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Marine ecosystems with elevated temperature and terrestrial input support simplified food webs

Ludi Parwadani Aji[1,2,3,4,*], Christiaan A. de Leeuw[1], Philip Riekenberg[5,6], Agustin Capriati[1,2,7], Diede L. Maas[1], Marjolijn J. A. Christianen[7], Albertinka J. Murk[1], Marcel T. J. van der Meer[5], Leontine E. Becking[2,4]

[1]Marine Animal Ecology group, Wageningen University, Wageningen 6700 AH, The Netherlands
[2]Aquaculture and Fisheries group, Wageningen University, Wageningen 6700 AH, The Netherlands
[3]Research Center for Oceanography, National Research and Innovation Agency, Jakarta 14430, Indonesia
[4]Naturalis Biodiversity Center, Leiden 2333 CR, The Netherlands
[5]NIOZ Royal Netherlands Institute for Sea Research, Texel 1790 AB, The Netherlands
[6]CAIS Center for Applied Isotope Studies, University of Georgia, Athens, GA 30602, USA
[7]Aquatic Ecology and Water Quality Management group, Wageningen University, Wageningen 6700 AA, The Netherlands

ABSTRACT: Tropical coastal ecosystems are increasingly threatened by rising seawater temperatures and terrestrial nutrient input, yet the combined impact of these stressors on food web complexity remains poorly understood. Using marine lakes in Raja Ampat, Indonesia, as natural analogs for varying environmental conditions, we investigated how temperature and terrestrial influence shape food web structure and carbon source utilization. We applied an approach at 2 scales, combining whole food web stable isotope analysis in 2 contrasting lakes — one with elevated temperature and high terrestrial input, the other with ocean-like conditions — with a broader survey of 16 additional lakes using the filter-feeding mussel *Brachidontes* as a proxy for baseline carbon sources. Biodiversity, food web complexity, and functional redundancy were reduced in the marine lake with higher temperatures and greater terrestrial input. Bulk stable carbon and nitrogen isotope values from *Brachidontes* from 16 different marine lakes revealed a shift in the main food source underlying the food web from marine to terrestrial organic matter, with a shift from particulate organic matter to the use of sponge-derived material (reworked/recycled organic material) in environments with high temperatures and high terrestrial inputs. The use of *Brachidontes* as an integrative indicator of basal carbon sources offers a valuable tool for monitoring and managing the ecological impacts of environmental change in tropical coastal systems. Extrapolating our findings to coastal marine systems, our results suggest a potential shift toward simplified, less resilient trophic structures in ecosystems with combined thermal and terrestrial stressors.

KEY WORDS: Climate change · Eutrophication · Carbon food source · Marine lakes · Mussels · *Brachidontes* · Stable isotopes

1. INTRODUCTION

Over the past decades, the reduction and change in biodiversity of tropical coastal ecosystems have been widely documented and linked to anthropogenic activities on land and climate change (Hughes 1994, Bellwood et al. 2004, de Bakker et al. 2016, Duprey et al. 2016, Hughes et al. 2017, Tebbett et al. 2023). Activities such as deforestation and coastal development contribute to eutrophication by increasing terrestrial runoff, enriching coastal waters with organic and inorganic nutrients (Smith et al. 2003, Fabricius 2005). This enrichment elevates the productivity of algae (Cloern 2001, Fabricius 2005, den Haan et al. 2016), potentially allowing algae to outcompete corals, which rely on nutrient-poor, oligotrophic con-

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[*]Corresponding author: ludi.aji.biak@gmail.com

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ditions (Tomascik & Sander 1987, Fabricius 2005, Zhao et al. 2021). These local disturbances are further exacerbated by ocean warming, driven by global climate change (Hughes et al. 2003, Knowlton & Jackson 2008, Hall et al. 2018). However, the combined effect of increased water temperature and terrestrial input on tropical coastal ecosystems has yet to be thoroughly understood.

Concerns have been raised that reefs worldwide are shifting to states dominated by macroalgae (Bellwood et al. 2004, Pandolfi et al. 2005, Graham et al. 2015). Meanwhile, there is growing evidence that 2 other benthic groups are increasing in abundance on coral reefs, namely sponges and benthic cyanobacterial mats (BCMs) (de Bakker et al. 2016, 2017, Goatley et al. 2016, Ford et al. 2018, Pawlik & McMurray 2020). Cyanobacterial blooms are repeatedly linked to climate change and human-induced eutrophication (Sato et al. 2010, O'Neil et al. 2012, Huisman et al. 2018). BCMs and sponges may be more resilient to environmental change than corals or macroalgae (Bell et al. 2013, 2018, Huisman et al. 2018, Mumby & Steneck 2018). The question remains what effects these shifts away from coral dominance will have on the functioning of food webs in coastal settings.

The high biodiversity of tropical coastal ecosystems supports complex food webs, enabling the transfer of energy and nutrients between species through numerous trophic pathways (Hughes et al. 2017, Bellwood et al. 2019). A reduction in species richness and trophic interactions can lead to lower functional redundancy, compromising ecosystem resilience (Donázar-Aramendía et al. 2019, Li et al. 2022). Microbialization, a shift in ecosystem trophic structure of biomass and energy from higher trophic levels to the microbial loop (Haas et al. 2016) has been predicted as a possible future scenario for current coral reefs due to a combination of overfishing and eutrophication. This shift results in hypoxia and increased CO_2 emission from microbial respiration, fundamentally altering ecosystem function (Haas et al. 2016, Pezner et al. 2023). In this light, it is important to understand how the food webs of tropical coastal ecosystems will be impacted by a combination of globally increasing temperatures and local disturbances from increased terrestrial nutrient inputs.

Understanding the effects of environmental change at the ecosystem level requires an approach that considers complex ecological communities with multiple species across different trophic levels. However, it can be challenging to simulate whole ecosystem responses in small-scale experiments, and large-scale experimental interventions on open-system coral reefs are impractical (Knowlton & Jackson 2008). Marine lakes, with naturally occurring variation in temperatures and input of terrestrial organic matter, offer a promising setting to study ecosystem responses on a larger scale (Becking et al. 2011). Marine lakes are isolated from the surrounding ocean, with subterranean channels and fissures forming the only connection to the sea (Holthuis 1973, Dawson et al. 2009). As a result, they are under the influence of the inflow of terrestrial nutrients from the adjacent karst landscape covered with tropical rainforest. The extent to which nutrients are brought in via ocean currents or originate from terrestrial runoff and subsequently retained in the marine lake system depends on the degree of connection between the marine lake and the adjacent sea and corresponds to the extent of oceanic water inflow into the system. A highly connected marine lake experiences minimal retention of terrestrial runoff, as it is rapidly diluted by the exchange with seawater, making it akin to a conventional lagoon. In contrast, poorly connected marine lakes, despite receiving the same amount of terrestrial runoff, will be more impacted due to greater retention of terrestrial material within the system (Becking et al. 2011). Thus, marine lakes with high connectivity to the sea could serve as proxies for coastal conditions, experiencing lower terrestrial influence than those with limited connectivity. Temperatures of marine lakes range from current ocean conditions (29–31°C) to those predicted in the future under different climate change models (31–36°C), with each marine lake maintaining a relatively stable temperature year-round (Becking et al. 2011, 2015, Maas et al. 2018, de Leeuw et al. 2020). These characteristics make marine lakes uniquely suited to study the effects of temperature and land–sea coupling on marine food webs and ecosystem resilience.

Marine lakes predominantly harbor coastal marine species (Tomascik & Mah 1994, Dawson 2016). One species commonly found in marine lakes is the bivalve *Brachidontes* (de Leeuw et al. 2020, Aji et al. 2023). *Brachidontes* mussels are filter-feeders that feed on particulate organic matter (POM) and phytoplankton, thereby indirectly also incorporating dissolved organic matter (DOM) in their tissue (Sarà et al. 2003). Mussels can use almost all carbon sources available in the water column; previous work has shown that the filter-feeding mussels *B. pharaonis* and *Mytilus edulis* are reliable proxies for the carbon pools supporting food webs in coastal ecosystems since they can integrate the variation in $\delta^{13}C$ over time (Cabana & Rasmussen 1996, Vander Zanden et al. 1999, Middelburg 2014, Christianen et al. 2017).

With the marine lake model system, we can investigate a gradient in the relative contribution of terrestrial organic matter to the total organic carbon content, as well as temperature, to test whether the stable isotopic values of the mussels reflect this gradient.

By comparing marine lakes in Raja Ampat, Southwest Papua, Indonesia, of similar sizes and ages but differing in environmental conditions, we studied the combined influence of temperature and terrestrial input on the trophic structure and complexity of the ecosystem. We studied the resources supporting the food web and trophic interactions using stable isotope analysis by investigating patterns at fine and coarse scales. For the fine-scale approach, we studied the food web by sampling possible influxes such as POM, producers, and consumers contributing to the food web in a marine lake with a high temperature (33°C) and large influence of terrestrial input, and in a marine lake with current coastal conditions (30°C) and relatively low terrestrial influence. As a coarse-scale approach, we sampled the mussel *Brachidontes*, to serve as a proxy for the organic carbon base of the food web, from 16 marine lakes, which varied in temperature and terrestrial influence. Additionally, we investigated the diversity of major benthic groups in these marine lakes to assess the key components of the food web. We hypothesized that higher temperatures and greater terrestrial input will reduce trophic complexity and biodiversity, potentially leading to simplified and less resilient food webs.

