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Spatial and temporal variability in tropical off-reef zooplankton across broad spatial and temporal scales

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ABSTRACT

Productivity of oligotrophic coral reefs is largely dependent on the constant influx of zooplankton. However, our understanding of how zooplankton communities in tropical reef-associated regions vary over large spatial and temporal scales is limited. Using the Australian continuous plankton recorder dataset, we explored if, and to what extent, the off-reef zooplankton community along the Queensland shelf (including most of the Great Barrier Reef lagoon) varied with latitude, month, and diel time. The zooplankton community was consistently dominated by copepods (~60%) which, with appendicularians, chaetognaths, non-copepod crustaceans, and thaliaceans, comprised ~98% of the zooplankton. However, the abundance of these taxonomic groups did not vary predictably across latitude, month, or diel time, with these gradients only explaining 5% of community variation. At the scales sampled herein the composition of zooplankton was highly predictable in terms of broad taxonomic groups but variation in the relative abundance of these groups was not predictable.

1. Introduction

Plankton dominate the biomass of marine systems and are ubiquitous throughout the worlds approximately 1 billion km^3 pelagic zone (Schminke 2007; Batten et al., 2019). Consequently, almost all marine food webs depend on this abundant pelagic resource (Batten et al., 2019), with oligotrophic ecosystems, such as coral reefs, being particularly reliant on plankton as nutrient vectors (see Shakya and Allgeier 2023). Indeed, by connecting reefs to off-reef resources, planktonic subsidies allow nutrient poor reefs to circumvent the limitations of their environment (Odum and Odum 1955; Hamner et al. 1988, 2007; Heidelberg et al., 2004; Skinner et al., 2021). For example, Morais and Bellwood (2019) revealed that this influx of pelagic nutrients supports reef productivity, supplying on average 41% of the energy required for fish growth on a windward coral reef. As a result, the maximum carrying capacity, in terms of fish biomass, of coral reefs is determined, in part, by the abundance and composition of the plankton that is continuously transported to these systems (Marquis et al., 2011).

The community composition of zooplankton is of particular importance to reef ecosystems as planktivorous reef fishes (the dominant planktivores in these ecosystems [Allgeier et al., 2017]) are predominantly zooplanktivorous (Hiatt and Strasburg 1960; Lazzaro, 1987; Hobson 1991), and the nutritional composition of zooplankton is known to vary markedly between taxa (Wang and Jeffs 2014), while taxon-specific traits, such as size, can affect availability to planktivorous fishes (Gahan et al., 2023). Consequently, changes or variability in zooplankton taxonomic composition may have significant implications for reef fish productivity. For example, dominance shifts away from the readily digestible Copepoda to the gastronomically challenging Cnidaria may result in a decline in abundance of fish lacking sufficient trophic flexibility to utilise the dominant food resource (Huertas and Bellwood 2020).

The taxonomic composition and abundance of zooplankton is, however, notoriously variable, with their distribution and community structure influenced by ocean currents (Hammer and Hauri 1977; Kingsford and Suthers 1996), temperature (Mackas et al., 2012; Zhao et al., 2020), salinity (Kelly et al., 2016; Hall and Lewandowska 2022), sunlight intensity (Brierley 2014; Hobbs et al., 2021), and chemical composition (Hansson et al., 2007; Garzke et al., 2017). Despite the potential for 'patchy' distribution, zooplankton are thought to vary in predictable spatial (cross-shelf [Sammarco and Crenshaw 1984; Williams et al., 1988], latitudinal [Campbell et al., 2021; Brandão et al., 2021; Fraser et al., 2021]) and temporal patterns (diel [Jacoby and Greenwood 1988; Nakajima et al., 2008] and seasonal [Dakin and

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Colefax 1940; Sammarco and Crenshaw 1984; Puelles et al., 2003]). Planktonic organisms thus provide variable but functionally consistent prey for coral reef planktivores. Yet, to-date, our knowledge of these distribution patterns has been extrapolated from relatively small scale — spatial and temporal — surveys (e.g. 1 location, 1 site, 46 days [Hamner et al., 1988]; 1 location, 2 sites, 46 days [Jacoby and Greenwood 1988]; 11 locations, 2 to 11 sites per location, over 22 months [Fraser et al., 2021]), or from mathematical models based on these data (Skerratt et al., 2019; Heneghan et al., 2023). This knowledge gap is due, in part, to the challenges of sampling plankton within certain habitats such as the complex reef mosaic (Santos et al., 2017), exposed windward reef faces (Brito-Lolaia et al., 2020), or in close proximity to the benthos (Sponaugle et al., 2021). As a result, we have little understanding of the plankton community predictability across these various scales. This is particularly true for tropical plankton communities that are associated with reefs and are key to underpinning the productivity of these ecosystems.

Evidently, plankton are an integral component of marine systems and can fuel trophic pathways in critical marine ecosystems such as coral reefs. It is, therefore, surprising that we currently lack a comprehensive understanding of how tropical off-reef plankton communities vary across key temporal and spatial scales. To address this knowledge gap, the aim of this study was to investigate if, and to what extent, patterns in zooplankton community structure vary over large spatial and temporal scales. Specifically, we utilised the Australian continuous plankton recorder dataset which provides the largest consistent spatially and temporally extensive plankton dataset for Australasian waters. This allowed us to examine patterns in off-reef zooplankton distribution across large spatial (i.e. latitudinal gradients along most of Australia's Queensland coast including the majority of the Great Barrier Reef [GBR] lagoon) and temporal (i.e. seasonal, diel) scales. Based on the findings of previous smaller-scale studies, we hypothesis that the composition of zooplankton would exhibit clear variations across broad spatial and temporal scales. This variation may manifest as differences in the relative abundance of taxa between diurnal and nocturnal periods as well as clear shifts in taxa abundance along a latitudinal gradient.

