



Gelatinous versus non-gelatinous zooplankton: their value as food for planktivorous coral reef fishes

James Gahan^{1,2} · David R. Bellwood^{1,2} · Orpha Bellwood^{1,2} · Jodie Schlaefer^{1,2,3}

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Abstract Coral reefs are highly productive ecosystems, in part due to the productivity of planktivorous fishes. The planktivorous fish community contains two distinct groups which target either the gelatinous or the non-gelatinous fractions of the incoming zooplankton. However, the nutritional value of these prey fractions and, consequently, their potential contribution to planktivorous fish productivity are poorly understood. We explored the zooplankton fractions potential contribution to planktivorous fish productivity (our function of interest), by quantifying the nutritional content a key trait of the gelatinous and non-gelatinous prey fractions which are accessible to reef-associated diurnal planktivores. By combining vertical plankton tows with stoichiometric analyses, we found that the three zooplankton community fractions—gelatinous, > 2 mm non-gelatinous and < 2 mm non-gelatinous—were all relatively good sources of nitrogen, with median C:N values of 4.81:1, 4.22:1 and 4.62:1, respectively. The delivery of gN m⁻² to our study reef over a flood tide was then estimated. The abundant < 2 mm non-gelatinous community delivered the largest gN m⁻² (median: 0.88 gN m⁻² 6 h⁻¹), which was estimated to be one to two orders of magnitude greater than the delivery

from the > 2 mm non-gelatinous (0.06 gN) and gelatinous (0.03 gN) communities, respectively. Overall, our results highlight the quality of both gelatinous and non-gelatinous zooplankton as prey for planktivorous fishes, emphasizing the potential importance of the often-overlooked gelatinous fraction.

Keywords Gelatinous plankton · Ecosystem function · Zooplankton · Great Barrier Reef · Planktivory · Productivity

Introduction

Coral reefs are one of the most biologically diverse and economically important ecosystems on the planet (Moberg and Folke 1999; Wilkinson 2004; Fisher et al. 2015; Grafeld et al. 2017). They are capable of supporting a large standing biomass of fishes and sustaining the rapid replacement of consumed prey (Halpern and Warner 2002; MacNeil et al. 2015; Morais et al. 2021). Coral reef fish productivity may be dependent, at least in part, on the availability of nitrogen, an essential element that is required for the formation of amino acids and protein that underpin the growth and maintenance of fishes (Wilson 2003). As nitrogen must be obtained in sufficient quantities from prey, it may, in some circumstances, be limiting (Vitousek and Howarth 1991; Nixon 1992; Tyrell 1999). On coral reefs the availability of sufficient nitrogen and other nutrients to support their high productivity has been linked to the assimilation of off-reef resources (Hamner et al. 1988; Pinnegar and Polunin 2006; Wyatt et al. 2010). These may be termed pelagic or spatial subsidies, referring to the current-driven transport of new nutrients (i.e. organisms) into reef waters (Morais and Bellwood 2019; Morais et al. 2021). Consumed and assimilated

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✉ James Gahan
james.gahan@my.jcu.edu.au

- ¹ Research Hub for Coral Reef Ecosystem Functions, James Cook University, Townsville, QLD 4811, Australia
- ² College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia
- ³ Commonwealth Scientific and Industrial Research Organisation (CSIRO), Environment, Townsville, QLD 4811, Australia

by filter feeders and planktivores, these organisms link off-reef resources to coral reefs (Young et al. 2015). On coral reefs, planktivorous fishes represent a key trophic conduit for ingestion and assimilation of off-reef resources (DeMartini et al. 2008; Young et al. 2015). Morais and Bellwood (2019) found that planktivorous fishes were responsible for nearly half (~41%) of the total fish productivity of a windward facing reef section, a pattern that may be replicated across the Indo-Pacific (see Morais et al. 2021).

However, not all planktivorous fishes target the same planktonic resources. The differential targeting of planktonic resources by fishes is suggested by morphological adaptations, which appear to facilitate predation on either the gelatinous or non-gelatinous fraction of the incoming zooplankton (Hamner et al. 1988; Huertas and Bellwood 2020). Gelatinous zooplankton refers to planktonic organisms united through a high body water content, including ctenophores, cnidarians, and pelagic tunicates (Hamner et al. 1975; Jaspers et al. 2015). By contrast, non-gelatinous zooplankton are all other zooplankton united by their comparatively lower body water content, such as copepods and other crustaceans (Sommer et al. 2002). The reasons why planktivorous fishes partition these two components of the zooplankton supply are currently unclear. Indeed, the functional biology of planktivores is particularly poorly understood (Bellwood et al. 2019). Given the importance of nitrogen on reefs, and the preferential selection of prey by planktivores, partitioning could be related to the nitrogen content (i.e. the nutritional quality) of gelatinous and non-gelatinous planktonic prey fractions. However, evidence for this potential variation in nutritional quality is currently limited, partly because the gelatinous fraction of the zooplankton has often been overlooked in past research (cf. Mills 2001; Cardona et al. 2012; Aubert et al. 2018).