2. MATERIALS AND METHODS

2.1. Sampling locations

In this study, we examined the food webs of 2 marine lakes (Papua01 and Papua24, Fig. 1) through an intensive sampling campaign in April 2016. These 2 marine lakes were selected because they strongly differ in water temperature and degree of connection to the surrounding sea.

Papua01 is a highly isolated marine lake, resulting in long water retention times and, thus, a relatively large contribution of terrestrial nutrient runoff and erosion to the total carbon content of the marine lake. Papua01 is located on Mansuar Island in the Dampier Strait, Raja Ampat, Southwest Papua, Indonesia. It retains a marine character through an underground connection in the limestone karst with the surrounding sea. The limited connection is evident in the delayed and dampened tides compared to the surrounding sea (Becking et al. 2011). An influx of rainwater reduces the overall salinity and, combined with the limited mixing of the water column, causes the marine lake to be permanently stratified. It contains an anoxic layer at a depth of 5 m below the surface, and a dense accumulation of purple sulfur bacteria marks the transition zone between the oxic and anoxic zones. The mean temperature of the oxygenated water layer is 32.5°C, which decreases to 28°C in the anoxic layer. In the oxic zone, the hard substrate is covered mostly by dense mussel beds (*Brachidontes* sp.), together with sponges (13 species), macroalgae, and ascidians. Other notable organisms include small omnivorous fish (*Exyrias* sp. and *Atheriniformes* sp.), tunicates, starfish, and crabs. Marine lake Papua01 represents coastal waters with high temperatures and terrestrial inputs.

In contrast, Papua24 is a highly connected marine lake, resulting in relatively short water retention times and conditions more similar to the surrounding sea. Papua24 is located on the western side of Meos Mansar in Raja Ampat. The water characteristics are similar to the surrounding sea (average temperature 30.3°C, salinity 32 ppt). A subterranean cave connects the marine lake to its adjacent sea, the water column is mixed, and the maximum tidal fluctuation in the marine lake is similar to that in the surrounding sea. The substrate is covered by scleractinian coral, large patches of macroalgae (*Caulerpa* sp.), and an abundant and diverse sponge community (23 species). The marine lake contains at least 12 fish species, including predatory *Lutjanus* sp. Marine lake Papua24 represents a setting similar to current ocean conditions with relatively low terrestrial input retention.

Additionally, we sampled a filter-feeding mussel (*Brachidontes* sp.) from 16 marine lakes and 4 coastal locations in Raja Ampat to obtain information on the relative contribution of terrestrial carbon input between these marine environments (Fig. 1). Mussels from coastal locations were found in reef flat zones. *Brachidontes* sp. were used to serve as a proxy to examine the use of particulate carbon resources within each site to indirectly characterize baseline resources supporting the ecosystem.

Benthic communities were surveyed in all marine lakes using photographic transects. For benthic group richness, 15 m long transect lines (n = 3) were laid out horizontally along the wall of each marine lake, 1 m below the low tide line, with the 3 replicates evenly spread around the perimeter. Photographs of 25 × 25 cm were taken along both sides of the transect line with a digital camera (Olympus TG-4). Per transect, 120 pictures were taken, resulting in a total of 360 photos per marine lake. Half of the obtained photo-

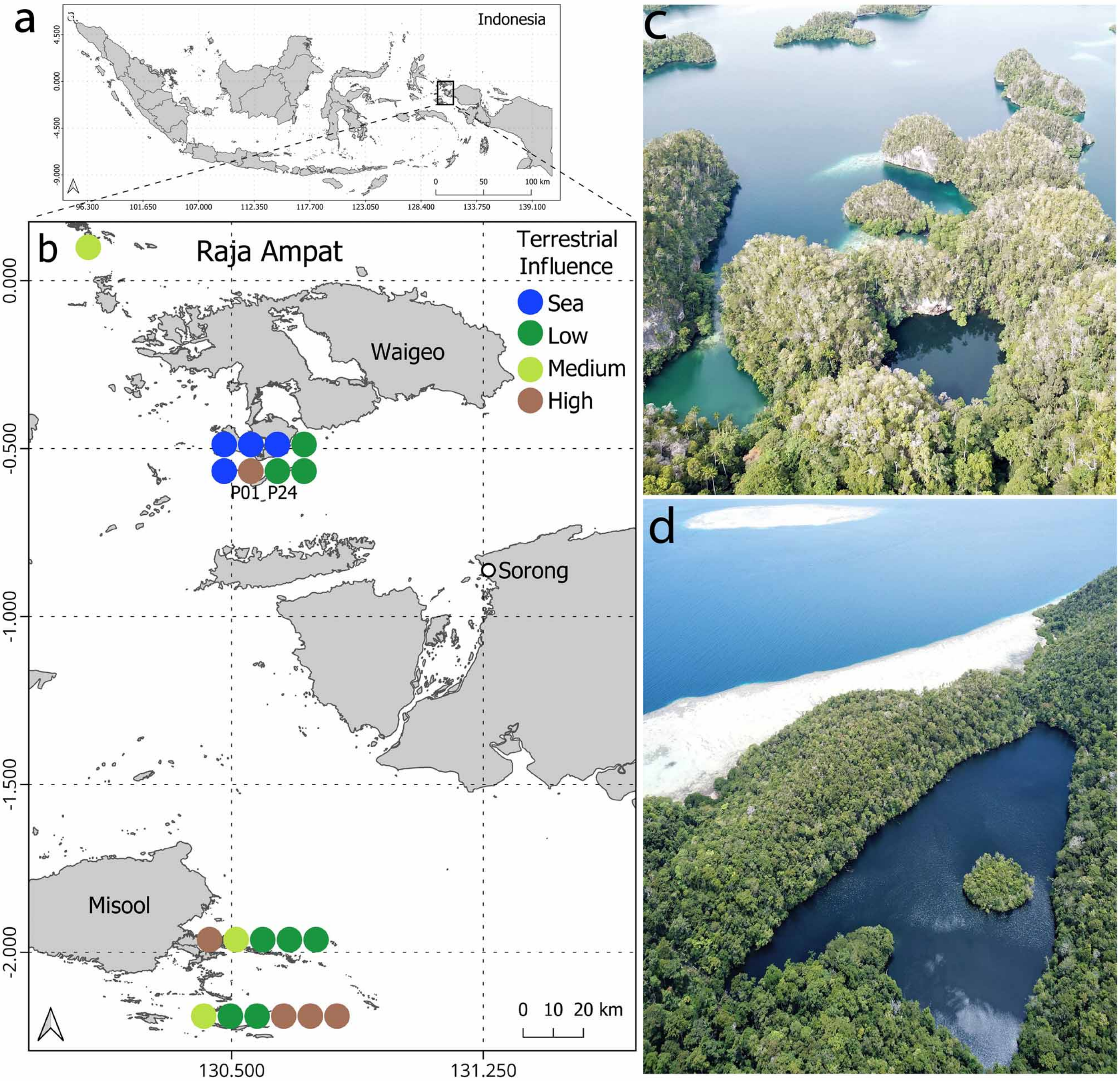

Fig. 1. Sampling locations in (a) Indonesia, with (b) overview of sampling locations in Raja Ampat, Southwest Papua province. Marine lakes are indicated by closed circles, colored according to estimated relative terrestrial nutrient input based on water retention in each marine lake (see key). Blue closed circles indicate sampling sites in the surrounding coastal seas. Marine lakes (c) Papua24 (P24) and (d) Papua01 (P01) were intensively sampled for food web analysis. In the remaining locations, only *Brachidontes* sp. mussels were sampled

graphs were analyzed, alternating between above and below the transect line. Coral Point Count with Excel extension (CPCE) Version 4.1 software (Kohler & Gill 2006) was used, with a uniform grid of 25 points per photo, to count the presence of 10 benthic groups (hard corals, sponges, macroalgae, crustose coralline algae, BCMs, bivalves, gastropods, polychaetes, tunicates, and echinoderms) as benthic group richness.

