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Stable isotopes reveal *sargassum* rafts provide a trophic subsidy to juvenile pelagic fishes

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ABSTRACT

Floating macroalgal rafts can form extensive habitat in coastal waters and support abundant and diverse communities of juvenile fishes. Rafts comprised predominantly of *Sargassum* spp. are common within the Ningaloo Coast World Heritage Area, Western Australia, and may be an important transitional habitat for pre-settlement coastal fishes. We had three aims: 1) to quantify the diversity and abundance of fishes associated with *Sargassum* rafts; 2) to use stable isotopes to determine whether fishes associating with rafts preyed on nearby plankton or on prey associated with *Sargassum*; and 3) to determine whether the food web fishes relied upon was ultimately supported by primary production of *Sargassum* or planktonic phytoplankton (measured as seston). Fishes and macroinvertebrates associating with *Sargassum* rafts, zooplankton, and seston were collected at six sites in the Ningaloo Marine Park and analysed for δ^{15}N and δ^{13}C, and the diets of the most common fishes were analysed using MixSIAR. Fishes were more abundant around macroalgal rafts than in open water. Eleven species of juvenile fishes associated with *Sargassum* rafts, with one species (*Histrio histrio* (Antennariidae)) represented by juveniles and adults. Four of the five fishes most sampled around *Sargassum* spp. rafts, (*Abudefduf vaigiensis* (Pomacentridae), *Helotes sexlineatus* (Terapontidae), *Colurodontis paxmani* (Monacanthidae) and *Petroscirtes breviceps* (Blenniidae)) had generalist diets whose food webs were ultimately supported by greater contributions of primary production from *Sargassum* spp. (55–72%) than planktonic seston. *H. histrio* was predominantly piscivorous but still derived most (64%) of its organic matter indirectly from *Sargassum* spp. Our results reveal the importance of *Sargassum* rafts as habitat that provides shelter and food for juvenile fishes and adult *H. histrio*. Moreover, the prevalence of juvenile fishes associating with *Sargassum* rafts highlights a bidirectional form of benthic-pelagic coupling whereby macroalgae that detach from the benthos provide habitat and a trophic subsidy for pelagic juvenile fishes before they the transition into benthic coastal habitats.

1. Introduction

Drifting rafts of macroalgae, such as *Sargassum* spp., support diverse flora and fauna in the open ocean where structure and food can be sparse (Kingsford, 1993; Kim et al., 2019; Turner and Rooker, 2006). Macroalgal rafts form when benthic macroalgae that have pneumatocysts (air bladders) detach from the benthos and float to the surface (Hees et al., 2019). Some *Sargassum* species (*Sargassum natans* & *Sargassum fluitans*) are also holopelagic and reproduce vegetatively by fragmentation, thereby completing their entire life cycle in the pelagic realm (Dooley, 1972). Macroalgal rafts can comprise a single lamina but large rafts exceeding 1000 m^2 (Marmorino et al., 2011; Ody et al., 2019) can form when currents or wind cause individual algae to converge (Liu et al., 2013). Macroalgal rafts can thus provide extensive habitat in some regions and are important for supporting biodiversity in marine ecosystems (Thiel and Gutow, 2004).

Fishes reside in macroalgal rafts as adults (Nishida et al., 2008), use rafts as transitional habitats prior to settlement (Antoni and Saillant, 2017) or visit rafts opportunistically for food (Wells and Rooker, 2009). Most fishes found closely associated with macroalgal rafts are juveniles (Druce and Kingsford, 1995; Kingsford, 1995; Wells and Rooker, 2004). These include pre-settlement reef fishes seeking shelter in the vast pelagic environment and juvenile pelagic species, which use the physical structure provided by rafts as shelter from predators (Dooley, 1972; Nishida et al., 2008), to maintain schools at night, and possibly as assembly points for school formation (Hasegawa et al., 2017). Some fishes

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associating with *Sargassum* rafts are harvested, such as tuna, wahoo, dolphinfish and billfish (NMFS, 2022), which highlights the potential importance of this habitat for sustaining commercial fisheries.