While planktivorous reef fishes have been widely reported to prey on gelatinous zooplankton (Ates 1988; Hamner et al. 1988; Harbinson 1993; Purcell and Arai 2001), it is generally viewed as a minor part of their diet (Sommer et al. 2002; Cardona et al. 2012). Indeed, gelatinous zooplankton, especially large gelatinous zooplankton, are often considered a trophic 'dead end' due to their high water-low protein content. They are thus assumed to be of lower nutritional value when compared to non-gelatinous zooplankton (Arai 2005; Hamilton 2016). The assumption that non-gelatinous zooplankton have a greater nutritional value compared to gelatinous zooplankton has endured despite the limited quantification of the nutritional content of both groups. Past studies on the nutritional content of zooplankton have primarily focussed on individual taxa such as larvaceans, ctenophores, thaliaceans, and copepods (e.g. Martin and Knauer 1973; Alldredge 1976; Gorsky et al. 1988; Bailey et al. 1995; Dubischar et al. 2012), or the entire pelagic community, without specific consideration of the various components

or predatory pathways (e.g. Wyatt et al. 2013). As a result, there is a clear gap in our understanding of zooplankton nutritional content at a level relevant to their consumption by planktivorous reef fishes.

As nitrogen is an essential element that may underpin fish productivity, the ratio of carbon to nitrogen is often used as an indicator of nutritional quality (Platt et al. 1969; Karasov and Martínez del Río 2007). Consequently, the variable contribution of gelatinous and non-gelatinous zooplankton to planktivorous reef fish productivity could be reflected in their stoichiometry and, specifically, their carbon to nitrogen (C:N) ratios. The broad aim of this study, therefore, was to quantify the value of gelatinous and non-gelatinous zooplankton as food sources and to evaluate their potential contribution to planktivore productivity. This was achieved through two specific objectives: firstly, to assess the composition of a near-reef zooplankton community, and secondly, to quantify the nitrogen supplied to planktivorous fishes by the gelatinous and non-gelatinous zooplankton fractions based on their stoichiometry. In doing so, this study contributes to an enhanced understanding of the nutritional content of the gelatinous and non-gelatinous community fractions which characterize the zooplankton supply available to coral reef planktivores.

Methods

Study site

Zooplankton samples were collected from Pioneer Bay, Orpheus Island, Central Great Barrier Reef, Australia (18° 34' S, 146° 29' E) between 20 and 26 November 2021. Pioneer Bay is an inner shelf reef, on the leeward (western) side of Orpheus Island. Hydrodynamic processes are dominated by strong tidal streaming in the adjacent channel which separates Orpheus Island from the mainland. The tidal stream flows to the north on ebb tides and to the south on flood tides (Parnell 1988). Interactions of the tidal stream with the geomorphology of Pioneer Bay result in an oblique delivery of current to the reef face, with an average flood tide current speed of 0.0996 m s⁻¹. This average flood current speed was calculated using data from Schlaefer et al. (2022) who deployed 27 Marionette HS drag-tilt current metres on the benthos and in the water column in a three-dimensional grid pattern in the immediate vicinity of our sampling site (details in Schlaefer et al. 2022).

Sample collection

Samples were collected using 18 m vertical plankton hauls close to the reef (within 20 m). The plankton net had a 240 µm mesh and a diameter of 0.3 m. To ensure a vertical

descent, a 1 kg weight was attached at the bottom of the 750 ml cod end. Once the net had descended to the desired depth, it was hauled up by hand at a target rate of 1 m s^{-1} . Daily sampling was conducted over the 7-day period, with all samples collected during the first diel flood tide at peak run (when flow was the strongest). The daily samples comprised of: (A) two 18 m hauls for analysing community composition and (B) 20 hauls (each 18 m) pooled (the combined 20 hauls = 1 day replicate) for nutrient delivery analyses. In total, 14 replicates were collected for the community composition analysis (2×7 days) and 7-day replicates (per fraction) for the nutrient delivery analyses. Community composition samples were preserved in 4% phosphate-buffered formaldehyde. Samples were subsampled, with individuals identified to major categories, and counted using a dissecting microscope. Taxa counts were then standardized into density of individuals per cubic metre.