2.2. Environmental measurements

Water temperatures were measured using a YSI Professional Plus multimeter at 1 m intervals from the surface to the bottom of each marine lake (Table 1). Marine lakes were classified into 3 groups based on the influence of terrestrial input (Fig. 1). The terrestrial influence was estimated based on the degree of

Table 1. Marine lake characterization. Measurements of water temperature and salinity are mean values based on sampling at 1, 2, and 3 m depths. Codes for the marine lakes are based on de Leeuw et al. (2020) and Aji et al. (2023). The 2 marine lakes in **bold** were studied in more detail

Marine lake code	Relative tidal fluctuation	Terrestrial influence	Temperature (°C)	Salinity (ppt)	Benthic group richness	Coral present	Mangrove present
Papua26	0.9	Low	30	30	7	Y	Y
Papua15	0.9	Low	31	30	10	Y	Y
Papua24	0.8	Low	30	31	8	Y	Y
Papua11	0.8	Low	31	28	9	Y	Y
Papua18	0.8	Low	31	28	7	N	Y
Papua25	0.8	Low	32	30	8	Y	Y
Papua06	0.8	Low	32	28	8	N	N
Papua04	0.8	Low	32	26	8	N	N
Papua30	0.7	Medium	32	29	7	N	Y
Papua03	0.5	Medium	32	27	8	N	Y
Papua05	0.3	Medium	32	29	7	N	N
Papua02	0.2	High	34	25	7	N	Y
Papua01	0.1	High	33	24	6	N	Y
Papua21	0.1	High	35	24	7	N	Y
Papua19	0.1	High	35	20	7	N	Y
Papua22	0.1	High	36	18	6	N	Y

marine lake connectivity to the sea. The higher the relative tidal amplitude or connection to the sea, the lower the terrestrial influence due to the higher chance of terrestrial input being diluted by increased seawater turnover. Following Maas et al. (2018), this metric was assessed by measuring the tidal fluctuation in a marine lake with water level loggers, expressed as a relative value to the tidal fluctuation in the surrounding sea. The 'relative tidal amplitude' is calculated by ($\text{Lake}_{\text{max}} - \text{Lake}_{\text{min}}$) / ($\text{Sea}_{\text{max}} - \text{Sea}_{\text{min}}$), where Lake_{max} and Lake_{min} refer to the maximum and minimum water level in the marine lake over a 48 h period, and Sea_{max} and Sea_{min} represent the maximum and minimum water level in the adjacent open sea during that period. Marine lakes with a relative tidal fluctuation >0.75 were classified as having low terrestrial influence, marine lakes with values between 0.25 and 0.75 as medium, and marine lakes with <0.25 as having high terrestrial influence. The sea locations were categorized as a reference group, representing conditions in current open-sea environments. The location selection was restricted by the natural occurrence of (1) marine lakes and (2) populations of *Brachidontes* mussels in coastal locations. Regarding the geographical spread of lakes, which are a rare find even in this global hotspot for marine lakes, earlier research suggests limited effects of geographical distance in shaping populations in these lakes (de Leeuw et al. 2020). Regarding the 4 coastal locations, finding *Brachidontes* in the remote coastal areas of Raja Ampat is challenging and requires considerable time and effort. We searched for *Brachidontes* along stretches of coast, particularly in areas surrounding or near the lakes within our study sites. However, we were only able to locate these mussels in 4 coastal areas. Furthermore, coral and mangrove presence were included as a qualitative measure to reflect ecological differences. The presence of hard coral in marine lakes would mean a higher connection to the sea, while mangrove trees contribute to terrestrial input through their leaves and roots.

2.3. Sample collection, processing, and stable isotope analysis

For the food web analysis, replicates of each species of benthic groups, fish, terrestrial trees (fresh leaves and leaf litter), mangroves (leaves and roots), dead wood, and potential nutrient sources were sampled for the 2 marine lakes that were studied in more detail, i.e. Papua01 and Papua24 (Table 2). We sampled all representative species that we could find in the field. We had replicates for benthic organisms, but it was difficult for fish. Most species were collected by hand, while moving species such as fish were collected by fishing, traps, and hand nets. We collected adductor muscle tissue from bivalves; foot tissue from gastropods and nudibranchs; bell (umbrella) tissue from jellyfish; body column tissue from anemones; body wall tissue from tunicates and echinoderms; leg muscle tissue from

Table 2. Summary of stable isotope values for samples from 2 marine lakes with low (Papua24) or high (Papua01) terrestrial influence. Mean (±SD, when n > 1) stable isotope values of δ^{15}N and δ^{13}C are shown for all sources and consumer functional groups. Species were sampled in triplicate where possible. BCMs: benthic cyanobacterial mats; POM: particulate organic matter

Sources and consumers	Papua24				Papua01			
	n samples	n species	$\delta^{13}C_{VPDB}$ (‰)	$\delta^{15}N_{AIR}$ (‰)	n samples	n species	$\delta^{13}C_{VPDB}$ (‰)	$\delta^{15}N_{AIR}$ (‰)
Macroalgae	12	4	−18.2 ± 4.4	3.2 ± 0.7	6	2	−32.4 ± 1.7	−0.8 ± 2.3
Dead wood	1	–	−25.7	3.1	3	–	−30.2 ± 1.1	1.7 ± 2.2
Litter	3	–	−30.1 ± 1.1	−1.6 ± 2.7	3	–	−29.6 ± 0.5	−0.7 ± 0.5
Mangrove roots	3	1	−30.4 ± 1.1	1.9 ± 0.8	3	1	−29.8 ± 0.7	4.7 ± 1.6
Mangrove leaves	3	1	−31.6 ± 0.5	0.8 ± 1.3	3	1	−30.3 ± 1	3.7 ± 0.4
Trees	8	5	−31.2 ± 1.6	−1.3 ± 2	14	5	−27.5 ± 2.5	−0.6 ± 1.7
Sediment	1	–	−28.1	4.2	1	–	−26.3	2.0
BCMs	2	–	−24.6 ± 3	2.4 ± 0.6	1	–	−27.5	4.8
POM	1	–	−28.3	0.5	4	–	−28.1 ± 3.8	2.6 ± 1.7
Sponges	58	24	−24.2 ± 1.7	5.7 ± 1.5	37	13	−29.7 ± 0.7	6.9 ± 1.5
Bivalves	22	6	−22.0 ± 1.1	5.3 ± 0.7	5	1	−30.9 ± 0.6	6.2 ± 0.2
Gastropods	9	3	−19.4 ± 2.5	5.3 ± 1.7	3	1	−24.4 ± 0.8	3.3 ± 0.3
Fish	12	12	−19.5 ± 2.1	8.4 ± 1.3	6	2	−27.0 ± 0.9	10.1 ± 0.9
Anemones	2	1	−24.5 ± 0.01	6.4 ± 0.4	–	–	–	–
Hydroids	3	1	−23.0 ± 0.05	4.9 ± 0.2	–	–	–	–
Nudibranchs	3	1	−35.4 ± 0.7	4.7 ± 0.9	–	–	–	–
Coral	1	1	−22.2	5.1	–	–	–	–
Jellyfish	1	1	−18.3	3.8	–	–	–	–
Tunicates	–	–	–	–	2	1	−28.9 ± 0.2	6.4 ± 0.1
Echinoderms	–	–	–	–	3	1	−23.7 ± 1.7	9.0 ± 0.2
Crabs	–	–	–	–	3	1	−23.2 ± 1.2	7.2 ± 0.4

crabs; polyp tissue from corals and hydroids; body tissue from sponges; and tail muscle tissue from fish. POM was sampled by filtering 1 l water samples (from 1 m depth) over Whatman^{TM} glass microfiber filters (GF/F, 0.6–0.8 µm particle). In Papua01, additional water samples were taken from the anoxic layer at 5 m depth. For the between-site comparison across the 20 study locations (16 marine lakes and 4 coastal sites), 5 individuals of *Brachidontes* sp. were sampled from an intertidal area at each site.

Immediately after collection, materials were placed in aluminum foil envelopes and dried in a rice cooker at approximately 80°C for 24 h in the field until dry. Due to the remoteness of the field setting, after the initial drying period, bags were stored at ambient temperature for up to 1 mo before being stored at −20°C. Before further analysis, samples were dried again for 24 h at 60°C in a drying oven to remove any residual moisture that may have accumulated due to storage in humid field settings prior to freezing. Sample materials were ground (except samples on GF/F filters) using a mortar and pestle and stored in glass vials at room temperature prior to analysis. Samples potentially containing inorganic carbon (sponges, hard corals, BCMs, calcareous algae, mollusks, crabs, starfish, water filters) were decalcified by adding a 1 M HCl solution (Tue et al. 2012, Le et al. 2017, Di Trapani et al. 2020). Subsequently, the samples were dried in a vacuum oven at 70°C for 48 h to remove any remaining HCl. Samples were weighed in either tin or silver cups for non-calcareous and HCl-treated calcareous samples. Tissue samples for the ecological community data set were analyzed with a CN elemental analyzer (EA NA1500 - EA 1110, Carlo Erba and Thermo Fisher Scientific) coupled to an isotope ratio mass spectrometer (IRMS; Finnigan DeltaPlus) at Radboud University, Nijmegen, The Netherlands. Water filters and *Brachidontes* mussels for the coarse-scale data set were analyzed at the Royal Netherlands Institute for Sea Research (NIOZ, Texel, The Netherlands) with an organic elemental analyzer (Flash 2000) that was coupled to an IRMS (Delta V Advantage). Stable isotope ratios were expressed in the conventional δ notation according to the following equation: $\delta X = (R_{sample}/R_{standard} - 1)$, where X is ^{13}C or ^{15}N, and R is the ratio of the heavy (^{13}C and ^{15}N) over the light (^{12}C and ^{14}N) isotope. The δ^{13}C and δ^{15}N values are reported in per mille notation (‰) relative to Vienna Pee Dee belemnite and atmospheric nitrogen standards, respectively, and normalized to international standards (IAEA N1 and IAEA-CH-6).

Average precision for internal standards (acetanilide, casein, benzoic acid, beet sugar, and urea) and replicate samples were calculated from the runs comprising this data set and were found to be within ±0.2‰ for δ^{13}C and ±0.3‰ for δ^{15}N. We did not adjust δ^{13}C values in consumer tissues for lipid inclusion because the C:N ratio of our consumers ranged between 3 and 6, which does not indicate a relevant amount of lipid storage in the consumers to shift isotopic values away from proteinaceous dominated values.