The high biodiversity of macroalgal rafts creates a complex food web that supports many pre-settlement reef fishes and pelagic fishes in the open ocean (NMFS, 2022; Rooker et al., 2006; Turner and Rooker, 2006). Phytoplankton and particulate organic matter (POM) such as detritus and pico-plankton, are the dominant sources of organic matter in the pelagic environment (Davenport and Bax, 2002; Sommer et al., 2002) but macroalgal rafts may also be an important source of organic matter in certain regions. For example, in the Gulf of Mexico, stable isotope and fatty acid analyses revealed that primary consumers within *Sargassum* rafts, including small shrimp and crabs, acquired up to 53% (*Leander tenuicornis* (Palaemonidae)) of their organic matter from *Sargassum* spp. and *Sargassum* spp. contributed up to 45% of organic matter to juvenile apex pelagic fishes including dolphinfish, sailfish and blue marlin (Wells and Rooker, 2009).

Ningaloo Reef in Western Australia is the world's longest fringing coral reef and is part of the Ningaloo Coast World Heritage Area. The region lies on an ecotone where tropical and temperate waters converge, facilitating high pelagic biodiversity. Each year large quantities of benthic *Sargassum* spp. detach from the substratum in Autumn-Winter and form rafts (Fulton et al., 2014) that may stay afloat for weeks to months (Yatsuya, 2007) or be deposited in intertidal and subtidal zones (Fulton et al., 2014). *Sargassum* rafts at Ningaloo Reef may thus represent an important trophic subsidy to the pelagic environment. Indeed, *Sargassum* spp. have recently been identified as a food source for whale sharks, which probably ingest *Sargassum* spp. when ram filter feeding in waters adjacent to Ningaloo Reef (Meekan et al., 2022). Despite the prevalence of *Sargassum* rafts in this World Heritage Area, the fish fauna that associate with rafts and the potential trophic importance of rafts for bony fishes have never been studied.

The objective of this study was to determine the trophic importance of *Sargassum* rafts to fishes that associate with rafts within the Ningaloo Marine Park. Our specific aims were 1) to quantify the diversity and abundances of fishes associated with *Sargassum* rafts compared to open water, 2) use stable isotope analyses to determine if *Sargassum* spp. are an ultimate source of organic matter or direct prey source for fishes associated with *Sargassum* rafts, and 3) to compare the isotopic niches and trophic levels of common fishes associated with *Sargassum* rafts.

2. Materials and methods

2.1. Sample collection

Primary producers including *Sargassum* spp., epiphytes of *Sargassum*, and seston (phytoplankton and POM) and consumers (zooplankton, macroinvertebrates and fishes) were sampled from 24th to 27th April, 2022, at six different sites off the northern tip of Ningaloo Reef (21° 45′ 16″S, 114° 7′ 41″ E), Western Australia. Three *Sargassum* rafts were collected at each site using a purse seine net (10 m × 2 m; mesh size = 2 mm). The selected rafts were 5 m from all other rafts, less than 1 m in surface diameter and located drifting at the surface in water depths of 10–40 m. The seine net was deployed by two snorkellers, with the boat maintained >10 m downwind from the raft to minimise disturbance. The seine net was also deployed three times in open water where no *Sargassum* rafts occurred to control for potentially collecting organisms not associated with *Sargassum* rafts.

Fishes and invertebrates were removed from the algae, identified to the lowest taxonomic level possible and counted. The total and standard length of fishes were measured. Two specimens of each taxon from each raft were kept and euthanised in an ice slurry; this provided representative sampling from the six sites. Each raft was weighed to the nearest gram and a sample (15 cm^2 section) of thallus was taken. Seston was collected using a small plankton net (diameter = 30 cm; mesh size = 53 μm). Two larger plankton nets (diameter = 51 cm; mesh size = 100 μm and diameter = 51 cm; mesh size = 200 μm) were used to collect zooplankton. Plankton nets were towed just below the surface for approximately 5 min. Duplicate tows were done at each of the six sites. All samples were stored on ice while transported to the laboratory for processing.

2.2. Preparation of samples for stable isotope analyses

Samples for stable isotope analyses were processed fresh. Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) were measured for subsamples of the most abundant fishes and invertebrates, *Sargassum* spp., two size classes of mesozooplankton, and seston (Table 1). Fishes were dissected to obtain samples of their muscle between the dorsal and caudal fins but if they were too small to gain an adequate tissue sample they were decapitated and gutted, and the remainder of the sample was processed. Crustaceans were too small to gain adequate tissue samples so were processed whole. Epiphytes were removed from the *Sargassum* spp. samples and the epiphytes and *Sargassum* spp. were rinsed with distilled water. Seston was filtered through 100 μm mesh to remove any large material and was collected by passing the filtrate through precombusted Whatman GF/F filters using a vacuum pump. Zooplankton samples from the 100 μm and 200 μm nets were combined and separated into 100–300 μm and 300+ μm fractions using sieves. The 100–300 μm fraction was collected on pre-combusted GF/F filter papers whilst the 300+ μm fraction formed enough material to obtain a homogenous paste. All samples were stored at −80 °C in cryogenic vials before being dried in an oven at 56 °C for 48 h or until they reached constant weight. Dried samples, excluding those on filter papers, were ground into a fine powder using a mortar and pestle.