2. Methods

2.1. Continuous plankton recorder data

Data were extracted from the Australian Plankton Survey which is based on Continuous Plankton Recorders (CPR) (IMOS, 2023). For a complete methodology see Richardson et al. (2006). The CPR data is collected by towing a self-contained mechanical automatic sampler approximately 10 m deep and 100 m behind the research vessel. Tows were conducted within the GBR lagoon where the water depth averages ~30 m (Larcombe and Carter 2004), at an approximate depth of 10 m. Each tow covered approximately 450 nautical miles (~833 km), at the ships 'regular' speed, taking on average approximately 14 h to complete. As the CPR is towed, plankton enters through a 1.27 × 1.27 cm aperture and is then trapped between two sheets of 270 μm mesh silk, 6.1 m long x 15 cm wide, loaded in a removeable internal cassette. As water passes through, it turns the internal propeller, winding the silk on to a take-up spool within a formalin preservation chamber. The sheets of silk are wound at a fixed rate of 1 cm for every nautical mile travelled (450 NM = 450 cm). The silk is processed in 5 NM equivalent samples (average equivalent sample volume ~1.5 m^3, ranging 0.4–1.6 m^3 [range dependent on water flow]) with microscopic counts of all the plankton on each sample. To limit spatial autocorrelation, only the first sample and then every fourth sample thereafter is counted (i.e. 1, 5, 9, 13, etc continuing to the length of tow), with the last sample always excluded to avoid the accumulation of trapped zooplankton (F. Coman, personal communication, June 29, 2023). Metadata outlining the time, date and position (i.e. coordinates) are included for each sample. Sample zooplankton counts are then converted to number per cubic meter (ind. m^{-3}) (Richardson et al., 2006). As we wanted to focus on Tropical-subtropical plankton communities that are more likely to be associated with coral reefs, we subsampled the data to include only those samples from the GBR lagoon (16.7°S) to the Queensland-New South Wales border (28.1°S) (Fig. 1), yielding 574 zooplankton tow samples from 2009 to 2022. Given the zero-inflated nature of the data, taxa were pooled into 10 taxonomic groups (that were functionally relevant, especially as prey for reef fishes): copepods, appendicularians, chaetognaths, thaliaceans, non-copepod crustaceans (i.e. meroplanktonic larvae), other non-gelatinous, other gelatinous, molluscs, cnidarians, and echinoderm larvae (Table S4).

2.2. Statistical analyses

Initially, we explored large scale trends in community composition along the entire length of the study area. Firstly, we calculated the average zooplankton community using the entire dataset (~1265 km, 542 samples). Secondly, we collated the zooplankton community into 12 sites, averaged across 1° of latitude with each site consisting of ~111 km and 9–104 samples (Table S1). Next, we explored variation in the entire zooplankton community (i.e. all 10 taxonomic groups) using multivariate analyses. The primary gradients of interest were latitude, time of day (diel), and season. To account for non-linearity and the potential for cyclical temporal patterns, month and time were converted to magnitude, with month standardised to months from January (hottest month to coldest [i.e. 1-7]), and diel time to time from 12 p.m. (i.e. 0-12). The relationships between the multivariate zooplankton assemblage and the three key variables were then formally tested using distance-based permutational multivariate analysis of variance (adonis) (Oksanen et al., 2020). The results of this analysis were then visualised using a distance-based redundancy analysis (dbRDA), constrained by significant variables (Oksanen et al., 2020). All multivariate analyses were based on a Bray-Curtis similarity matrix calculated from fourth-root transformed, row-standardised data.

Following the multivariate analyses, we used generalised linear mixed effects models (GLMMs) to specifically explore relationships between key zooplankton taxonomic groups and the gradients of interest (Brooks et al., 2017). The key zooplankton groups were the five most abundant discrete taxonomic groups (i.e. copepods, appendicularians, chaetognaths, non-copepod crustaceans, and thaliaceans). To ensure any spatial or temporal variation in these zooplankton groups was comprehensively captured in our analyses we examined variation in both the a) density (ind. m^{-3}) and b) relative abundance (percent of total community) for each group. Specifically, separate models included the response variables of taxa density or relative abundance, and fixed continuous factors of latitude, month, and diel time (all scaled and mean centred). Month and diel time were treated as above. All models also included sampling year and trip ID as a random factors, with trip ID nested within year, to account for any non-independence at these scales. All models were based on a Tweedie distribution with a log-link function. In terms of the relative abundance data, the Tweedie distribution was superior to a betabinomial distribution here due to the nature of the data (i.e. the data contained exact zeroes and the non-zero data were continuous with very few observations at the upper bounds [i.e. close to 100%]). Model fit and assumptions were assessed using DHARMa simulated residual plots which were satisfactory in all cases (Hartig 2022). All statistical analyses were performed within the R 4.1.0 Statistical and Graphical Environment (R Core Team, 2021), using the *vegan* (Oksanen et al., 2020), and *glmmTMB* (Brooks et al., 2017) packages.