2.4. Data analysis

All analyses were performed in R version 4.4.2 (R Core Team 2024). Data were checked for deviations from normality and homogeneity using a Shapiro-Wilk test and the *F*-test variability as implemented by the 'var.test' function in the base R 'stats' package, respectively. The difference between stable isotope values between marine lakes and environments was then tested with unpaired sample *t*-tests in case of normally distributed data with homogeneous variance, and with Wilcoxon tests in case of non-normally distributed data or heterogeneous variance. For the comparisons between categories of terrestrial influence, a Kruskal-Wallis test with a post hoc Dunn test with Bonferroni correction was performed. In addition, the difference in benthic group richness of 3 marine lake categories (low, medium, and high terrestrial influence) was tested by 1-way ANOVA and Tukey's HSD test at a confidence level of 95%. An alpha level of $\alpha = 0.05$ was maintained to indicate significance. The contributions of the underlying resources being used by the filter-feeding mussel *Brachidontes* and other consumers (gastropods and fish) in the 2 contrasting marine lakes, Papua24 and Papua01, were assessed from the stable isotope analysis using the R package 'Stable Isotope Mixing Models in R' ('SIMMR'). The 'SIMMR' package utilizes Bayesian techniques to solve for unknown consumer mixes given known resource values for C and N isotope compositions and concentrations (Parnell 2019). This package is an upgrade of the 'SIAR' R package (Parnell et al. 2010, Parnell & Jackson 2013) and uses Markov chain Monte Carlo analyses to solve for all possible contributions from each resource for each consumer as probability distributions (iterations: 200 000; burn-in: 50 000; thinned by: 10). To assess the models' performance, we examined Gelman-Rubin convergence statistics to ensure that the R-hat values were close to 1 for each of the 3- and 5-source models that were performed for each site. Matrix output from the models was examined for strong and weak correlations to determine whether the inclusion of individual sources was appropriate (Figs. S1–S4 and Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m771p015_supp.pdf). To examine whether the 5-source model had significant autocorrelation due to relatively comparable source values for 3 sources, we combined source values for each site to investigate terrestrial versus marine resource use and found similar output for resource use between the 2 models. The 3-source model has the limitation that not all consumers were contained in the mixing envelope, but the lowered complexity further confirmed the robustness of the conclusions provided by the 5-source modeling at both sites. The combined output from these 2 modeling approaches (complex and simplified) strengthens the likelihood that model output reflects natural patterns within the examined ecosystems (Fry 2013). For the 5-source model, we provide probability ratios for the use of terrestrial resources as determined by δ^{13}C values indicating strongly terrestrial values (<-25‰) that were combined post hoc. Probabilities for resource use are provided with source densities for each consumer from the 3-source modeling (Figs. S5 & S6).

The contribution of 5 sources to the diet of the mussel *Brachidontes* sp. as a filter-feeding primary consumer in both marine lakes was assessed by running 2 independent models in 'SIMMR.' The sources used for Papua24 and Papua01 were sponges, macroalgae, litter, POM, and BCMs. Macroalgae from both marine lakes belong to green algae (Phylum Chlorophyta) and have the same photosynthetic pathways. We included sponges (mixotrophic organisms) as a source of the reworked material (DOM) that re-enters the system (Hanz et al. 2022). Sponge DOM and litter were classified as terrestrial sources from marine lakes Papua24 and Papua01, largely due to their comparatively low δ^{13}C values, while non-terrestrial sources were BCMs and POM with higher δ^{13}C values. Trophic enrichment factors (TEFs) were applied to consumers to allow for the relative contribution of resources to their diets: 3.4‰ for δ^{15}N and 1‰ δ^{13}C (Post 2002, McCutchan et al. 2003). Resource contribution from terrestrial sources were calculated post hoc by combining probabilities for resources with similar δ^{13}C values, and propagation of uncertainties was done using the 'propagate' R package. In Papua01, the terrestrial sources were represented by a combination of sponges, litter, and macroalgae, while in Papua 24, terrestrial sources were a combination of sponges and litter.

3. RESULTS

3.1. Environmental conditions and characteristics of marine lakes

The environmental conditions and characteristics of 16 marine lakes in Raja Ampat are presented in Table 1. In general, the temperature of low terrestrial influence marine lakes ranged from 30 to 32°C, followed by medium marine lakes at 32°C and high terrestrial influence marine lakes from 34 to 37°C. Benthic group richness from low terrestrial influence marine lakes ranged from 8 and 10, medium from 7 to 8, and high terrestrial influence marine lakes from 6 to 7. In addition, hard coral colonies were only found in 5 marine lakes with low terrestrial influence (Table 1), whereas mangrove trees as part of terrestrial input for the marine lakes were found in marine lakes from all 3 terrestrial influence categories.

3.2. Whole food web differences

The 2 marine lakes selected for more detailed comparison showed very distinct differences in community diversity and food web complexity (Fig. 2). The food web in Papua24, the cooler and higher seawater turnover lake, was more complex, with a higher number of species and functional groups and a larger range of $\delta^{13}C$ values compared to Papua01, the relatively warmer and more isolated marine lake (Papua24: −36 to −9‰; vs Papua01: −35 to −23‰). Filter-feeders such as sponges, bivalves, and anemones clustered together in the stable isotope plot representing $\delta^{13}C$ and $\delta^{15}N$ values. The marine lake representing high temperature and terrestrial influence (Papua01) had less community diversity, with only 2 fish species, 3 mollusks, and no other groups represented (e.g. anemones, hydroids). In addition, the total range of $\delta^{15}N$ values of consumers was comparable in both marine lakes, despite the absence of some top predators in Papua01 (Papua24: 2.1 to 10.6‰; Papua01: 2.5 to 11.5‰). Sponges and fish had the lowest and highest $\delta^{15}N$ values, respectively, in both marine lakes. The highest trophic level in Papua01 consisted of small gobies and a starfish, while in Papua24, large predatory fish and a predatory gastropod (*Muricodrupa* sp.) represented the highest trophic level. The benthic group richness of Papua01 (6 groups) was less diverse than that of Papua24 (8 groups), and there was a higher coverage of bare substrate in Papua01. Dense beds of *Brachidontes* mussels covered most of the hard substrate, while the soft substrate harbored macroalgae and thin biofilms of BCMs. Papua01 had larger gaps in isotopic niche space than Papua24 (Fig. 2).

3.3. Stable isotope compositions of primary producers

The trees and terrestrial litter surrounding the marine lakes showed similar ranges in stable isotope values for both marine lakes, with most $\delta^{13}C$ values around −30‰, except for 1 tree species at Papua01: −23 ± 0.1‰ (Table 2). The $\delta^{15}N$ for these terrestrial sources ranged from −4 to 2‰ in both marine lakes. Mangrove roots and leaves (combined) showed comparable $\delta^{13}C$ values for both marine lakes as well (Papua01: −30.1 ± 1‰ vs. Papua24: −31 ± 1‰) (*t*-test: $t_{10} = 1.8$, $p = 0.11$), but the mangrove $\delta^{15}N$ value was higher in Papua01 (4.2 ± 1.2‰) when compared to Papua24 (1.4 ± 1.1‰) (*t*-test: $t_{10} = 4.2$, $p = 0.002$). Macroalgae in Papua01 had a mean $\delta^{13}C$ value of −32 ± 1.7‰, while those in Papua24 had a mean value of −18 ± 4.4‰, which was significantly different (Wilcoxon test: $W = 0$, $p < 0.001$). The macroalgal $\delta^{15}N$ values also significantly differed between sites (Wilcoxon test: $W = 1$, $p = 0.001$), with −0.8 ± 2.3‰ for Papua01 and 3.2 ± 0.7‰ for Papua24. BCMs were found in both marine lakes, and these had a slightly lower $\delta^{13}C$ value in Papua01 (−27.5‰) compared to Papua24 (−24.6 ± 3‰). However, BCM $\delta^{15}N$ values showed the opposite trend, with a lower value of 2.4 ± 0.6‰ for Papua24 and 4.8‰ for Papua01. Lastly, POM taken from a depth of 1 m showed similar $\delta^{13}C$ values in both marine lakes (Papua01: −28.1 ± 3.8‰ and Papua24: −28.3‰) but had different $\delta^{15}N$ values (Papua01: 2.6 ± 1.7‰ and Papua24: 0.5‰).