Samples for δ^{15}N were placed into Sercon tin capsules. Fauna (1–2 mg), flora (5–7 mg) and one half of each sample collected on filter papers were analysed. Some samples for δ^{13}C analysis underwent additional treatment, including decalcification to remove inorganic carbon and/or removal of lipids. Samples of seston, zooplankton and crustaceans were decalcified by adding drops of 0.1 M hydrochloric acid until any bubbling stopped (Carabel et al., 2006). Samples collected on filter papers (i.e., seston and 100–300 μm plankton fraction) were submerged in 0.1 M hydrochloric acid until any bubbling ceased and rinsed in distilled water. All decalcified samples were redried at 60 °C. Lipids were extracted from fish, acid-treated invertebrates, and acid-treated 300+ μm zooplankton samples. Samples were transferred into 2 ml microcentrifuge tubes and lipids extracted using methods modified from Bligh and Dyer (1959) and Elliott et al. (2017). Samples were homogenised in 600 ml methanol using an ultrasonic processor (130 W at 20 kHz, 1 s pulse, 40%) for 10 intervals. Chloroform was added (1200 ml) and samples were vortexed for 10 s. Homogenous solutions were centrifuged for 15 min at 15,000 rpm and the supernatants containing solvents and lipids were discarded using a pipet. Lipids were extracted 2–4 times or until the supernatant was clear. Lipids were extracted from acid-treated 100–300 μm zooplankton samples by submersing filter papers in 2:1 chloroform/methanol solution for 24 h and the lipid-containing solvent was discarded. Lipid-free samples were freeze dried overnight at −80 °C and weighed into 5 mm, Sercon tin capsules. All samples were analysed at the Stable Isotope Laboratory (SIL) at Griffith University using a Sercon Hydra 20–22 with a Europa EA-GSL sample preparation system.

2.3. Statistical analyses

All statistical analyses were performed using the software R (version 4.2.0). Isotopic analyses were performed using untreated δ^{15}N values for all taxa, lipid-extracted δ^{13}C values for fishes, decalcified δ^{13}C values for seston, and decalcified and lipid-extracted δ^{13}C values for macroinvertebrates and zooplankton (Table 1). Paired t-tests were used to test for significant differences between δ^{13}C values of untreated samples and samples that had lipids extracted, were decalcified, or that had been

Table 1

Species associated with *Sargassum* rafts at Ningaloo Reef (N = number of individuals caught; n = number of untreated stable isotope samples, **n** = number of samples used for stable isotope analyses (based on number available after treatment (i.e., decalcification and/or lipid extraction) where appropriate; see methods 2.3). J = juvenile, A = adult, I = Initial phase, U = unknown, NA = not applicable, (*) = significant difference between treated and untreated δ^{13}C values. Isotope values are given as mean ± SD and shading indicates test type (dark grey = Wilcoxon signed rank test, light grey = Paired *t*-test). Total length measurements were based on N.