3. Results

Initial exploration of the data revealed the overwhelming contribution of copepods to zooplankton community composition across the entire length of the Queensland coast examined (Fig. 2). Indeed, copepods comprised, on average, nearly 60% of the total zooplankton

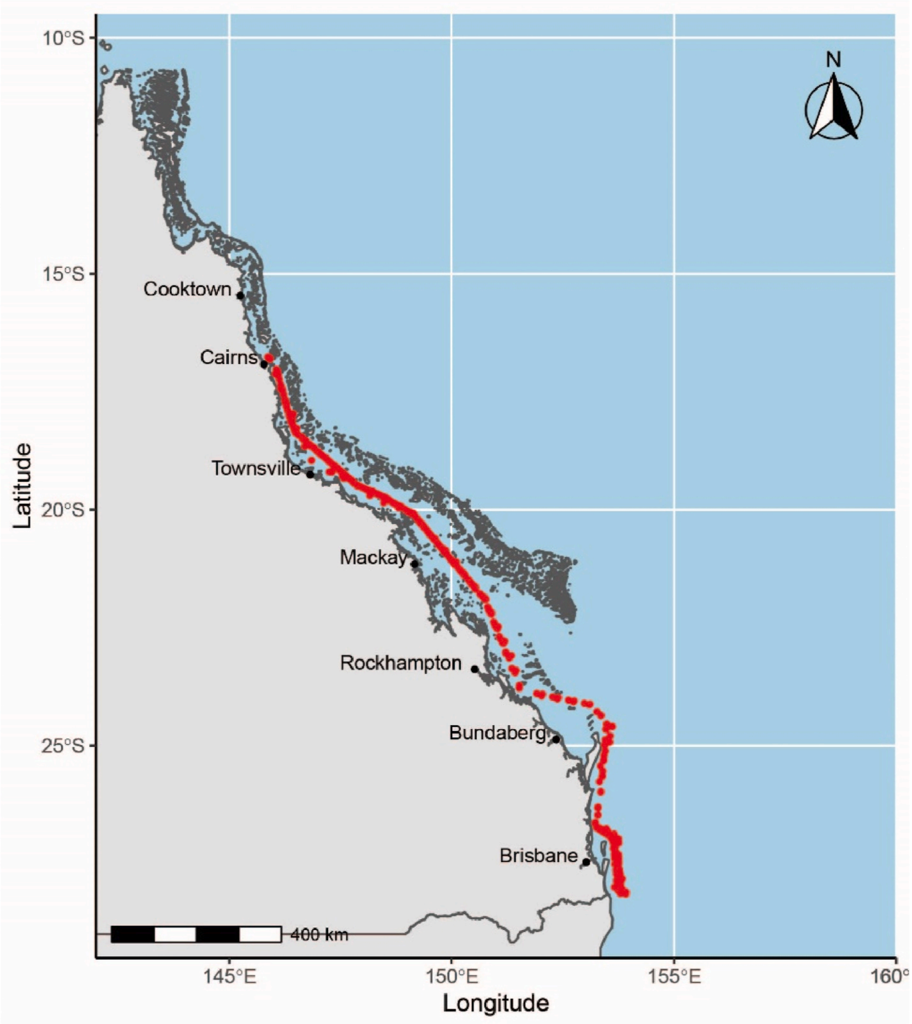

Fig. 1. A map of the sample locations off the east coast of Queensland Australia. Red dots indicate discrete samples.

community, followed by appendicularians (13.2%), chaetognaths (11.3%), non-copepod crustaceans (10.2%), and thaliaceans (4.4%) (Fig. 2b). Together these five taxonomic groups comprised ~98% of the zooplankton community (Fig. 2b). This community structure appeared to be relatively consistent across latitudes, with copepods always the dominant taxon, followed by varying relative abundances of appendicularians, chaetognaths, non-copepod crustaceans, and thaliaceans (Fig. 2a).

No distinct spatial structure was apparent in the zooplankton community. While significantly correlated with the functional groupings of the zooplankton community, the environmental variables when combined only explained ~5% of the variation in the community structure (Table S2). To explore trends within this explained variability, the zooplankton community was ordinated in a multivariate space using a dbRDA constrained by latitude, months from January, and time from 12 p.m. (Fig. 3a). Latitude and months from January were positively correlated with the relative abundance of copepods, appendicularians, and other gelatinous taxa. While echinoderm larvae, non-copepod crustaceans, molluscs, cnidarians, and other non-gelatinous taxa were positively correlated with time of day. In contrast, thaliaceans and chaetognaths did not appear to be strongly correlated with any of the environmental variables (Fig. 3b). Overall, while there was a significant correlation between the environmental variables and the zooplankton community, but the amount of variance explained was limited (just 5%) (Fig. 3a), indicating a lack of predictable variability across the chosen gradients.

The general lack of strong clear patterns across the key environmental gradients was reflected in the results of our GLMMs which examined the density and relative abundance of key taxonomic groups (Fig. 4, S1–S4). In terms of copepods (i.e. the dominant zooplankton taxa), we detected no significant trends across latitudes or months for both density and relative abundance (Fig. 4, Table S1). There was, however, a statistically significant positive relationship between copepod density ($p < 0.0001$; Table S1) as well as relative abundance ($p = 0.012$; Table S1), with diel time, although there was a substantial degree of variability around this relationship (Fig. 4).