3.4. Stable isotope compositions of consumers

A higher diversity of mollusk species was found in Papua24 (10 species: gastropods, bivalves, and nudibranchs), with $\delta^{13}C$ values ranging from −35 to −16‰ compared to Papua01 (2 species: gastropod and bivalve *Brachidontes*), where $\delta^{13}C$ values ranged from −32 to −24‰, resulting in a significantly larger $\delta^{13}C$ variation for mollusks in marine lake Papua24 (Wilcoxon test: $W = 26$, $p < 0.001$), while the $\delta^{15}N$ of mollusks from Papua24 (3.2 to 7.9‰) and Papua01 (3.1 to 6.4‰) were similar (Wilcoxon test: $W = 142$, $p = 0.86$). Both the $\delta^{15}N$ values and $\delta^{13}C$ values of gastropods were lower in Papua01 ($\delta^{15}N$: 3.3 ± 0.3‰ vs. 5.3 ± 1.7‰; Wilcoxon test: $W = 2$, $p = 004$; $\delta^{13}C$: −24.4 ±

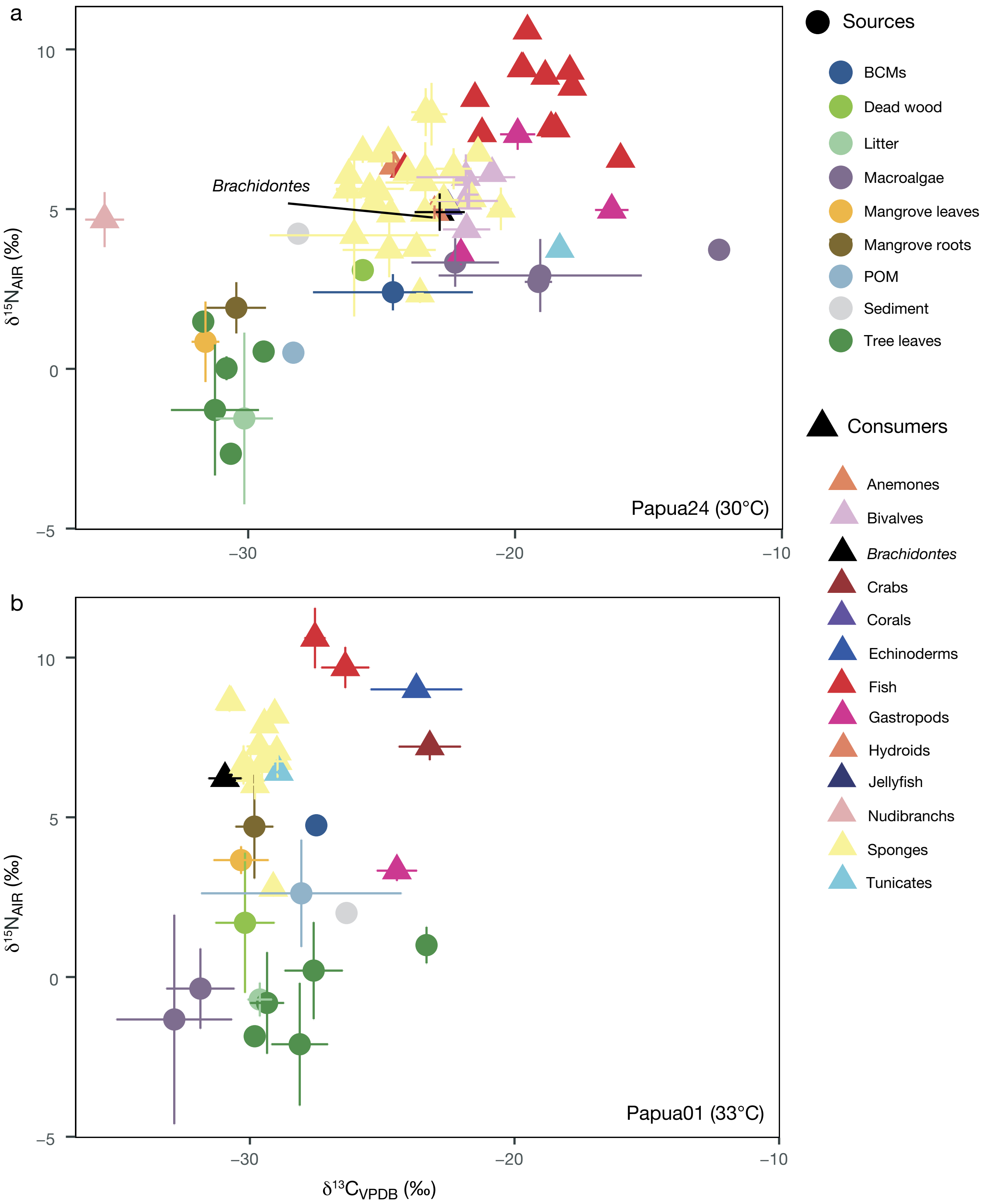

Fig. 2. Stable isotope values of ecological communities with primary producers, detrital resources, and consumers potentially contributing to the food web in (a) a marine lake close to current ocean conditions (Papua24) and (b) a marine lake with high temperature and a high influence of terrestrial input (Papua01). Error bars represent standard deviations of biological replicates (n = 3–14). Black arrow in (a) points to *Brachidontes*. BCMs: benthic cyanobacterial mats; POM: particulate organic matter; VPDB: Vienna Pee Dee belemnite

0.8 vs. −19.4 ± 2.5‰; Wilcoxon test: $W = 0$, $p = 0.02$). Bivalves had lower $\delta^{13}C$ values in Papua01 (−30.9 ± 0.6‰) than in Papua24 (−22 ± 1.1‰) (Wilcoxon test: $W = 0$, $p < 0.001$), but higher $\delta^{15}N$ values (Papua01: 6.2 ± 0.2‰ and Papua24: 5.3 ± 0.7‰, respectively; Wilcoxon test: $W = 95$, $p = 0.01$). Similarly, the $\delta^{13}C$ values of fish in Papua01 were lower than in Papua24 (−27 ± 0.9 and −19.5 ± 2.1‰; t-test: $t_{16} = -8.3$, $p < 0.001$), but the $\delta^{15}N$ values were higher (10.1 ± 0.9 and 8.4 ± 1.3‰, respectively) (t-test: $t_{16} = 3.0$, $p = 0.008$). Sponges were the most species-rich taxon in both marine lakes (n: 13 in Papua01 and n: 24 in Papua24). There was no overlap in the isotopic niche space between sponges of the 2 marine lakes, as $\delta^{13}C$ values were considerably lower in Papua01 than Papua24 (−29.7 ± 0.7 vs. −24.2 ± 1.7‰; Wilcoxon test: $W = 0$, $p < 0.001$) and higher for $\delta^{15}N$ values (Papua24: 5.7 ± 1.5‰ vs. Papua01 6.9 ± 1.5‰; Wilcoxon test: $W = 1620$, $p < 0.001$). The primary consumers (mean values of $\delta^{13}C$ and $\delta^{15}N$) such as anemones (−24.5 and 6.1‰), hard coral (−22.2 and 5.09‰), hydroids (−23.1 and 4.88‰), jellyfish (−18.3 and 3.75‰), and nudibranchs (−35.4 and 4.67‰) were only found in Papua24, while consumers that only occurred in Papua01 were echinoderms (−23.7 and 9‰), crabs (−23.2 and 7.21‰), and tunicates (−28.9 and 6.41‰) (Fig. 2).

3.5. Food source proportion

The stable isotope mixing model indicated that marine POM was the most essential food source for *Brachidontes* sp. in Papua24, while sponge-derived material contributed the least as a dietary resource. In contrast, in the high temperature and high terrestrial influence marine lake Papua01, sponge-derived material was the dominant food source for *Brachidontes* sp., with macroalgae as their second most important dietary component, while POM contributed the least (Fig. 3). We classified sources of terrestrial origin based on their $\delta^{13}C$ values (Papua24: sponge and litter; Papua01: sponge, litter, and macroalgae) as well as non-terrestrial sources (Papua24: BCMs, POM, and macroalgae; Papua01: BCMs and POM). Macroalgae were classified as a terrestrial source in Papua01, but not in Papua24. This classification is based on the significantly lower $\delta^{13}C$ values in Papua01 (−32.4 ± 1.7‰) compared to those in Papua24 (−18.2 ± 4.4‰). Overall, the food source contribution from terrestrial sources to the mussel *Brachidontes* is higher in Papua01 (Fig. 4). Fig. 4 shows that food sources for consumers (Gastropoda, fish, *Brachidontes*) in Papua24 are mostly non-terrestrial. Meanwhile, in Papua01, food sources are mainly terrestrial (indirectly from sponge-derived material).

3.6. *Brachidontes* resource use and benthic group richness

Benthic group richness was higher in marine lakes with larger tidal fluctuations (lower terrestrial influence) and lower in higher terrestrial input marine lakes (ANOVA: $F_{2,13} = 5.39$, $p = 0.02$) (Fig. 5a). Furthermore, there was a difference in group richness between marine lakes with low and high terrestrial influence (Tukey's HSD: $p = 0.01$, CI = 0.29, 2.76), but not between marine lakes with medium and low, or medium and high terrestrial influence.

The filter-feeding mussel *Brachidontes* sp. was collected from 16 marine lakes and 4 coastal locations. Categories reflecting the degree of terrestrial influence (high, medium, low, and coastal) were established based on the extent of tidal fluctuation. The highest $\delta^{13}C$ values were observed in the open ocean (−11.8 ± 3.3‰) and the lowest in the marine lakes with the highest terrestrial influence (−26 ± 2.9‰). The marine lakes with low (−22.8 ± 1.7‰) and medium (−20.9 ± 1.7‰) terrestrial influence were similar and in between the 2 extremes. Significant differences exist between $\delta^{13}C$ values among the categories of terrestrial influence (Kruskal–Wallis: $H_3 = 72.3$, $p < 0.001$). In particular, the marine lakes with high terrestrial influence were significantly lower in $\delta^{13}C$ than all other categories (Dunn tests: versus medium: $Z = -4.7$, $p < 0.001$, versus low: $Z = -3.5$, $p < 0.001$, versus coastal locations: $Z = -8.2$, $p < 0.001$). Additionally, the coastal locations were significantly higher in $\delta^{13}C$ values than all other categories (Dunn tests: versus medium: $Z = -2.7$, $p = 0.04$, versus low: $Z = -5.9$, $p < 0.001$).

