophic to heterotrophic communities. We observed that the most significant factor effecting the trophic niche was the consistently higher $\delta^{15}N$ values in the host compared to the symbiont across all sites and in both sampling times. This highlights the crucial role of nitrogen in the coral symbiosis (Conti-Jerpe et al., 2020). Similar $\delta^{15}N$ values of the coral host and its symbiont imply a shared nitrogen source that potentially involves nitrogen recycling within the holobiont (Tanaka et al., 2006; Gustafsson et al., 2013). This underscores the limiting role of nitrogen on reefs (Muscatine and Porter, 1977) and illustrates how corals have evolved symbiosis as an adaptive response to oligotrophic conditions (Conti-Jerpe et al., 2020). Generally, autotrophic coral will have higher $\delta^{15}N$

levels and lower $\delta^{13}C$ in the host tissue compared to their symbiont algae as a result of isotopic fractionation and mutual exchanges of carbon and nitrogen between the coral host and its symbiont algae (Muscatine et al., 1989; Muscatine & Kaplan, 1994; Swart et al., 2005a). When heterotrophy is the more dominant feeding strategy used by the coral, the difference in $\delta^{13}C$ values between the coral hosts and their symbiont algae will be greater and the host signatures will more closely resemble the $\delta^{13}C$ values of their heterotrophic feeding sources (i.e., zooplankton $\delta^{13}C$ <-16‰) (Muscatine et al., 1989). We see these associations in *A. tenuis* at the more turbid sites, Somerville and Eva, where coral host $\delta^{13}C$ average is -16.7 ± 0.8, and phytoplankton and zooplankton $\delta^{13}C$ signature was -17. However, this was less evident at Tantabiddi, were $\delta^{13}C$ signature of phyto/zooplankton was -7 whereas in the coral host tissue it was -13.4 ± 0.6. The reduced association between host signatures and feeding sources is likely due to other important factors such as the isotopic values of the dissolved inorganic carbon and nitrogen sources (Heikoop et al., 2000; Risk et al., 2009), nutrient concentrations (Hoegh-Guldberg et al., 2004; Fox et al., 2019), respiration rates (Swart et al., 2005b) and light availability (Grottoli and Wellington, 1999), all of which influence $\delta^{13}C$ and $\delta^{15}N$ values of Scleractinia corals. In summary, despite the dominance of a heterotrophic energy acquisition strategy across all sites, the lack of an increase with rising turbidity could be explained by one or a combination of the following:

1) *Acropora* physiology

The ability to capture particulate organic matter, along with feeding rate and strategy vary among species potentially in relation to their polyp size and surface area (Palardy et al., 2005), as well feeding rates (Houlbrèque and Ferrier-Pagès, 2009). The Acroporidea family when compared to other families such as Montiporidae or Pocilloporidae, likely has a limited heterotrophic capacity due to small polyps (<2 mm) and short tentacles, which limits their ability to feed on larger organic matter (Palardy et al., 2008; Conti-Jerpe et al., 2020; Sangmanee et al., 2020). In contrast, those species with larger polyps (e.g., *Galaxea* sp., *Lobophyllia* sp., *Euphyllia* sp.) are found to be more efficient at heterotrophic feeding (Anthony and Fabricius, 2000). Consequently, the lower than expected coral host $\delta^{15}N$ values at the more turbid sites may not be due to the lack of nitrogen sources available in the water column, but rather from the reduced ability of *A. tenuis* to capture the particles. Further, turbidity levels at Somerville were highly variable characterised by extreme high turbidity events of 36 NTU followed by very low turbidity levels of ~1 NTU the following day. These highly variable conditions for a coral species that are less tolerant to sediments, may further stress these corals resulting in reduced nitrogen intake via heterotrophy. Alternatively, it could be that the periodic extreme turbidity events in Somerville do not reach the required threshold to increase heterotrophic feeding in *A.tenuis*. This suggests that sustained high levels of turbidity pressure may be necessary for a shift in its feeding strategy.

2) Variable sediment loads and composition

Both Somerville and Eva experience elevated turbidity and resuspension events all year round with a weak pattern of higher values during winter and lower values during summer (Cartwright et al., 2021). This sediment is mostly composed of quartz and calcite sand that are recycled and resuspended locally due to strong wind driven waves and tidal regime in the area (Massel et al., 1997; Brunskill et al., 2001). Sediment loads at certain times of the year may be exceeding heterotrophic thresholds of *A. tenuis*. In Somerville, host-symbiont SEA_C overlap indicated transition from mixotrophy (23% overlap) in February2021, the wet season (rainfall = 2 mm, <11.3 NTU, <0.41 Kd490), to heterotrophy (0% overlap) in October 2021, the dry season (rainfall = 0 mm, <0.35 Kd490). These data suggest that during the wet season when more sediments are delivered to coastal waters, the sediment stress threshold for *A.tenuis* has been exceeded resulting in a decline in heterotrophy. The observed $\delta^{15}N$ enrichment of coral host and symbiont in Tantabiddi suggests that turbidity is not the only driver effecting trophic levels but also supports the notion that the isotopic composition of nitrogen sources differs between sites (Heikoop et al., 2000; Baker et al., 2011).