The limited capacity for broad spatial and temporal gradients to explain variability in zooplankton abundance was also apparent in the models used to examine variation in appendicularian, chaetognath, non-copepod crustacean, and thaliacean density and relative abundance (Figs. S1–S4). In most cases, no significant relationships with latitude nor month were detected (apart from the relationship between thaliacean relative abundance and latitude) (Table S1), while in some cases (thaliacean density, chaetognath relative abundance, non-copepod crustacean relative abundance) a significant relationship with diel time was detected, with the nature of these relationships dependent on the taxonomic group involved (Figs. S1–S4; Table S1). In all other cases there was no significant relationship between diel time and the density or relative abundance of the taxonomic groups (Table S1). Overall, these results suggest that tropical reef-associated zooplankton communities do not vary to any great extent spatially or temporally nor do they vary in a predictable manner across key gradients, especially across latitude and

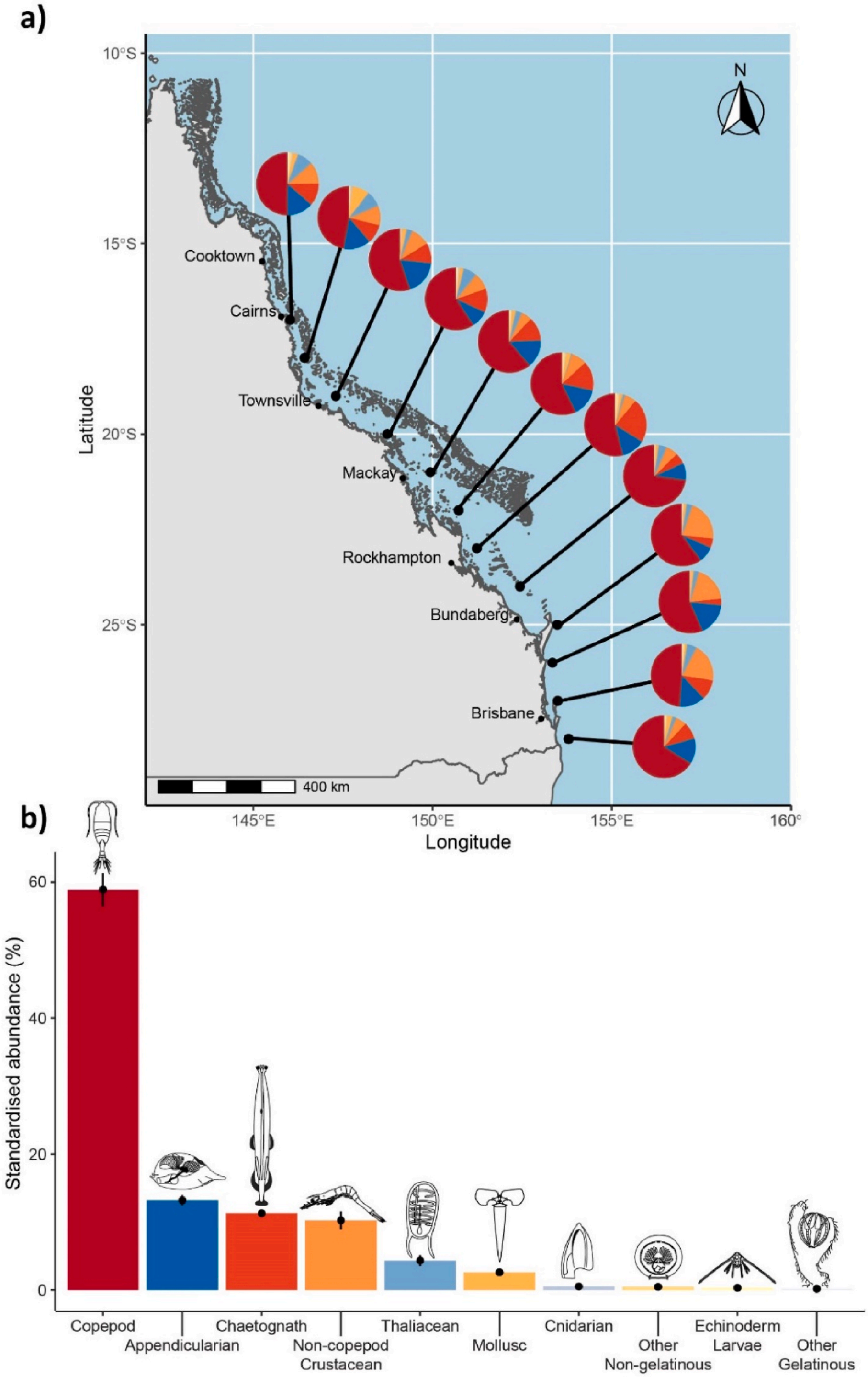

Fig. 2. The composition of the sampled zooplankton community (percentage of total zooplankton abundance) averaged across **a** 1° latitude, and **b** total dataset (see Table S1 for further details).

season.