	Scientific name	Common name / description	N	n	**n**	Life Stage	δ^{13}C (‰) (untreated)	δ^{13}C (‰) treated	δ^{15}N (‰) (untreated)	Total length (mm)
Fishes	*Abudefduf vaiginesis*	Indo-Pacific sergeant	177	14	14	J	-18.4±0.4	-18.1± 0.3	7.4± 0.5	13–29
	Scaridae sp.	Parrot fish	1			I				120
	Blenniidae sp.	Blenny	10			J				6–7
	Histrio histrio	Sargassum fish	34	10	9	J/A	-18.5± 1.5	-18.1±0.6	8.2±0.7	11.5–64
	Clurodontis paxmani	Paxman’s leatherjacket	10	5	4	J	-18.5±0.8	-18.1±0.9	7.2±1.1	9.0–23
	Helotes sexlineatus	Eastern striped grunter	27	5	5	J	-18.8±0.5	-18.3±0.3	7.2±0.3	23–50
	Petroscirtes breviceps	Shorthead sabretooth blenny	9	3	3	J	-18.8±0.5	-18.4±0.4	6.5±0.5	40–43
	Serranidae sp.	Grouper	1			J				11
	Syphraena barracuda	Great barracuda	1	1	1	J	-18.0±NA	-18.3±NA	7.7±NA	27
	Trachinotus anak	Oyster pompano	1			J				6
	Verulux cypselurus	Swallowtail cardinalfish	1			A				47
Invertebrates	Nudibranchia sp.	Nudibranch	3			A				
	Octopoda	Octopus	1			J				
	Decapodiformes	Squid	2			J				
	Cymothoida sp.	Isopod	1			U				
	Bryozoa sp.	Bryozoan	NA	1	1	U	-19.7±NA	-19.9±NA	5.1±NA	
	Larval Portunidae sp.	Megalopa	5	2	0	J	-18.4±1.3		6.0±1.4	
	Portunus sp.	Swimmer crab	26	7	6	J	-16.4±0.5	-19.0±0.6*	5.8±0.8	
	Portunidae sp.	Swimmer crab	1	1	1	J	-17.5±NA	-20.8±NA	7.1+NA	
	Penaeidae sp.	Penaeid shrimp	9	5	5	A	-14.1±0.9	-15.9±0.8*	5.3±0.8	
	Dendrobranchiata sp.	Prawn	8			U				
	Zooplankton (300+ μm)	Zooplankton	12	12	12		-18.9±0.8	-20.8±1.1*	5.8±0.5	
	Zooplankton (100–300 μm)	Zooplankton	12	12	5		-18.5±0.8	-20.1±0.4*	4.7±1.2	
Flora	Seston	Phytoplankton & POM	12	12	12		-17.9±2.7	-20.7±0.7*	1.9±3.2	
	Epiphyte 1	Filamentous brown macroalgae	8	8	8		-12.6±1.4		3.5±0.8	
	Epiphyte 2	Filamentous red macroalgae	3	3	3		-11.7±1.1		3.5±0.6	
	Sargassum spp.	Macroalgae	12	12	12		-17.2±1.5		3.4±0.8	

decalcified and had lipids extracted. The assumption of normality was tested using a Shapiro-Wilk normality test and was met for all variables, except seston, which was analysed using a non-parametric Wilcoxon signed rank test.

MixSIAR models and trophic level estimates were calculated using trophic enrichment factors (TEFs) from the aquatic environment: 0.4 ± 0.17‰ for carbon and 2.3 ± 0.28‰ for nitrogen (McCutchan et al., 2003). Trophic level (TL) was estimated for consumer species (macroinvertebrates, zooplankton and fishes) using a dual baseline approach due to the unknown significance of *Sargassum* spp. to the food web. Seston and *Sargassum* spp. were used as baseline primary producers in Equation (1):

$$\mathrm{TL} = \lambda + (\delta^{15}\mathrm{Nconsumer} - [\delta^{15}\mathrm{Nbase}_1 \times \alpha + \delta^{15}\mathrm{Nbase}_2 \times (1 - \alpha)]) \,/\, \mathrm{NTEF} \qquad 1$$

EQUATION 1. MODIFIED FROM (POST, 2002).

λ Denotes the trophic level of the baseline organisms (i.e., 1), δ^{15}Nconsumer is the δ^{15}N value of the consumer organism, and δ^{15}Nbase is the average δ^{15}N value of baseline organism 1 (seston) and baseline organism 2 (*Sargassum* spp.). NTEF is the trophic enrichment factor of nitrogen. α (the proportion of nitrogen in the consumer derived from baseline one) was calculated using Equation (2).

$$\alpha = (\delta^{13}\mathrm{Cconsumer} - \delta^{13}\mathrm{Cbase2}) / (\delta^{13}\mathrm{Cbase1} - \delta^{13}\mathrm{Cbase2}) \qquad 2$$

EQUATION 2. MODIFIED FROM (POST, 2002).

δ^{13}Cconsumer is the δ^{13}C value of the consumer organism, and δ^{13}Cbase is the average δ^{13}C value of seston and *Sargassum* spp. respectively.

After calculating an approximate TL using equations (1) and (2), an iterative process using Equation (1) to find TL and Equation (3) to find α was used to estimate trophic level for each consumer species.

$$\alpha = [\delta^{13}\mathrm{Cbase2} - (\delta^{13}\mathrm{Cconsumer} + \mathrm{CTEF\ x\ TL})] \,/\, (\delta^{13}\mathrm{Cbase2} - \delta^{13}\mathrm{Cbase1}) \qquad 3$$

EQUATION 3. MODIFIED FROM (POST, 2002).