Samples for stoichiometric analyses were processed fresh, with samples initially separated into $> 2 \text{ mm}$ and $< 2 \text{ mm}$ size fractions using a 2-mm sieve. The in situ size fractioning was done on ice to slow the activity of the zooplankton and to minimize within-sample predation. Post-fractioning, the samples were stored in an ice-filled cooler for euthanasia and to slow gelatinous zooplankton breakdown. Field size fractioned samples were then manually examined, using a dissecting microscope and a 1000- μL micro-pipette, to further separate them into gelatinous and non-gelatinous community fractions. To avoid gelatinous zooplankton decomposition, processing was restricted to 5 min per 20 ml sample. Following processing, samples were briefly rinsed on mesh with reverse osmosis water (RO) to remove any salt adhering to the outside of the zooplankton. Samples were then stored in a $-80 \text{ }^\circ\text{C}$ freezer for a minimum of 72 h, freeze-dried (Martin Christ Alpha 1-2 LDplus freeze dryer), homogenized and weighed to the nearest 0.1 mg (Mettler AE240) to get their dry weights. The daily $> 2 \text{ mm}$ and $< 2 \text{ mm}$ gelatinous size fractions were combined to reach the $> 2 \text{ mg}$ dry weight guideline for stoichiometric analysis (Fig. S1). This created three distinct prey groups: gelatinous, $> 2 \text{ mm}$ non-gelatinous and $< 2 \text{ mm}$ non-gelatinous zooplankton. Although the pooling of the gelatinous fraction was necessary for the analysis, it resulted in a loss of resolution and restricted the analyses to the entire gelatinous fraction, preventing an assessment of the differences between the $> 2 \text{ mm}$ and $< 2 \text{ mm}$ size fractions. Stoichiometric analyses were conducted using a continuous-flow gas source mass spectrometer (Finnegan Delta-V), coupled to an elemental analyser (Costech) with a zero-blank auto-sampler suitable for small sample measurements of organic matter in biological material, at the James Cook University Analytical Centre, Cairns.

The potential nitrogen supply to planktivores from the three zooplankton fractions was evaluated by determining their respective delivery of N. This was done by: (A)

calculating the total amount of nitrogen (gN) in each sample (by multiplying the dry weight of each sample by the per cent nitrogen [expressed as a % of dry weight = biomass]; e.g. if $8\% \text{ N} = 0.08 \times 0.05 \text{ g dry mass} = 0.004 \text{ gN}$). (B) The total grams of nitrogen per sample were then converted to the concentration of nitrogen (gN m^{-3}) by dividing it by the volume of water sampled in each replicate (25.45 m^3) (e.g. $0.004 \text{ gN}/25.45 \text{ m}^3 = 0.000157 \text{ gN m}^{-3}$). (C) The concentration of nitrogen was then multiplied by the average flood tide current speed at the study site (0.0996 m s^{-1}) and the typical duration of a flood tide (6 h or 21, 600 s) to estimate the total amount of nitrogen potentially supplied to planktivores (e.g. $0.000157 \text{ gN m}^{-3} \times 0.0996 \text{ m s}^{-1} \times 21, 600 \text{ s flood}^{-1} = 0.338 \text{ gN m}^{-2} \text{ flood}^{-1}$). This assumes that fish are able to feed within a 1 m^3 area adjacent to the reef, giving the final estimate of the potential grams nitrogen available for planktivorous organisms from the various zooplankton community fractions over a flood tide, across a standardized square metre of the water column ($\text{gN m}^{-2} \text{ flood}^{-1}$).

Statistical analyses

Individual Bayesian generalized linear mixed effect models were used to assess the data. Specifically, for the community composition data we used two separate models to examine variation in density (response variable) of the different gelatinous and non-gelatinous taxa (fixed factors). In addition, for the nutrition delivery data separate models were used to examine variation in the carbon to nitrogen mass ratio (C:N) and grams nitrogen contribution per square metre (gN m^{-2}) (response variables) of the zooplankton community fractions (fixed factors). In all models, the random effect of day (varying effect) was used to account for the lack of temporal independence. All models used a Gamma distribution with a log link (Gelman et al. 2004). Although a Gaussian distribution, with identity link, to accommodate zero values, could have been used for the community composition samples, doing so resulted in a poorly fit model. Instead, as the zero values most likely represented rare species lost due to subsampling, a small value (+ 1) was added to the entire dataset. This allowed a Gamma distribution with a log link to be used for the community composition data, improving model fit. All models incorporated the default weakly informative priors from the *brms* package (Bürkner 2021) for the fixed effects and included three chains each of 10, 000 iterations (2000 warmup, thinning rate of 5). The models were validated through visual examination, ensuring that the priors were correctly defined, chains were well mixed and converged on a stable posterior (Rhat < 1.05) and showed no evidence of within-chain autocorrelation. Furthermore, posterior predictive checks and simulated residuals using the *DHARMA* package (Hartig 2021) were also used to assess model fits. An overly influential outlier was detected in the

nutritional composition data and removed. The outlier had an exceptionally small dry weight (well below the recommended > 2 mg guideline) and a large C:N ratio that compromised the integrity of the results (Fig. S2). The median, lower, upper 50% and 95% highest posterior density (HPD) interval for each model were calculated. Evidence of a strong effect was made through examination of these HPD ratios. All statistical analyses were performed within the R 4.1.0 Statistical and Graphical Environment (R Core Team 2021), using the *brms* (Bürkner 2021), *emmeans* (Lenth 2021) and *rstan* (Stan Development Team 2020) packages.