The values of $\delta^{15}N$ varied less, with marine lakes with low terrestrial influence showing 5.2 ± 2.1‰, marine lakes with medium terrestrial influence showing 6.1 ± 1.4‰, marine lakes with high terrestrial influence showing 4.5 ± 3.2‰, and the coastal locations showing 5.3 ± 0.8‰. Still, significant differences were observed (Kruskal-Wallis: $H_3 = 13.7$, $p = 0.003$). In particular, marine lakes with medium terrestrial influence showed significantly higher $\delta^{15}N$ values than marine lakes with low terrestrial influence (Dunn test: $Z = -3.2$, $p = 0.007$), and marine lakes with high terrestrial influence (Dunn test: $Z = -2.9$, $p = 0.02$).

Marine lakes with low and medium terrestrial influence exhibited more or less similar $\delta^{13}C$ values

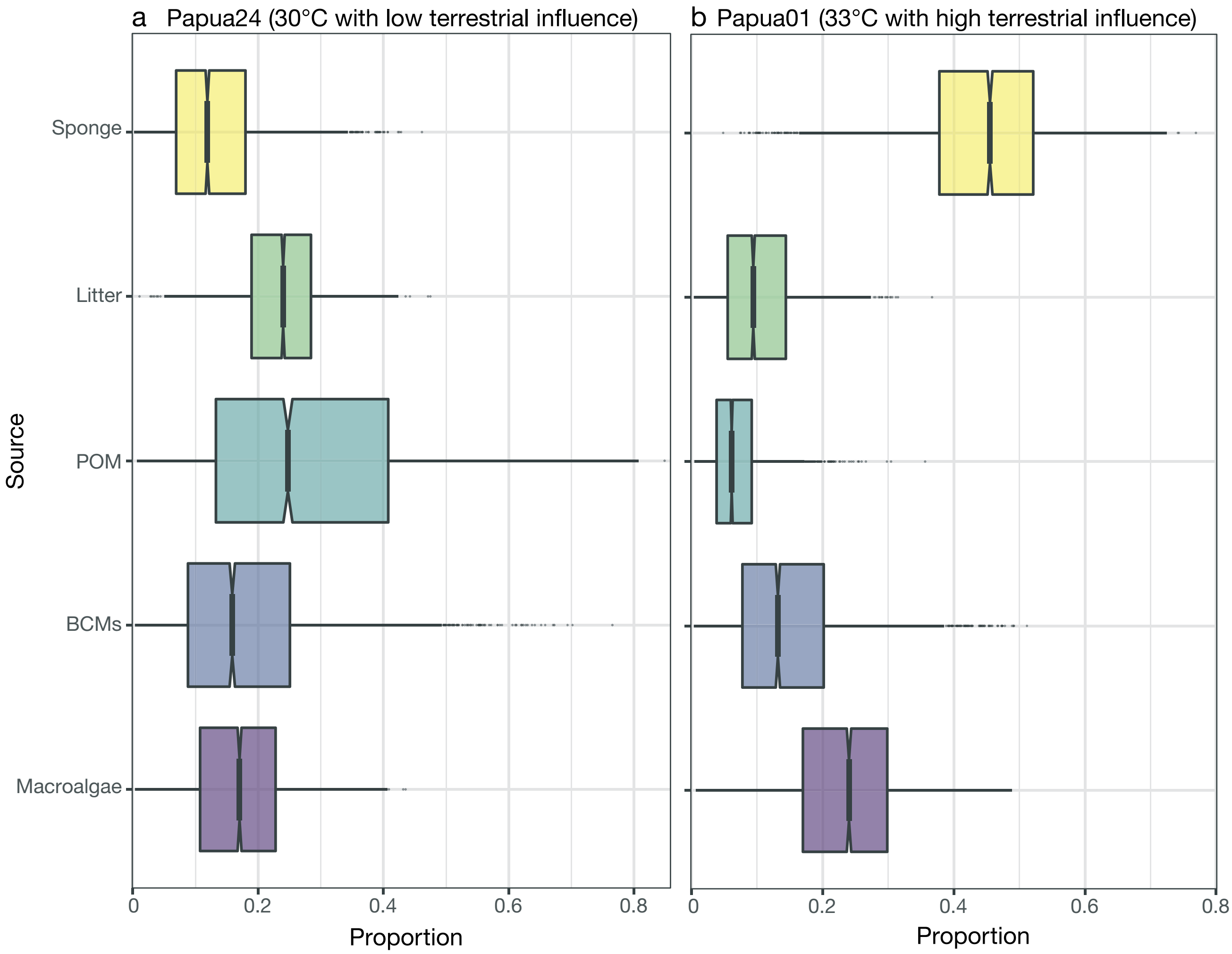

Fig. 3. Fractional contributions of sources to the mussel *Brachidontes* sp. modeled using the 'SIMMR' package. Five sources are included in the model: sponge, litter, particulate organic matter (POM), benthic cyanobacterial mats (BCMs), and macroalgae. The box represents the interquartile range (Q1, 25th percentile to Q3, 75th percentile), vertical line inside the box indicates the median (Q2) of the data, whiskers extend from the box to the minimum and maximum, and dots are considered potential outliers

(Fig. 5b), while $\delta^{15}N$ did not show a clear pattern. The value of $\delta^{15}N$ from low and medium terrestrial influence marine lakes was similar to those from the sea locations. Furthermore, *Brachidontes* sp. populations in the sea exhibited higher $\delta^{13}C$ values than those in marine lakes and showed a large range in $\delta^{13}C$ values (−16 to −8‰) between the 4 sea locations. Stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ for *Brachidontes* sp. varied considerably (22 and 11‰) across 20 sampling locations (marine lake and sea locations) (Fig. 5b).

4. DISCUSSION

As global temperatures rise and regional disturbances increase (e.g. land erosion, runoff), understanding the combined effects of elevated water temperature and terrestrial runoff on tropical coastal ecosystems becomes increasingly important. Here, we compared the trophic structure and food webs in marine lakes across a gradient of environmental conditions to assess the influence of elevated temperature combined with input of terrestrial resources. We found that lakes with higher temperature and stronger terrestrial influence supported lower benthic group richness and simpler food webs, with fewer species per trophic level and narrower isotopic niche space. The filter-feeding mussel *Brachidontes* sp. served as a useful proxy to examine baseline resources supporting the food web in each lake. Our study shows a clear shift in resource use: in lakes with high temperature and terrestrial input, mussels relied more on reworked terrestrial organic matter, while in more con-

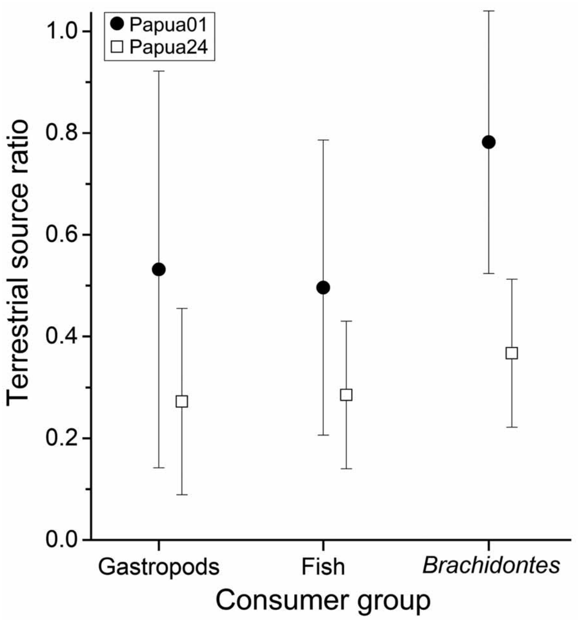

Fig. 4. Terrestrial resource ratio of consumers (gastropods, fish, and *Brachidontes*) from 2 marine lakes in Indonesia, Papua01 (33°C) and Papua24 (30°C), from the 5-source mixing model. Error bars are for propagated probability ranges for combined sources

nected, cooler lakes, marine POM was the dominant source. This change in carbon sources reflects both increased availability of terrestrial material and reduced dilution by seawater in less-connected systems. Below, we discuss the potential implications of extrapolating these findings to coastal marine systems under climate change scenarios and with increased local disturbances.