CTEF is the trophic enrichment factor of carbon.

Three models were run to quantify the contribution of different dietary sources to each consumer species using the MixSIAR modelling package (Stock et al., 2018). Species were pooled across sites, due to insufficient samples at each site and uninformative priors were used, as the contribution of dietary sources to consumers was unknown (Stock et al., 2018). The first model estimated the ultimate amount of primary production contributed by *Sargassum* spp. and seston to consumers (macroinvertebrates, zooplankton and fishes). Epiphytes were not included because their biomass was considered too small to represent a major dietary source. Primary producers were corrected for trophic enrichment between trophic levels as a proportion of the average trophic level estimated for each fish species (Vander Zanden and Rasmussen, 2001). A sensitivity analysis was done to determine the potential change in *Sargassum* spp. versus seston-derived organic matter and coinciding trophic level change due to variation in TEFs for the five most abundant fishes (Indo-Pacific sergeant (Pomacentridae), *Abudefduf vaigiensis*; sargassum fish (Antennariidae), *Histrio histrio*; eastern striped grunter (Terapontidae), *Helotes sexlineatus*; Paxman’s leatherjacket (Monacanthidae), *Colurodontis paxmani* (Hutchins, 1977; and the shorthead sabretooth blenny (Blenniidae), *Petroscirtes breviceps* (Valenciennes, 1836)). TEFs were varied by ±0.25, ±0.5 and + 0.75 for carbon and ±0.5, +1 and + 1.5 for nitrogen, which encompassed the range of TEFs recommended for aquatic environments (Vander Zanden and Rasmussen, 2001) and those applied for *Sargassum*-associated fish in the Gulf of Mexico (Rooker et al., 2006; Wells and Rooker, 2009).

The second model estimated the possible dietary sources directly consumed by *A. vaigiensis, H. sexlineatus, C. paxmani,* and *P. breviceps*. Prey sources included the two most common primary producers (seston and *Sargassum* spp.), the two most observed macroinvertebrates associated with *Sargassum* rafts (*Portunus* sp. and Penaeidae sp.), and two size fractions of zooplankton (100–300 μm and 300+ μm). Since gut content analyses indicate *H. histrio* consumes larval fishes and shrimp (Ida et al., 1967b), a third model was run for that species, which included seston, *Sargassum* spp., both size fractions of zooplankton, Penaeidae sp. and fish (using the average δ^{13}C and δ^{15}N values for all fishes analysed in this study except *H. histrio*). MixSIAR models were run using the following parameters: chains = 3; chain length = 3,000,000; burn = 1,500,000; and thin = 500. Satisfaction of GelmanRubin and Geweke diagnostics was used to identify model convergence (Stock et al., 2018).

The isotopic niche overlap and standard ellipse areas corrected for small sample size (SEAc), were calculated for the three most abundant fish species (*A. vaigiensis*, *H. histrio* and *H. sexlineatus*) using the SIBER package (Jackson et al., 2011). Fish species were selected based on a minimum sample size of five to maintain adequate degrees of freedom for matrix and mean calculations. The Bayesian approach using multivariate ellipse-based metrics was used to develop SEAc, representing the core 40% of isotopic space occupied by each fish species.

3. Results

A total of 328 animals of 20 species, including 11 species of fishes, were recorded from the 18 *Sargassum* rafts sampled (Table 1). The average weight of the rafts sampled was 435 g (±839 SD) and an average of 15.1 (±19.8 SD) fish associated with each raft, all of which were juveniles except for *H. histrio,* that also included adults, and a single small initial phase parrot fish (Scaridae). *A. vaigiensis* were the most abundant fish species and occurred at 78% of *Sargassum* rafts followed by *H. histrio* (at 61% of rafts) and *H. sexlineatus*, *C. paxmani* and *P. breviceps*, each of which occurred at 28% of rafts. No fish were caught in the control seines done in open water away from rafts.

δ^{13}C values of fishes that had lipids extracted were not significantly different to untreated δ^{13}C values (Table 1). Seston samples were significantly depleted by an average of −2.8‰ after decalcification and all lipid-extracted and decalcified macroinvertebrates and zooplankton samples were significantly depleted in ^{13}C after treatment. *Portunus* sp. were most depleted after they were both decalcified and had lipids extracted (−2.6‰), followed by 300+ μm zooplankton, Penaeidae sp., and 100–300 μm zooplankton which were depleted by −1.9, −1.7 and −1.6‰ respectively.