Results

Community composition

The Orpheus Island zooplankton community composition was characterized by the abundance of a few dominant taxa (Fig. 1). Larvaceans and cnidarians were the primary

contributors to gelatinous zooplankton densities (median: $234.6 \text{ ind. m}^{-3}$, $163.5\text{--}333.6$; $112.8 \text{ ind. m}^{-3}$, $81.5\text{--}165.7$, respectively), contributing 92% of the total mean gelatinous abundances (62% larvaceans, 30% cnidarians). In comparison, the non-gelatinous community composition was dominated by a single taxon, copepods (median: $992.3 \text{ ind. m}^{-3}$, $713.4\text{--}1408.1$), which contributed 71% of the total mean non-gelatinous abundance.

Nutritional quality

The carbon: nitrogen (C:N) ratios demonstrated that the zooplankton community fractions all had comparable C:N ratios, indicating the fractions to be of similar nutritional quality (Fig. 2). The > 2 mm non-gelatinous zooplankton fraction contained the lowest C:N ratio (median: $4.22:1$, $3.86:1\text{--}4.62:1$), followed by < 2 mm non-gelatinous (median: $4.62:1$, $4.26:1\text{--}5.10:1$) and gelatinous community fractions (median: $4.81:1$, $4.39:1\text{--}5.31:1$). However, there was only evidence of a difference in C:N ratios between the > 2 mm

Fig. 1 Zooplankton density of **a** gelatinous and **b** non-gelatinous zooplankton taxa. Black bar and black dots represent the median and mean density from the posterior distribution, respectively. Thick coloured bars represent the 50% credible intervals, and the thin coloured bars represent the 95% credible intervals. Raw data are overlaid as grey dots

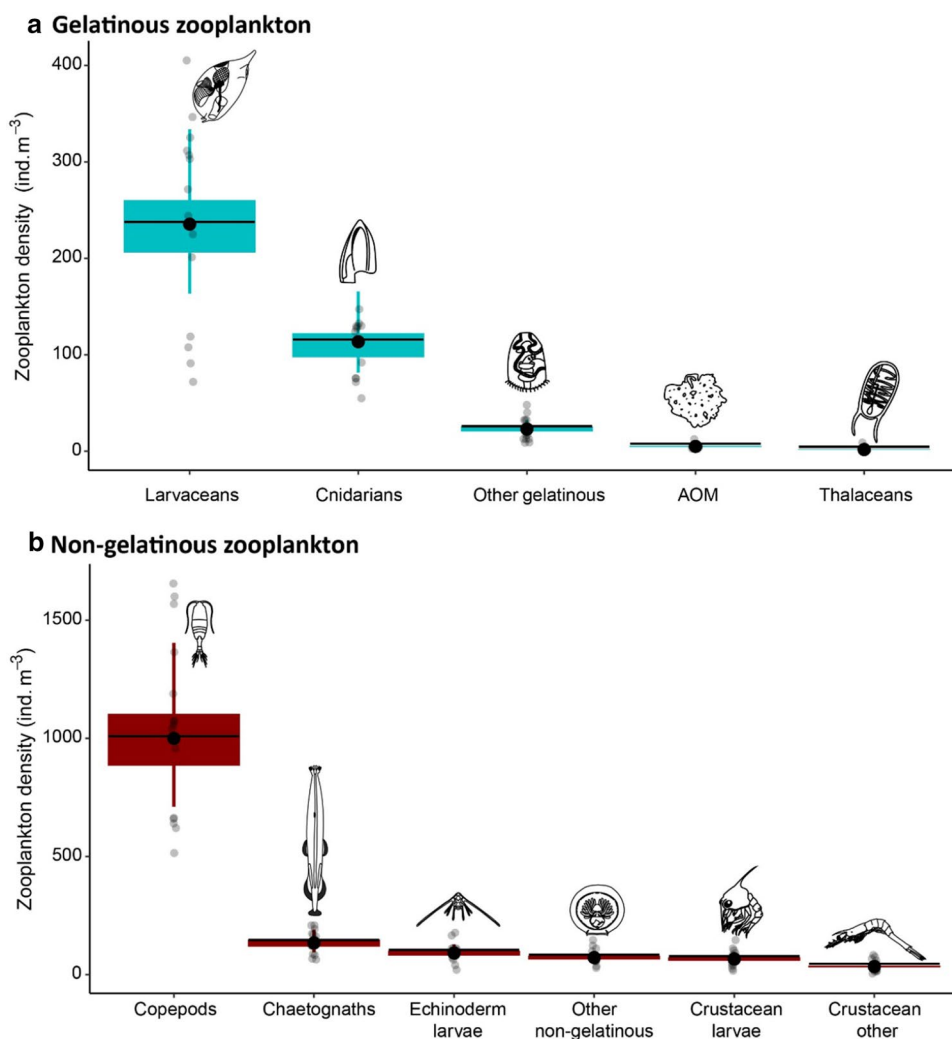
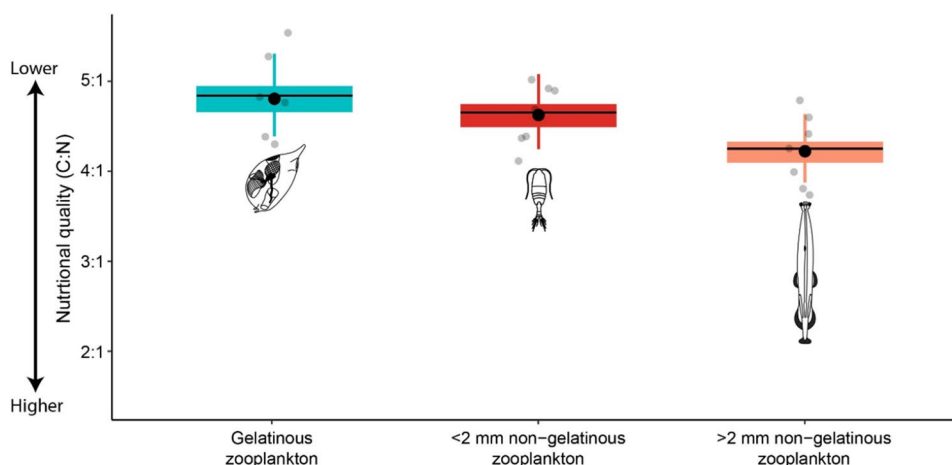