4. Discussion

We examined 574 zooplankton tow samples spanning 13 years and spread across ~12° of latitude in the GBR lagoon to explore if, and to what extent, zooplankton community structure was related to key spatial and temporal gradients. We revealed that the abundance of key zooplankton taxonomic groups were highly consistent, with limited variability being explained by relationships to key spatial and temporal gradients (just 5% total). Indeed, the lack of clear and consistent latitudinal, seasonal, or diel patterns in zooplankton composition is remarkable given the extensive nature of the CPR dataset and its associated statistical power. Furthermore, despite variability in abundance across all gradients, the overwhelming contribution of copepods, as well as other key taxa (i.e. appendicularians, chaetognaths, non-copepod crustaceans, and thaliaceans) was consistent. Indeed, copepods were the dominant taxon and generally comprised over 50% of the total zooplankton community across the entire spatial scale examined. The overwhelming contribution of copepods to the community composition

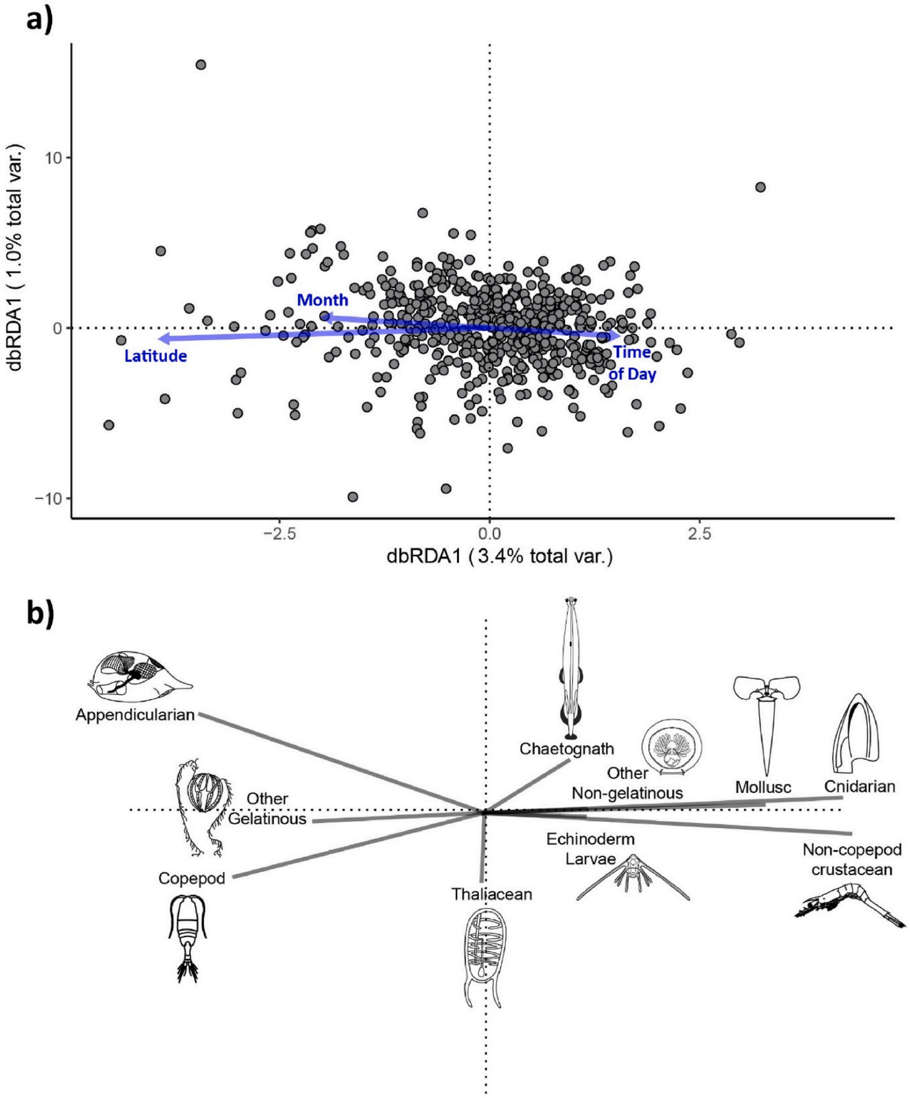

Fig. 3. **a** dbRDA ordination of the zooplankton community, constrained by the environmental variables: latitude, months from January, and time from 12 p.m. (blue vectors). **b** species vectors showing correlations between the taxonomic groupings and how they contribute to the patterns observed in the dbRDA ordination.

of coral reef zooplankton aligns with the findings of past studies conducted at smaller spatial scales (e.g. Hamner et al., 1988; Roman et al., 1990; Heidelberg et al., 2004; Yahel et al., 2005), and suggests that the patterns extrapolated from these small-scale studies do hold along the length of the GBR lagoon. From a planktivorous reef fishes' perspective, these results suggest that copepods and to a lesser extent appendicularians, chaetognaths, non-copepod crustaceans, and thaliceans represent, on average, a consistently abundant nutritional resource with limited and unexplained variability across latitude, month, and diel cycles.