The isotopic values of the two primary producers were distinct (Fig. 1). Compared to seston, the *Sargassum* spp. were on average 3.5‰ enriched in ^{13}C and 1.5‰ enriched in ^{15}N. The nitrogen isotope values of seston varied greatly and ranged from −2.8‰ to 6.1‰. Macroinvertebrates and zooplankton mostly occupied intermediate trophic levels (range: 1.5–2.5) with larger zooplankton (i.e. 300+ μm) occupying a higher trophic level than the 100–300 μm size fraction (Table 2; Fig. 1). Fishes were secondary or tertiary level consumers (trophic levels 2.4–3.0), with *H. histrio* occupying the highest trophic level of the fishes (Table 2). Fishes collectively occupied a small isotopic space compared to other taxa, such as crustaceans (Fig. 1).

Primary production by *Sargassum* spp. provided 55–72% of the organic matter ultimately consumed by fishes and 93% of organic matter ultimately consumed by the penaeid shrimp (Table 2). Except for the

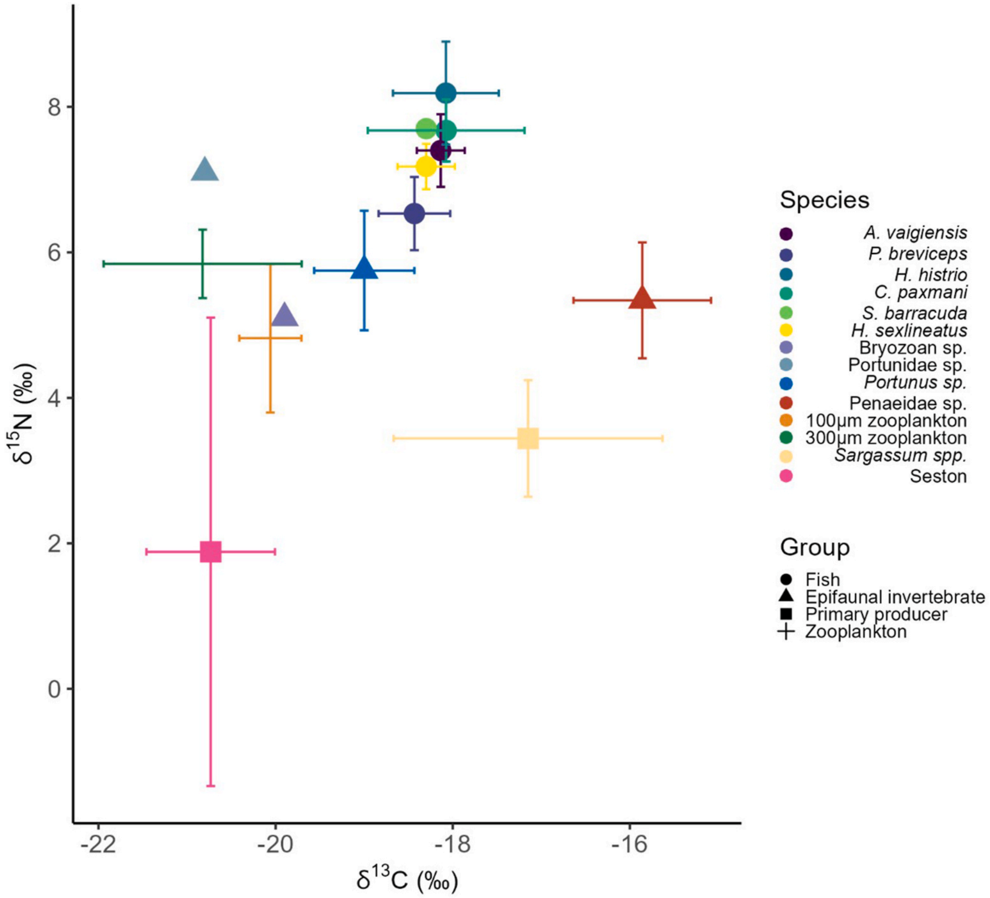

Fig. 1. Isotopic biplot illustrating mean values (±SD) for δ^{13}C and δ^{15}N of primary producers, zooplankton, and invertebrates and fishes associated with *Sargassum* rafts.

Table 2
Trophic level estimates and MixSIAR model results that compared the percentage contributions of primary production derived from *Sargassum* spp. And seston to the diet of *Sargassum*-associated fauna. Dietary contributions are shown as medians (95% confidence interval), n = sample size and TL = trophic level. When n > 2, samples were collected from more than one site.