Fig. 2 Zooplankton community fraction carbon:nitrogen (C:N) ratios. Black bar and black dots represent the median and mean density from the posterior distribution, respectively. Thick coloured bars represent the 50% credible intervals, and the thin coloured bars represent the 95% credible intervals. Raw data are overlaid as grey dots



non-gelatinous and gelatinous fractions (median [95% credible interval]: -0.13, -0.2253 to -0.0267), with the gelatinous fraction having the higher C:N ratio of the two.

N delivery

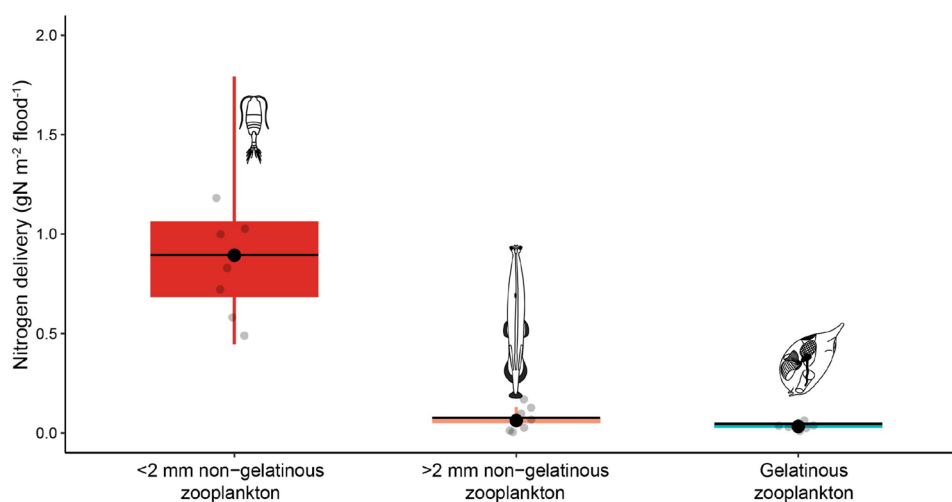
The potential N delivery to the reef from the zooplankton community fractions was explored through an estimation of the grams nitrogen delivered per square metre to planktivorous organisms over a flood tide (6 h) at an average flood tide current speed of 0.0996 m s⁻¹ (Fig. 3). The <2 mm non-gelatinous community fraction was found to be the largest source of gN m⁻² (median: 0.88 gN m⁻² 6 h⁻¹, 0.45–1.791), which was one and two orders of magnitude greater than the delivery from the > 2 mm non-gelatinous (median: 0.06 gN m⁻² 6 h⁻¹, 0.03–0.13) and the gelatinous community fraction, respectively (median: 0.03 gN m⁻² 6 h⁻¹, 0.02–0.07). This difference in nitrogen delivery was further evidenced by a strong positive effect between <2 mm non-gelatinous zooplankton and the other fractions (median [95% credible

interval]: gelatinous - <2 mm non-gelatinous: -3.3, -4.1 to -2.5; > 2 mm non-gelatinous - <2 mm non-gelatinous: -2.7, -3.5 to -1.9).