The zooplankton community composition was found to be primarily composed of five key taxonomic groupings, copepods (~60%), appendicularians (13.2%), chaetognaths (11.3%), non-copepod crustaceans (10.2%) and thaliaceans (4.4%), together comprising on average ~98% of the zooplankton community across the GBR lagoon. This is comparable to the community patterns described from previous smaller-scale studies which found copepods to be the dominant taxon followed by a varying dominance hierarchy in the other key taxa across the GBR (e.g. central GBR inner-shelf on-reef zooplankton communities; copepods 56.1%, appendicularians 13.3%, chaetognaths 7.7%, cnidarians 6.4%, and non-copepod crustaceans 5.8% [Gahan et al., 2023], central GBR mid-shelf on-reef zooplankton communities; copepods 64.1%, appendicularians 31.8%, cnidarians 1.9%. thaliaceans 2.2% [Hamner et al., 1988], southern GBR outer-shelf off-reef zooplankton communities; copepods 44.4%, appendicularians 33.5%, other zooplankton 15.0%, non-copepod crustaceans 7.1% [Sale et al., 1976]). Indeed, copepod dominance appears to be ubiquitous throughout marine systems, with consistent dominance regardless of habitat preference (on-reef; Hamner et al., 1988, pelagic; Turner 2004, benthic; Kramer et al., 2013), diel habit (night; Heidelberg et al., 2004, day; Hamner et al., 1988), or latitude (tropics; Hamner et al., 1988, temperate; Duggan and White 2010, polar; Kosobokova et al., 2011). This prevalence suggests that copepods may be key nutrient vectors and readily available for planktivorous organisms in marine systems.

Copepods are considered one of the most broadly palatable zooplankton taxa to planktivorous fishes (Hiatt and Strasburg 1960; Hobson and Chess 1978; Hobson 1991) and are considered a nutritionally complete prey item (Kleppel 1993). However, despite the prevalence of copepods in zooplankton communities, as well as their palatability and nutritional quality, many of these copepods may be unusable as nutritional resources for planktivorous fishes. This is because, while copepods occupy a broad range of size spectra (e.g. 0.001–6 mm; Hopcroft et al., 2001), the majority of marine copepods are small (i.e. over 90% of zooplankton are <450 μm; Hopcroft et al., 2001).