3) Nutrient sources

Heterotrophy by corals can be enhanced by the increase of available particulate nutrient sources in turbid environments to counteract the reduction in autotrophy by the photosymbionts and allow the corals to maintain a positive energy budget (Anthony, 2000). Here, Somerville corals were found to acquire most of their energy from heterotrophy as indicated by the range in $\Delta^{13}C$ (-0.84 ± 0.87 in February 2021 and -0.21 ± 0.56 in October 2021), as well as the highest $\Delta^{15}N$ in both sampling times. Still, the fact that corals were the most $\delta^{15}N$ enriched at Tantabiddi compared to corals from Somerville, $\Delta^{15}N$ variability among sites was not significant, and $\Delta^{13}C$ at Somerville remained small, suggests no additional increase in heterotrophic feeding strategy at the turbid sites (Einbinder et al., 2009; Nahon et al., 2013). Importantly, Tantabiddi experiences the Ningaloo current which leads to upwelling during the summer months. Deep-water upwelling is essential in generating fluxes of inorganic nutrients, contributing to increased reef-wide primary productivity and the availability of particulate resources (Leichter and Genovese, 2006; Stuhldreier et al., 2015; Radice et al., 2019b). Consequently, the variability in nutrient and particulate concentrations can impact the trophic strategies adopted by symbiotic corals (Porter, 1976). This may explain increasing nitrogen levels and nutrient influx to the NMP waters and might be a contributing factor to why the *A.tenius* community at the clear water site is the most heterotrophic, with SEA_C 0% overlap between coral host and symbiont in February 2021 (summer) and with 11% in October 2021 (winter). In contrast, Somerville and Eva are found in a more coastal – protected location, with little supply of freshwater from land or terrestrial runoff, and thus nutrient supply may be very low and limited (Brunskill et al., 2001).

5 Conclusion

Although limited in distribution, corals from naturally extreme environments are invaluable to understanding the mechanisms that support higher tolerance to future climate change. The spatial variability in turbidity of the shallow inshore waters of Exmouth

Gulf provided the opportunity to assess how an important coral species can adapt to variable light and sediment conditions. We assumed that as turbidity increased, corals would increase their heterotrophic feeding rates to compensate for the reduction in carbon from photosynthesis. However, our results suggest that increased heterotrophy by coral hosts in turbid coral reef areas is not a universal pattern. Stable isotopic compositions of several coral species show variability through space and time, suggesting that adjustments in the heterotrophic pathway is a species-specific phenomenon.

A.tenuis was able to acquire additional energy through non-photosynthetic means and, as such, was classed as a mixotroph. However, highly variable and elevated sediment loads at the most turbid site negatively influenced *A. tenuis* ability to ingest sources of nitrogen by decreasing rates of heterotrophy during the most turbid months. Moreover, it seems that the loss of carbon due to low light at the turbid sites is not accompanied by nitrogen intake, which might suggest lower coral growth and reproduction as well as increased vulnerability to climate stressors. The main finding of this study is that *A. tenuis* feeding pattern varied mostly spatially rather than between the two sampling times, being more heterotrophic (than mixotrophic) at times of lower turbidity on sites within the Exmouth Gulf, and at the Ningaloo site during times of likely higher nutrient supply. This highlights the fact that Exmouth Gulf is a dynamic environment with variable environmental conditions and nutrient supply, which in combination has led to an opportunistic *A. tenuis* coral community that frequently changes its feeding strategy in response to varying turbidity and light levels. Yet, it is crucial to acknowledge that this conclusion may be influenced by varying environmental conditions at different study sites.

Despite the limitations posed by small sample sizes, the incorporation of both carbon and nitrogen isotope values in SIBER facilitated the exploration of trophic dynamics for both nutrients within the coral holobiont. To enhance our understanding of trophic strategies of corals in turbid environments, future research should consider a larger sample size and a broader range of taxa. The diverse findings reported in other studies from various regions, highlight the constraints associated with transferring results between different systems (Travaglione et al., 2023). Therefore, conservation and management plans should aim to include site-specific data on coral energy acquisition mechanisms along with long term environmental monitoring and examination of the different energy investment mechanisms of the coral to provide improved predictions of coral reef health under varying climate change scenarios.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because all necessary permits were obtained to conduct the research described in this manuscript. Coral sampling in Exmouth Gulf was conducted under permit 3619 from the Department of primary industries and regional development, Australia. Sampling at the Ningaloo Marine Park was conducted under permit FO25000277 from the Department of Biodiversity, Conservation and Attractions.

Author contributions

AZ: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. NB: Conceptualization, Project administration, Supervision, Validation, Writing – original draft, Writing – review & editing. OL: Conceptualization, Writing – review & editing. RH: Methodology, Writing – review & editing. MO: Conceptualization, Funding acquisition, Investigation, Methodology, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1288296/full#supplementary-material

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