Discussion

In contrast to previous studies of the nutritional quality of gelatinous zooplankton (e.g. Wang and Jeffs 2014; Luskow et al. 2021, 2022), the gelatinous and non-gelatinous fractions of the zooplankton community were found to be nutritionally comparable. However, the grams nitrogen delivered by the <2 mm non-gelatinous fraction was found to be one to two orders of magnitude greater than the > 2 mm non-gelatinous and gelatinous fractions. This disparity is likely to be due to the higher abundances and total biomass of the non-gelatinous taxa. These results highlight that each of the zooplankton fractions represents relatively rich sources of nitrogen for coral reef planktivores and that the primary

Fig. 3 Potential nitrogen delivery by zooplankton fractions at Orpheus Island. Grams nitrogen per standardized metre square of water column over a flood tide (6 h) at a current speed of 0.0996 m s⁻¹. Black bar and black dots represent the median and mean density from the posterior distribution, respectively. Thick coloured bars represent the 50% credible intervals, and the thin coloured bars represent the 95% credible intervals. Raw data are overlaid as grey dots



factor determining their potential contribution to productivity is abundance rather than nutritional quality.

Community composition

The Pioneer Bay zooplankton community was comprised of 11 broad taxonomic groups. The groups from the gelatinous community included larvaceans, cnidarians, thaliaceans and amorphous organic material (AOM). The non-gelatinous community included copepods, crustacean larvae, other crustaceans, echinoderm larvae and chaetognaths. However, larvaceans and copepods were found to numerically dominate gelatinous and non-gelatinous communities, respectively. This community structure is consistent with past studies on near-reef zooplankton. Hamner et al. (1988), for example, found gelatinous and non-gelatinous zooplankton communities to be defined primarily by larvacean and copepods, respectively, the two comprising up to 70% of the total incoming zooplankton assemblage. Variation in the remaining taxa is also well documented (Hamner et al. 1988; Roman et al. 1990; Heidelberg et al. 2004; Yahel et al. 2005a). Our findings suggest that the composition of the zooplankton community at Orpheus Island is similar to that of other near-reef planktonic communities, with both gelatinous and non-gelatinous zooplankton groups arranged in a similar hierarchical structure. As such, our results may be widely applicable across coral reef ecosystems.

Nutritional quality

Despite the prey fractions occupying distinct trophic levels, stoichiometric analyses revealed that their nutritional quality was largely comparable. The > 2 mm non-gelatinous fraction recorded the highest nutritional values (i.e. recording the lowest mean C:N ratios) of 4.22:1 followed by the < 2 mm non-gelatinous (4.63:1) and the gelatinous prey fractions (4.81:1). There was little evidence of nutritional quality changing between prey fractions, except between the > 2 mm non-gelatinous and gelatinous zooplankton with the former having more nitrogen. However, despite this slight variation in quality, each of the examined zooplankton fractions, including the often-overlooked gelatinous component, represents potentially high-quality food for planktivores.

When compared with other dominant coral reef prey groups the nutritional quality of the zooplankton prey fractions becomes apparent. The zooplankton community fractions from our study (C:N averaged across all zooplankton = 4.55:1) approximate the nutritional quality of reef-associated fish as prey, with an average C:N ratio of 4.1:1 (Wyatt et al. 2012). Moreover, the nutritional advantage of a planktivorous diet is clear when contrasted with sessile coral reef dietary items. For example, macroalgae is a vastly inferior nutritional resource with an average C:N

ratio of 25:1 (Wyatt et al. 2012), which reveals nitrogen proportions that are 5 times lower than the zooplankton in this study. The nutritional inferiority of macroalgae is supported by the fact that only a select few specialized herbivorous fishes exploit this challenging resource (Choat and Clements 1998). By contrast, most nominally herbivorous fishes on coral reefs exploit components of the algal turf community (Choat and Clements 1998; Wilson et al. 2003; Tebbett et al. 2022). Even key components of this community (i.e. turf algae and detritus) have lower nitrogen values compared to the zooplankton recorded herein (i.e. C:N ratios of 8.5:1 and 8.36:1, respectively; Purcell and Bellwood 2001). Overall, these comparisons demonstrate the nutritional superiority of all three zooplankton prey fractions. Clearly, all zooplankton fractions are nutrient-rich food sources on coral reefs when compared to other non-elusive prey, highlighting the potential for each to contribute significantly to coral reef productivity.