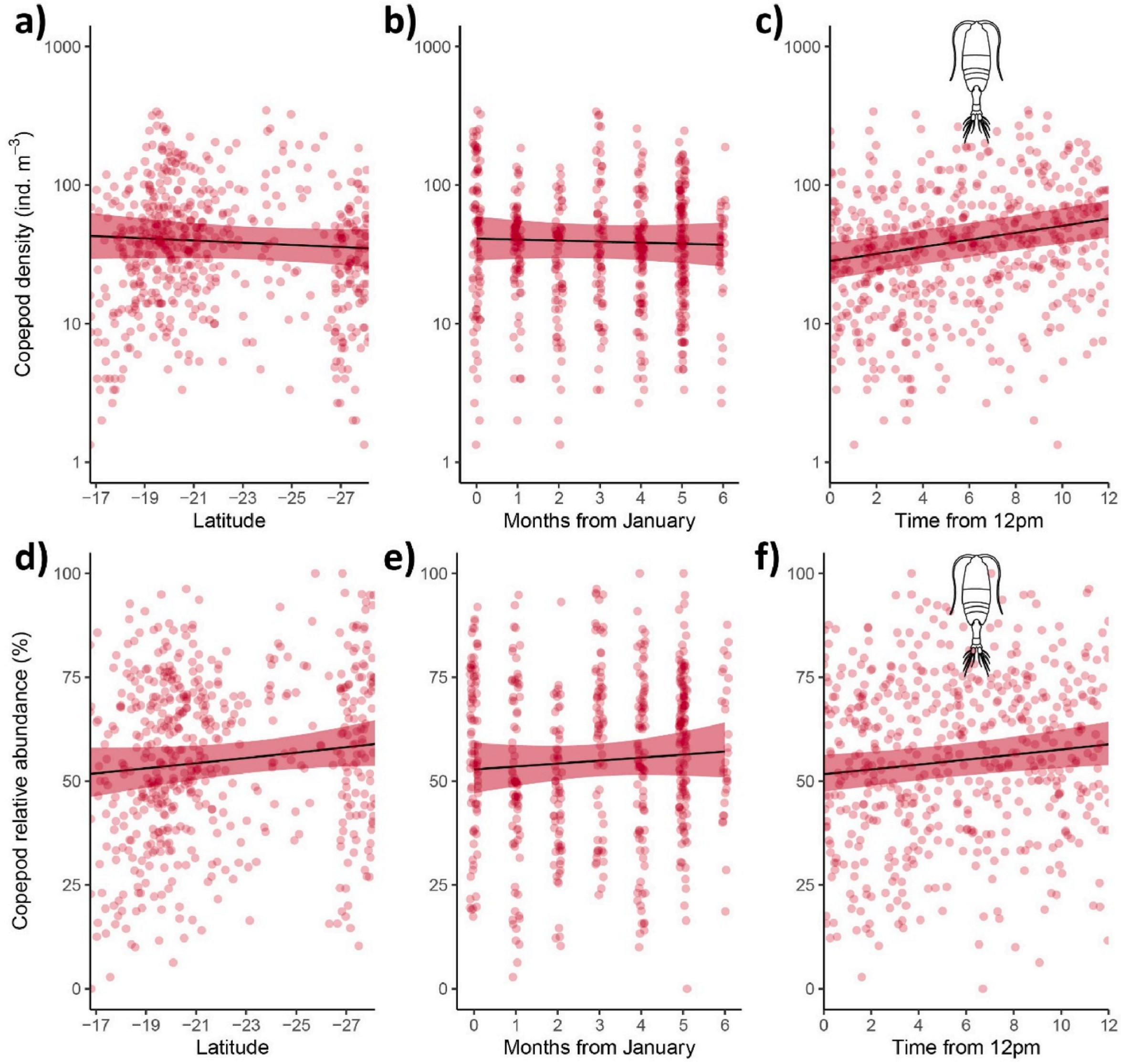

Fig. 4. Consistency in the relationships between copepod density and **a** latitude, **b** months from January, **c** time from 12pm, as well as copepod relative abundance (percent of total zooplankton abundance) and **d** latitude, **e** months from January, and **f** time from 12 p.m. Copepod silhouette indicates statistically significant effect. Black lines represent the mean predicted fits from the GLMMs, and the coloured ribbons and points represent the 95% confidence intervals and raw data, respectively. Note the y-axis for panels a-c are on the log10 scale.

Given the small size of many copepods they may not be detected and go unused by planktivorous fishes, especially larger species (Gardner 1981). Although, some smaller copepods do provide a critical nutritional resource for smaller planktivorous fishes, such as damselfishes (Frédérich et al., 2016). While copepods dominate zooplankton communities, and are highly palatable, other plankton taxa are also consumed (e.g. Hamner et al., 1988; Hamner et al., 2007) and contribute significantly to nutrient availability to planktivores (Gahan et al., 2023). As different species of fishes specialise in feeding on different components of the zooplankton (e.g. copepod-feeding damselfishes versus gelatinous plankton-feeding caesionids) (Hamner et al., 1988; Frédérich et al., 2016) variation in the structure of zooplankton communities may influence fish communities and the utilisation of planktonic resources on the reef.

A ‘baseline’ community structure of coral reef plankton has been inferred from past small-scale studies, however, there is limited data on broad scale community patterns of zooplankton on the GBR (Kingsford and Welch 2007). Some previous studies have suggested that zooplankton abundance varies with latitude (Brandão et al., 2021), seasonal (Dakin and Colefax 1940; Sammarco and Crenshaw 1984; Puelles et al., 2003) or diel cycles (Jacoby and Greenwood 1988; Nakajima et al., 2008). Interestingly, when we investigated these trends using the CPR dataset (the largest spatial and temporal dataset in Australasian waters) we found the zooplankton community patterns were highly consistent and did not vary in a predictable manner across any of these gradients. Instead, the abundance of zooplankton groups was remarkably consistent, on average, across the length of the GBR lagoon, and throughout diel and seasonal cycles. Indeed, while latitude, month, and time of day are proxies which encompass a suite of complex interactions between the physical, chemical, and biological components, when we investigated relationships between zooplankton abundance and the environmental variables of current velocity, temperature, temperature range, chlorophyll, salinity, and dissolved oxygen’s influence on the density and relative abundance of key zooplankton groups no clear, consistent, trends emerged (Figs. S5–S14). This incongruence with past studies may be due to the large-scale nature of our study, as sampling plankton in multi-kilometer multi-hour tows may have overshadowed finer scale patterns (e.g. diel migrations on a single reef [Jacoby and Greenwood 1988; Heidelberg et al., 2004; Nakajima et al., 2008]). Additionally, our use of higher taxonomic groupings overlooks the species-specific patterns documented across spatial and temporal gradients in past studies (Omori and Hamner 1982; Carleton and Doherty 1998; Wolfe et al., 2023).

While species-specific patterns for zooplankton may exist, we limited our study to broad taxonomic groups of plankton, as it is these broad groups, rather than specific species, which planktivorous fishes are likely to target on reefs (Hamner et al., 1988; Huertas and Bellwood 2020). Furthermore, the species gradients documented in past, smaller-scale studies, are largely based on plankton tows using nets in the vicinity of coral reefs (e.g. Hamner et al., 1988; Carleton and Doherty 1998; Nakajima et al., 2008; Gahan et al., 2023). However, this is where the pelagic off-reef zooplankton assemblage meets the on-reef (emergent/diurnal) community which means that plankton in these areas may be mixed, and it can be difficult to determine the relevant extent of pelagic (holoplanktonic) versus on-reef (meroplanktonic) supply. The CPR dataset focuses exclusively on the off-reef zooplankton community, which is the nutrient vector primarily responsible for powering coral reef productivity (Morais and Bellwood 2019). Our data analysis therefore represents spatial and temporal trends in the pelagic zooplankton supply without the noise from mixing of the on-reef and off-reef communities.