Our analysis of the food webs in 2 marine lakes shows that both lakes have representative consumers in the same trophic levels, but in the high temperature, high terrestrial input lake (Papua01), the diversity of species per trophic level was reduced, with top predators absent. In contrast, the cooler, better connected lake (Papua24), supported more fish species and a more complex food web structure. We also found that benthic group richness was lower in high terrestrial influence marine lakes (Fig. 5a). These patterns align with findings from coral reef and temperate systems where warming and eutrophication reduce biodiversity and food web complexity (Norderhaug et al. 2015, de Bakker et al. 2016, Gibert 2019, Smith et al. 2000). Low oxygen levels and stratification in Papua01 may also contribute to the absence of higher trophic levels, as hypoxia limits the presence of larger consumers (Breitburg et al. 2018). Since the functioning of marine ecosystems relies on both the biodiversity and energy transfer within the food web (Ullah et al. 2018), higher temperatures combined with terrestrial influence could result in a lower functional redundancy (Steneck et al. 2002,

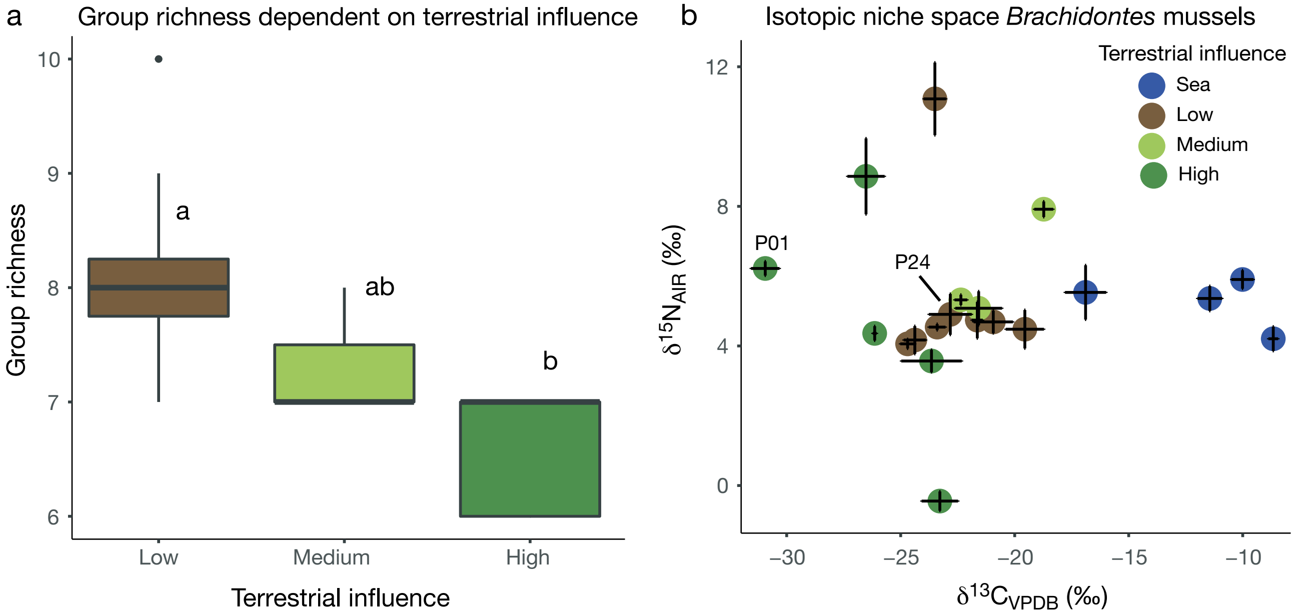

Fig. 5. (a) Number of benthic groups in marine lakes. Different letters above the boxplots indicate significant differences ($F_{2,13}$ = 5.39, p = 0.02). Boxplot parameters as in Fig. 3. (b) Isotopic niche space of the mussel *Brachidontes* sp. in marine lakes and coastal locations. Sampling locations are colored according to the estimated terrestrial influence. Blue dots indicate mussels collected at coastal locations in the open sea. Marine lake Papua01 and Papua24 (P01 and P24) are indicated in the figure. VPDB: Vienna PeeDee belemnite

Micheli & Halpern 2005). Overall, it has been found that increasing temperature directly impacts aquatic food webs (freshwater, estuarine, marine) with diminishing species richness and number of trophic interactions among species (Gibert 2019). Adding that elevated temperatures lead to higher metabolic growth costs (Barneche & Allen 2018), resulting in a greater portion of fixed carbon being released into the atmosphere, energy flow through the food chain could be reduced (Ullah et al. 2018, Nagelkerken et al. 2020).

As temperature and eutrophication continue to rise, the dominant benthic groups will likely shift towards more opportunistic species (Fabricius 2005, de Bakker et al. 2017, Ford et al. 2018). Although there was a similar spread in δ^{15}N of consumers (~9‰) between the 2 marine lakes, the number of different trophic interactions within the food web was lower in the environment with the combined high temperature and high terrestrial influence. Decreased trophic interactions may result from contraction to the center which is occupied by intermediate consumers because of a less diverse basal carbon source, resulting in low food web complexity (Figs. 2 & 6). Consequently, this alteration in energy flow within the food chain may drive shifts in food webs, potentially reducing functional redundancy and even causing the collapse of the food web (Ullah et al. 2018). Experiments in mesocosms demonstrated that temperature increase plays a crucial role in disrupting energy distribution within food webs, leading to an imbalance in the trophic structure (Nagelkerken et al. 2020). The warming impact encompassed increased populations of primary producers and reduced efficiency in primary consumer ingestion, resulting in a narrowing of the center of the food web, expansion of the top levels, and excessive resource consumption to meet metabolic demands. Within a food web, primary producers provide energy to intermediate consumers, which is subsequently transferred to top predators. Climate change, influencing the environmental conditions of marine ecosystems, can create conditions that favor certain species. For example, cyanobacteria, primary producers that can produce benthic mats, were more dominant in coverage compared to corals and macroalgae in marine lakes with higher temperatures (Aji et al. 2024). BCMs can incorporate nutrients efficiently, have a higher growth rate, and are more heat tolerant than macroalgae and corals (Thacker & Paul 2001, Tebbett et al. 2022).

Our isotope data show that δ^{13}C values of producers and consumers in Papua01 were more negative and less variable, indicating a narrower and more terrestrial-based carbon pool. This contrasts with Papua24, where the broader isotopic range reflects higher resource diversity and stronger marine influence. The reduced range of δ^{13}C values in high-influence lakes suggests a contraction in the diversity of basal carbon sources, which may underlie the observed simplification of the food web. With the reduced food web

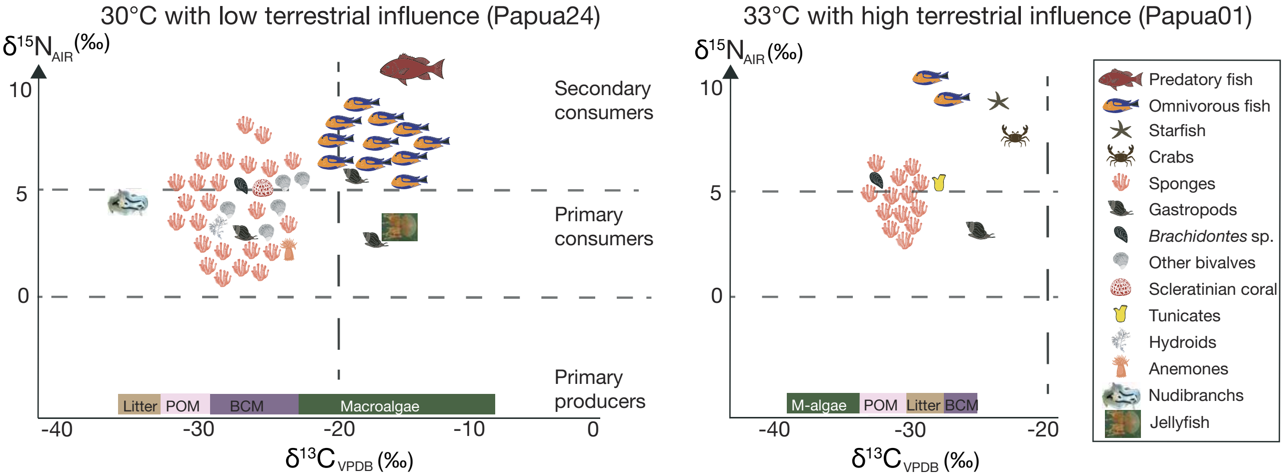

Fig. 6. Food web structure of the 2 scenarios of temperature (current temperature [30°C] versus increased temperature [33°C]) and terrestrial influence. Carbon sources included in the mixing model ('SIMMR') are shown at the bottom, with the width of the bar indicating the range in δ^{13}C along the *x*-axis and the vertical location indicative of relative δ^{15}N signatures amongst sources. Sponges as a dissolved carbon source are plotted in the graph. Each icon represents 1 species (see key) and schematically indicates the species' δ^{13}C and δ^{15}N values. Dashed horizontal lines delineate approximate trophic levels (based on a trophic enrichment factor of 3.4 for δ^{15}N). The dashed vertical line depicts where the δ^{13}C space ends in the marine lake with high temperature and high terrestrial input. BCMs: benthic cyanobacterial mats; POM: particulate organic matter; VPDB: Vienna Pee Dee belemnite