Nutritional quantity: nitrogen delivery

While each of the three zooplankton prey fractions had comparable C:N ratios, when scaled up to the delivery of nitrogen per square metre of water column, they differed greatly in their capacity to deliver nitrogen to coral reefs. The < 2 mm non-gelatinous prey fraction was estimated to deliver the most nitrogen over a 6 h flood tide, delivering 0.88 gN m^{-2} followed by > 2 mm non-gelatinous (0.06 gN m^{-2}) and the gelatinous fraction (0.03 gN m^{-2}) the least. The delivery of nitrogen from each community fraction was a function of the community-specific total gN in the sampled water volume (which is dependent on the number of individuals in each community, i.e. the abundance, and the gN contribution of each individual). In terms of abundances, the < 2 mm non-gelatinous zooplankton community was mostly made up of copepods, which were highly abundant at our study site. The much less abundant chaetognaths and the moderately abundant larvaceans and cnidarians dominated the > 2 mm non-gelatinous and gelatinous zooplankton communities, respectively. The high abundance of copepods at our study site may explain why the < 2 mm non-gelatinous zooplankton fraction was estimated to deliver so much more nitrogen compared to the other fractions. Interestingly, the > 2 mm non-gelatinous community fraction was estimated to deliver more gN m^{-2} than the more abundant gelatinous fraction. This could be explained at the individual level, where gelatinous zooplankton may be expected to contribute less gN per individual compared to non-gelatinous zooplankton of a similar size, given their high water content (Hamner et al. 1975; Jaspers et al. 2015).

Zooplankton abundances, especially gelatinous zooplankton abundances (Kingsford et al. 1991; Graham et al. 2001; Sola et al. 2019), are known to vary greatly in time and

space, and the potential impacts of this variability on our results should not be overlooked (Alvaro Morales and Muriello 1996; Heidelberg et al. 2004; Yahel et al. 2005b). The blooming dynamics of gelatinous zooplankton, in particular, is a well-studied phenomenon in the scientific literature (e.g. Boero et al. 2008). Indeed, despite this study only capturing a seven-day temporal snapshot, larvaceans were nearly 4 times more abundant on the last day of sampling compared to the first day (Fig. S3). Thus, our observations of moderate abundance of gelatinous zooplankton at the time of sampling may be a reflection of their temporal variability, rather than an indication of their maximum abundance in the community. So, while gelatinous zooplankton represented a moderately abundant food resource at our time of sampling, at other times they could potentially represent a highly abundant food resource. Thus, although variable, both gelatinous and non-gelatinous zooplankton have the capacity to be key vectors of nitrogen for reef planktivores.

The extent to which gelatinous zooplankton contribute to reef productivity may be also linked to physical characteristics, such as their structure, size and accessibility (Alldredge 1976). The key difference between potential and realized nitrogen delivery may depend on size-based accessibility. The nitrogen in the < 2 mm non-gelatinous component is delivered in small particles compared to those in the relatively larger > 2 mm non-gelatinous and gelatinous fractions. This is important because planktivorous fishes are well known to consume larger size classes of zooplankton in greater proportions (Brooks and Dodson 1965; Brooks 1968; Hall et al. 1976; Noda et al. 1992). Preferential size predation may reflect optimal foraging where the most energetically advantageous foraging pattern for a species will be selected (Werner and Hall 1974). Notably, planktivorous fish ~ 71 mm in length have been found to ignore < 2 mm prey in 70% of encounters, favouring a continued search (Gardner 1981). As fish increase in size, it may therefore become less and less energetically worthwhile to prey on the < 2 mm non-gelatinous fraction.

This does not imply the < 2 mm zooplankton goes unused. The 2 mm cut-off used in this study is relatively coarse when considering zooplankton (cf. the 0.001 to 6 mm sampled by Hopcraft et al. 2001), and < 2 mm non-gelatinous zooplankton have been identified as a substantial part of the diets of some planktivorous reef fishes (e.g. Noda et al. 1992; Alldredge and King 2009; Hanson et al. 2016). This may also be an important component of the diet of benthic invertebrates, notably corals (Houlbreque and Ferrier-Pages, 2009). The utilization of smaller size classes of plankton may be attributable to niche partitioning, where some planktivorous fishes target the challenging, but more abundant, small zooplankton resource, thus avoiding competition with more size-selective planktivores (Leray et al. 2019). Nevertheless, the realized consumption of nitrogen may vary substantially

from its theoretical availability, especially for those planktivorous fishes that selectively overlook the < 2 mm size fraction, regardless of the total nitrogen it delivers.