The mixing of planktonic communities near reefs may also influence the spatial and temporal patterns previously reported, notably, the nocturnal spikes resulting from emergent plankton (Jacoby and Greenwood 1988; Nakajima et al., 2008; Alldredge and King 1977). Zooplankton taxa, especially Crustacea (e.g. mysids, euphasiids, ostracods, copepods, and decapod larvae), Pteropoda, and Chaetognatha are well documented vertical migrators, exhibiting changes in behaviour and distribution between day and night (Jacoby and Greenwood 1988; Nakajima et al., 2008; Alldredge and King 1977). These migrations are believed to occur to avoid intense sunlight but are also often attributed to predator avoidance (see Hays 2003). However, it may be that some of these diel movements in coral reef plankton are more readily documented in on-reef zooplankton communities where it is shallow enough to allow sampling in relatively close proximity to the substratum (Jacoby and Greenwood 1988; Nakajima et al., 2008). Indeed, previous studies of nocturnal emergent zooplankton have used 'emergence traps' which are attached directly to the reef benthos (Alldredge and King 1977; Jacoby and Greenwood 1988; Kramer et al., 2013; Wolfe et al., 2023). By contrast, in our study, while we documented some significant relationships between zooplankton taxa and diel time, these relationships were not consistent nor strong, with no substantial spikes in nocturnal abundance evident. This may be because the CPR dataset was collected at ~10 m in the GBR lagoon where water depth averages ~30 m (Larcombe and Carter 2004), which means that emergent zooplankton may not have been quantified in this dataset.

The relatively low abundance of gelatinous zooplankton groups (i.e. appendicularians, thaliaceans, and cnidarians) in the CPR dataset was also surprising. This is because it is becoming increasingly clear that many groups of planktivorous reef fishes principally feed on gelatinous zooplankton; specifically wrasses (Huertas and Bellwood 2020), surgeonfishes (Choat et al., 2002), and fusiliers (Hamner et al., 1988). Given the high abundance of many of these fishes on the GBR (especially fusiliers [Williams and Hatcher 1983; Valenzuela et al., 2021]), one would expect that gelatinous zooplankton would be far more abundant to sustain such large fish population sizes. This relatively low abundance of gelatinous taxa may be due to the blooming dynamics of gelatinous zooplankton (see Boero et al., 2008). Specifically, the abundance of gelatinous zooplankton can be ephemeral, with dramatic temporal fluctuations (Hamner et al., 1988; Nakajima et al., 2013), making it difficult to quantify them in a consistent fashion. This means that while the methods underpinning the CPR data, are very versatile when it comes to quantifying copepods and other small zooplankton, they may not be as accurate for gelatinous zooplankton (Richardson et al., 2006). Moreover, it is important to highlight that the data in our analyses are based solely on plankton abundance and does not include plankton lengths, which may underestimate the relative contribution of groups with larger body sizes, such as gelatinous zooplankton, to pelagic-based food webs. Gelatinous zooplankton are typically large (>1 mm; Hamner et al., 1975), especially relative to highly abundant copepods. Moreover, the CPR data, as well as most surveys of plankton communities, are based on individual counts of gelatinous taxa, such as appendicularians, and do not quantify the empty mucous houses (which may be a particularly important nutritional resources to gelatinous feeders; Alldredge 1976). Therefore, a broader understanding of the distribution patterns of both gelatinous individuals and spent houses may be warranted in the future.

It is interesting to note that despite the limited variability in the average abundance of the off-reef zooplankton community, on-reef planktivorous reef fishes can vary considerably in the locations where they exploit this resource (Hamner et al., 1988; Morais and Bellwood 2019; Shakya and Allgeier 2023). These differences in variability may be due to the fact that oceanographic processes (e.g. tidal currents, wind-driven waves, upwelling), that can be highly variable, control the delivery of zooplankton at a local reef scale (Alldredge and Hamner, 1980; Alldredge and King 2009; Fox et al., 2023). As a result, the patterns and strength of plankton delivery to reefs is intrinsically linked to the local hydrodynamic conditions (White 1998; Lee et al., 2005), which can be variable within the complex mosaic of reefs that make up the GBR (Wolanski 2018). Planktivorous fishes exploit these heterogeneous water patterns, positioning themselves in areas of high-water movement, such as the reef crest, maximising their zooplankton encounter rate, and moving in response to changing current patterns (Hamner et al. 1988, 2007; Kingsford and MacDiarmid 1988; Streit et al., 2021). Overall, our study provides a baseline of plankton community compositions and emphasises a clear and consistent pattern of potential plankton delivery to reefs. Our findings support earlier descriptions of near-reef zooplankton community compositions that have been suggested by past smaller-scale studies (e.g. Hamner et al., 1988; Roman et al., 1990; Heidelberg et al., 2004; Yahel et al., 2005). Community composition appears to be consistent and is largely composed of the same five taxonomic groups; copepods were found to be the dominant taxon, comprising over half of the total zooplankton community, on average, followed by a variable dominance hierarchy of the other key groupings. This dominance in off-reef plankton communities suggests that these groups may represent critical nutritional resources for reef planktivores. However, limited to no relationships were found between these key zooplankton groups and the latitude, month, and time of day gradients examined. This demonstrates that at the large scales sampled herein the zooplankton community, at a coarse taxonomic level, is a consistent food source with limited and unexplained variability across latitude, month, and time of diel cycles. Given such limited variability, it suggests that when viewed from a coarse taxonomic level, the zooplankton community is a readily available food source, whose inherent variability is likely driven by species-specific patterns that may not directly affect reef-fish predation.

CRediT author statement

James Gahan: Conceptualization; Methodology; Data curation; Formal analysis; Visualisation; Writing – original draft. David R. Bellwood: Conceptualization; Methodology; Writing review & editing. Leo Nankervis: Conceptualization; Methodology; Writing review & editing. Sterling B. Tebbett: Conceptualization; Methodology; Writing review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2023.106169.

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