Species	n	TL	*Sargassum* spp. (%)	Seston (%)
Abudefduf vaiginesis	14	2.7	57.9 (42.6–84.1)	42.1 (15.9–57.4)
Histrio histrio	9	3.0	63.5 (38.7–93.3)	36.5 (6.7–61.3)
Colurodontis paxmani	4	2.6	71.8 (25.6–98.2)	28.2 (1.8–74.4)
Helotes sexlineatus	5	2.7	55.8 (32.6–87.9)	44.2 (12.1–67.4)
Petroscirtes breviceps	3	2.4	60.5 (20.6–96.3)	39.5 (3.7–79.4)
Syphraena barracuda	1	2.9	54.6 (6.3–96.4)	45.4 (3.6–93.7)
Bryozoa sp.	1	2.1	35.6 (2.3–93)	64.4 (7–97.7)
Portunus sp.	6	2.2	38.8 (16.2–73.5)	61.2 (26.5–83.8)
Portunidae sp.	1	2.1	20.9 (0.9–91.9)	79.1 (8.1–99.1)
Penaeidae sp.	5	1.5	92.6 (61.9–99.7)	7.4 (0.3–38.1)
Zooplankton (300+ μm)	12	2.5	7.1 (0.3–61)	92.9 (39–99.7)
Zooplankton (100–300 μm)	5	2.0	12.6 (1–47.6)	87.4 (52.4–99)

penaeid shrimp, seston contributed more (61–93%) organic matter to macroinvertebrates than *Sargassum* spp. Minimal changes in the contribution of *Sargassum*-derived organic matter to the diets of fishes was observed when the trophic enrichment factor of nitrogen was varied (Table 3). Increased fractionation of nitrogen increased the contribution of *Sargassum*-derived organic matter to fishes, whilst decreased fractionation of nitrogen reduced *Sargassum* spp. contributions. Conversely, variation in carbon fractionation caused the opposite effect on source contributions to fishes. *Sargassum*-derived organic matter still contributed substantially (i.e., >30%) to the overall diets of all five fish species when the carbon TEF was increased by 0.5 (i.e., to a value of 0.9) but increasing the carbon TEF by 0.75 reduced the contribution of *Sargassum* spp. to <30% in *A. vaigiensis*, *H. histrio*, and *H. sexlineatus* (Table 3).

A. vaigiensis, *H. sexlineatus, C. paxmani*, and *P. breviceps* had varied diets that were not dominated by any one source (Fig. 2). All prey sources contributed approximately equal amounts to the diet of *P. breviceps* with medians ranging from 12.8% for seston and 19.4% for 100–300 μm zooplankton. *A. vaigiensis*, *H* sexlineatus, and *C. paxmani* assimilated slightly greater proportions of zooplankton and macroinvertebrates than primary producers and they assimilated more *Sargassum* spp. than seston. The diet of *H. histrio* was dominated by fishes (41.2%) with smaller contributions (~14% each) from 300+ μm zooplankton and macroinvertebrates, and minimal contributions of seston (<5%; Fig. 3). *H. histrio* occupied a larger isotopic niche (SEAc = 0.75‰) and higher trophic level than *A. vaigiensis* (SEAc = 0.46‰) and *H. sexlineatus* (SEAc = 0.37‰; Fig. 4). The SEA of *H. histrio* marginally overlapped with *A. vaiginesis* (~5%), but the SEA of *A. vaigiensis* and *H. sexlineatus* overlapped by approximately 50%.

4. Discussion

The *Sargassum* rafts of Ningaloo Reef supported a diverse community of fishes. The sizes and conspicuous pigmentation of the fishes sampled indicated that most were juveniles that had probably settled into the *Sargassum* habitat at the end of their larval phase. Except for *H. histrio*, most fishes sampled occupy benthic habitats as adults, indicating that the fishes were probably using the *Sargassum* rafts as a transitional habitat between the pelagic and benthic stages of their life histories. Our findings thus highlight a unique form of bidirectional benthic-pelagic coupling whereby benthic macroalgae that detach from the substratum provide habitat and a trophic subsidy in the pelagic realm and, in turn, facilitates the transition of pelagic juvenile fishes to their benthic adult habitats.