System-level contributions

Planktivorous reef fishes are often one of the most diverse and abundant trophic groups on coral reefs (Williams and Hatcher 1983; Morais et al. 2021; Siqueira et al. 2021). They function as important trophic links, connecting coral reefs to off-reef resources by consuming the incoming nutrient-rich zooplankton (Morais and Bellwood 2019; Skinner et al. 2021). These assimilated nutrients are then transferred to other trophic levels through predation and excretion (Robertson 1982). Of these planktivorous fishes, damselfishes represent an abundant and particularly important group in the transfer of energy from pelagic to reef systems. This is because damselfishes are the primary source of food for many predatory reef fishes (Erez 1990; Frisch et al. 2014) and they can supply detritivorous fishes with nutritional resources via their supply of nutrient-rich faeces to the reef (Robertson 1982; Pinnegar and Polunin 2006). However, damselfishes have been documented preying on both gelatinous and non-gelatinous zooplankton and, therefore, may be considered relatively non-selective planktivores with diet restrictions imposed instead through prey availability (Dauby 1980; Hamner et al. 1988).

Given the potential importance of planktivorous damselfishes, and their non-selective feeding habits, it is interesting to consider the number of damselfish individuals that may be supported by the nutritionally rich zooplankton documented herein. It has been estimated that a planktivorous damselfish (*Chromis sp.*) requires, on average, 4.7% of their body mass in zooplankton per day, which is equivalent to 9.7 mg of nitrogen (Pinnegar et al. 2007). Applying this consumption rate to the grams nitrogen delivery calculated in this study allows for an estimation of the potential contribution of each of the zooplankton community fractions to planktivorous reef fish consumption and productivity. Thus, based on our estimates, each 6 h flood tide delivers, per m^2 , enough incoming zooplankton to provide the entire daily nitrogen ration for 99 damselfishes. Of this daily ration, the < 2 mm non-gelatinous fraction could, theoretically, sustain 90 individuals, with the > 2 mm non-gelatinous and gelatinous fractions feeding a further 6 and 3 individuals, respectively. However, when contextualized with the > 2 mm prey preference found in Gardner (1981) where planktivorous fish ~ 71 mm in length ignored < 2 mm size prey in 70% of encounters, the number of planktivorous fishes able to be sustained by the < 2 mm non-gelatinous fraction is reduced to 27 individuals. This rough calculation demonstrates the potential for each of the zooplankton fractions to underpin coral reef

trophodynamics and highlights how prey specificity may modify the potential of each fraction to contribute to reef fish productivity.

The importance of the zooplankton energetic pathway to coral reef productivity is highlighted when the values calculated above are compared to the grams nitrogen produced by turfing algae. Turfing algae are widely acknowledged as a major on-reef benthic primary producer that underpins herbivorous trophic pathways (Hatcher 1988; Klumpp and McKinnon 1992). However, turfing algae yield only $0.04 \text{ gN m}^{-2} \text{ day}^{-1}$ (Tebbett et al. 2018), a rate capable of sustaining a total of 4 damselfish $\text{m}^{-2} \text{ day}^{-1}$. This amount, when compared to the daily incoming zooplankton supply, represents only a small portion, roughly 2% of < 2 mm non-gelatinous, 33% of > 2 mm non-gelatinous and 67% of the gelatinous fraction. The importance of planktonic resources compared to those found on-reef is supported by previous research on trophic pathway energy flows, where fishes that rely on pelagic food webs are responsible for approximately 41% of the total fish productivity (Morais and Bellwood 2019). By contrast, epibenthic reef surfaces (grazing herbivores and sessile invertivores) contributed just 29% (Morais and Bellwood 2019). Clearly, the delivery of zooplankton to coral reefs, while spatially and temporally variable (Alldredge and Hamner 1980; White 1998; Lee et al. 2005; Alldredge and King 2009), is an important functional link that helps to sustain the high productivity of coral reef ecosystems (Morais et al. 2021). However, the difference between the theoretical supply of nitrogen and the nitrogen that can be ingested and assimilated needs to be addressed.

Conclusion

Our study demonstrated that gelatinous zooplankton are of a comparable nutritional value (in terms of C:N ratio) when compared to non-gelatinous zooplankton, contrary to previous expectations. Gelatinous zooplankton thus have the potential to contribute significantly to coral reef productivity. When the nutritional content of the zooplankton fractions was scaled up to nutrient delivery, the < 2 mm non-gelatinous zooplankton were found to deliver the most gN m^{-2} to the waters surrounding coral reefs; however, it may be energetically and nutritionally disadvantageous for planktivores to target these small items when larger prey items are available. Our findings provide novel insights into the trait–function relationship between the nutritional quality of zooplankton and the productivity of planktivorous reef fishes. In particular, they emphasize the potential importance of all zooplankton components, including the often-overlooked gelatinous fraction, in contributing to the high productivity of reef fish.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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