complexity in the marine lake with high temperature, lower seawater connectivity and turnover (Papua01), the dominant carbon source is supplied from terrestrial resources (POM: −28.1 ± 3.8‰; macroalgae: −32.4 ± 1.7‰; and litter: −29.6 ± 0.5‰). The use of food sources in marine lakes with higher water retention (due to lower connectivity) results in a more terrestrial-based carbon isotope value in the food web derived from the vegetation and soil surrounding the marine lakes. Leaves and litter of the more general C3 plants (such as mangroves) typically represent the tropical flora surrounding marine lakes, with δ^{13}C of approximately −28‰ (Bouillon et al. 2011), and are lower than marine producers. For example, the δ^{13}C of mangrove plants ranges from −29.4 to −27‰, which is much lower than the marine microalgae (−23 to −18‰), macroalgae (−23.1 to −16.4‰), and seagrasses (−10.7 to −5.5‰) (Rodelli et al. 1984, Lonerجagan et al. 1997, Bouillon et al. 2008). Terrestrial and mangrove plants have similar δ^{13}C values in both marine lakes. The δ^{13}C dependency of consumers on those sources is stronger in marine lakes with low marine connectivity (Papua01) (Fig. 4), suggesting that food webs within that system are supported by organic carbon originating from terrestrial carbon sources. The δ^{13}C values in consumers between the 2 marine lakes shift in the range of ~9‰ for bivalves, ~5‰ for sponges, ~5‰ for gastropods, and ~8‰ for fish. When the food web incorporates more carbon from terrestrial sources in a basin with reduced water turnover, the dissolved inorganic carbon (DIC) resulting from heterotrophic reworking of leaf litter and other organic matter is likely to accumulate and support macroalgal production. The use of terrestrial derived DIC by macroalgae in the more closed systems may help to explain the ~20‰ difference in green macroalgae sampled from similar clades between the 2 sites, likely due to remineralization of terrestrial organic matter. Moreover, the range of δ^{13}C values for primary producers is narrower in Papua01, indicating a more limited variety of food sources than in Papua24. The lower food source diversity supports a lower number of consumer species, possibly due to temperature stress resulting in reduced food web complexity (Gibert 2019). The lowered diversity is possibly also a result of co-correlating environmental parameters in the marine lakes, linked with temperature and terrestrial run-off as well as other possible environmental conditions. For example, some marine lakes with higher temperatures not only have higher terrestrial influence but also have lower salinity, due to higher relative rainwater influence and less water exchange with the sea. These factors could be separately studied by performing mesocosm experiments starting with clearly defined communities in combination with controlled environmental conditions (Ullah et al. 2018).

The carbon isotope values of the functional groups in both marine lakes were consistently lower than those found in the open ocean coastal locations, indicating isotopic niche differentiation. The δ^{13}C value of consumers in this study is lower than those reported for the open ocean. For example, the δ^{13}C value of crabs (−23 to −11‰) (Tue et al. 2012, Christianen et al. 2017), fish (−23 to −18‰) (Igulu et al. 2013, Qu et al. 2016, Le et al. 2017), echinoderms (−15 to −13‰) (Di Trapani et al. 2020), and gastropods (−22 to −12‰) (Wai et al. 2008, Piñón-Gimate et al. 2016) from the surrounding seas are higher than in the marine lakes (Table 2). These lower values confirm the recycling and use of terrestrial organic matter to support consumers, especially in the marine lake with high temperature and high terrestrial input.

A similar pattern was observed in lower δ^{13}C values for filter-feeding consumers, which rely on a limited number of sources that are disproportionately of terrestrial origin in marine lakes compared to those in the open ocean (Fig. 5b). For instance, the δ^{13}C value of primary consumer filter-feeders from the open ocean such as bivalves (−25 to −9‰) (Wai et al. 2008, Graniero et al. 2016, Christianen et al. 2017, Le et al. 2017), sponges (−21 to −16‰) (Freeman et al. 2014, Van Duyl et al. 2018), anemones (−21 to −15‰) (Zabala et al. 2013), and tunicates (−22 to −20‰) (Skinner et al. 2022) are approximately 20‰ higher compared to those found in marine lakes (Table 2). The lower values within the marine lakes are likely due to efficient recycling and use of terrestrial materials suspended in the water column of the marine lakes. The organic carbon of this terrestrial material accumulates in the littoral zone, where it will subsequently be degraded (Wang et al. 2006). Filter-feeders are abundant in littoral zones where they feed on the accumulated organic matter of terrestrial origin, and sponges in Papua01 appear to use carbon derived from terrestrial materials (δ^{13}C: −29.7 ± 0.7‰). This value may result from direct heterotrophy of newly fixed organic matter using recycled DIC or direct recycling of dissolved organic carbon by the sponge or resident symbionts (Rix et al. 2020, Hanz et al. 2022). In our study, there is less use of POM and use of sponge-derived material by the mussel *Brachidontes* in Papua01 compared to Papua24 (Fig. 3), which likely reflects what is available to be fed upon in the environment. Sponges likely play a role in subsidizing the local food web, either directly, through feeding by spongivores, or indirectly by recycling of sponge-derived materials that are being filtered out and used by the mussels. Sponges can take up dissolved and particulate resources as their food and convert them into particulate organic carbon in the ecosystem, namely the sponge loop (De Goeij et al. 2013), where particulate organic carbon produced by the sponge can subsequently be used by other organisms.

We used the filter-feeding mussel *Brachidontes* sp. as a proxy to compare the available sources supporting ~20 different sites (16 marine lakes and 4 coastal areas). Across the 16 marine lakes and 4 coastal sites, *Brachidontes* mussels reflected environmental gradients. $\delta^{13}C$ values were lowest in lakes with high terrestrial influence, intermediate in lakes with moderate connectivity, and highest in open coastal locations. This pattern supports the use of mussel $\delta^{13}C$ values to infer shifts in food web support from marine to terrestrial sources. These bivalves filter-feed on phytoplankton and suspended organic matter from the water column, thus revealing information about the organic carbon sources in their environment (Arapov et al. 2010). Bivalves are a prominent trophic link between primary producers and higher trophic consumers in aquatic ecosystems. They consume organic material in the ecosystem and are then eaten by secondary consumers such as crabs, fish, and predatory gastropods (Penchaszadeh et al. 2006, Quinn 2020). *Brachidontes* sp. in higher temperature and terrestrial influence conditions have lower $\delta^{13}C$ values (Fig. 5b). This suggests that carbon of terrestrial origin or soil runoff occupies a larger part of the carbon sources assimilated by *Brachidontes* sp. in the marine lakes compared to the adjacent sea, especially in the marine lakes with reduced connection to the sea. Previously, mussels from the genus *Mytilus* have been shown to be good proxies for pelagic producers in a coastal ecosystem, with the $\delta^{13}C$ of the mussels similar to suspended particulate matter (Vokhshoori et al. 2014, Christianen et al. 2017). A study on a related mussel, *B. pharaonis*, in the Mediterranean Sea showed that this species could exploit almost all of the predominant carbon sources available in the environment (Sarà et al. 2003).

The $\delta^{15}N$ values of *Brachidontes* mussels may reflect differences in nitrogen cycling among lakes, including denitrification and nitrogen fixation, especially in stratified or anoxic systems (Fry & Allen 2003, Bouillon et al. 2011). The stable isotope $\delta^{15}N$ value of *Brachidontes* from marine lake Papua01 is higher than that from Papua24, so this may reflect the impact of greater material recycling in the lower trophic levels. The more or less semi-closed characteristics of marine lakes can be expected to influence the impact of such processes as well as the recycling of materials that are likely to occur in this ecosystem. For example, depletion of ammonium during phytoplankton blooms is expected to be rapid in small and non-mixing environments (Vorobyeva et al. 2021). Alternatively, nutrient cycling characteristics may vary considerably between marine lakes, with some having anoxic water layers and high densities of purple sulfur bacteria. These bacteria can fix $CO_{2,}$ and many are also nitrogen fixers (Petersen & Yuen 2021), leading to more isotopically depleted values (Karlson et al. 2015). Hence, the negative $\delta^{15}N$ values of *Brachidontes* sp. mussels could be caused by the presence of nitrogen-fixing (diazotrophic) cyanobacteria. Nitrogen-fixing bacteria mainly fix nitrogen from their surrounding habitats, which have lighter nitrogen (Rolff & Elmgren 2000, Karlson et al. 2015). In addition, low salinity is one of the characteristics of isolated lakes, which is known to increase the activity of nitrogen-fixing bacteria in marine ecosystems (Rysgaard et al. 1999, Staal et al. 2003, Jabir et al. 2020). These nitrogen-fixing bacteria can live in symbiosis with bivalves, and the nitrogen they fixate is efficiently assimilated and transferred into marine food webs (Karlson et al. 2015, Petersen & Yuen 2021).

In conclusion, our results show that elevated temperature and terrestrial influence are associated with reduced resource diversity and simpler trophic networks. The shift in food web structure and resource use under elevated temperature and terrestrial input conditions suggests a decline in functional redundancy and energy transfer efficiency. While co-varying factors such as salinity and stratification may also play a role, our findings support the hypothesis that temperature and land–sea coupling jointly influence trophic complexity in coastal ecosystems. The widespread presence and feeding ecology of *Brachidontes* sp. make it a useful integrative proxy for monitoring baseline carbon sources across environmental gradients in tropical marine systems. The patterns observed in marine lakes are relevant for understanding potential trajectories in coral reef ecosystems facing similar environmental pressures. Like marine lakes, coral reefs in semi-enclosed bays or lagoons can experience elevated temperatures and terrestrial runoff. The shift in food web structure observed in isolated lakes — characterized by reduced trophic complexity, lower consumer diversity, and increased reliance on terrestrial organic matter — mirrors documented changes in degraded reef systems, where eutrophication and warming have led to declines in coral cover, reduced herbivore abundance, and altered energy flow (Hughes et al. 2017, Altieri & Diaz 2019). These findings suggest that reefs exposed to combined thermal stress and nutrient enrichment may similarly shift toward simplified, detritus-fueled systems with reduced resilience.

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