Some of the fishes sampled in the *Sargassum* rafts at Ningaloo Reef have been observed associating with *Sargassum* rafts elsewhere. *H. histrio* is widely distributed across the Atlantic, Indian and western Pacific Oceans (Kharin and Markevich, 2006). This species is considered an obligate associate of *Sargassum* rafts (Dooley, 1972) because they have rarely been observed in other habitats (Kharin and Markevich, 2006; Rogers et al., 2010), occur in *Sargassum* rafts as both juveniles and adults, and associate with *Sargassum* rafts throughout the year (Adams, 1960). Juvenile *A. vaigiensis* and *P. breviceps* were also abundant in the *Sargassum* rafts at Ningaloo Reef and have also been observed associating with *Sargassum* rafts in the coastal waters of Japan and Korea (Cho et al., 2001; Ida et al., 1967a; Nishida et al., 2008). Our study has, however, provided the first observations of juvenile *H. sexlineatus* and *C. paxmani* within *Sargassum* rafts. The terapontid, *H. sexlineatus* has only been reported in estuarine and inshore coastal waters, particularly associated with seagrass meadows e.g., (Clough, 2011; Heithaus, 2004) and *C. paxmani* is the only species of its genus and there are no records of its diet or habitat use. Hence our study demonstrates the use of a novel habitat for these species.

Our conclusion that *Sargassum* was the focal point for aggregations of fish was based on multiple taxa being abundant around macroalgal rafts and the absence of fish caught in open water. Demonstrating that fish did not occur in open water, however, is challenging. Although no fish were caught when the seine net was deployed in areas away from *Sargassum*, we cannot exclude the possibility that small fish were able to avoid the net, especially given the clarity of the pelagic waters we sampled. We are, however, confident that densities of fish were much greater when *Sargassum* was present.

An important finding of our study was that primary production originating from *Sargassum* spp. ultimately contributed more organic matter than plankton to the overall diets of fishes that associated with the *Sargassum* rafts at Ningaloo Reef. Most of this organic matter was probably acquired indirectly (e.g., by consuming prey that had, in turn, consumed the primary producers) because our models indicated that most fishes ingested slightly more macroinvertebrates and zooplankton

Table 3
Sensitivity analyses of MixSIAR models showing the organic matter derived from *Sargassum* spp. (medians relative to seston) to the diet of fishes and tropic level (shown in parentheses) when TEFs are varied. TEFs are shown as a deviation from the original TEFs [0.4‰ for carbon and 2.3‰ for nitrogen (McCutchan et al., 2003)] with the TEF used in italics. Original TEFs, tropic levels and estimates of the contribution *Sargassum*-derived organic matter to fish diets are displayed in bold.

	Change in TEF (‰)		*A. vaigiensis*	*H. histrio*	*C. paxmani*	*H. sexlineatus*	*P. breviceps*
Nitrogen	−0.5	*1.8*	(3.1) 52.2	(3.5) 56.2	(3.0) 68.3	(3.1) 50.8	(2.7) 58.3
	0	***2.3***	**(2.7) 57.9**	**(3.0) 63.5**	**(2.6) 71.8**	**(2.7) 55.8**	**(2.4) 60.5**
	+0.5	*2.8*	(2.4) 61.7	(2.7) 66.2	(2.3) 74.1	(2.4) 59.4	(2.2) 61.1
	+1	*3.3*	(2.2) 64.4	(2.4) 71.4	(2.2) 75.2	(2.2) 61.2	(2.0) 62.5
	+1.5	*3.8*	(2.1) 64.8	(2.3) 68.6	(2.0) 76.5	(2.0) 64.6	(1.9) 63.1
	−0.5	*0*	(2.9) 74.3	(3.3) 75.7	(2.9) 79.8	(2.9) 68.7	(2.6) 67.5
Carbon	−0.25	*0.15*	(2.8) 70.0	(3.2) 72.0	(2.7) 78.7	(2.8) 65.2	(2.5) 65.4
	0	***0.4***	**(2.7) 57.9**	**(3.0) 63.5**	**(2.6) 71.8**	**(2.7) 55.8**	**(2.4) 60.5**
	+0.25	*0.65*	(2.6) 45.4	(2.9) 46.9	(2.5) 63.5	(2.5) 45.6	(2.3) 54.5
	+0.5	*0.9*	(2.5) 35.5	(2.8) 33.2	(2.4) 54.3	(2.4) 35.8	(2.2) 48.3
	+0.75	*1.15*	(2.8) 27.6	(2.7) 23.2	(2.3) 47.9	(2.4) 25.5	(2.1) 42.9

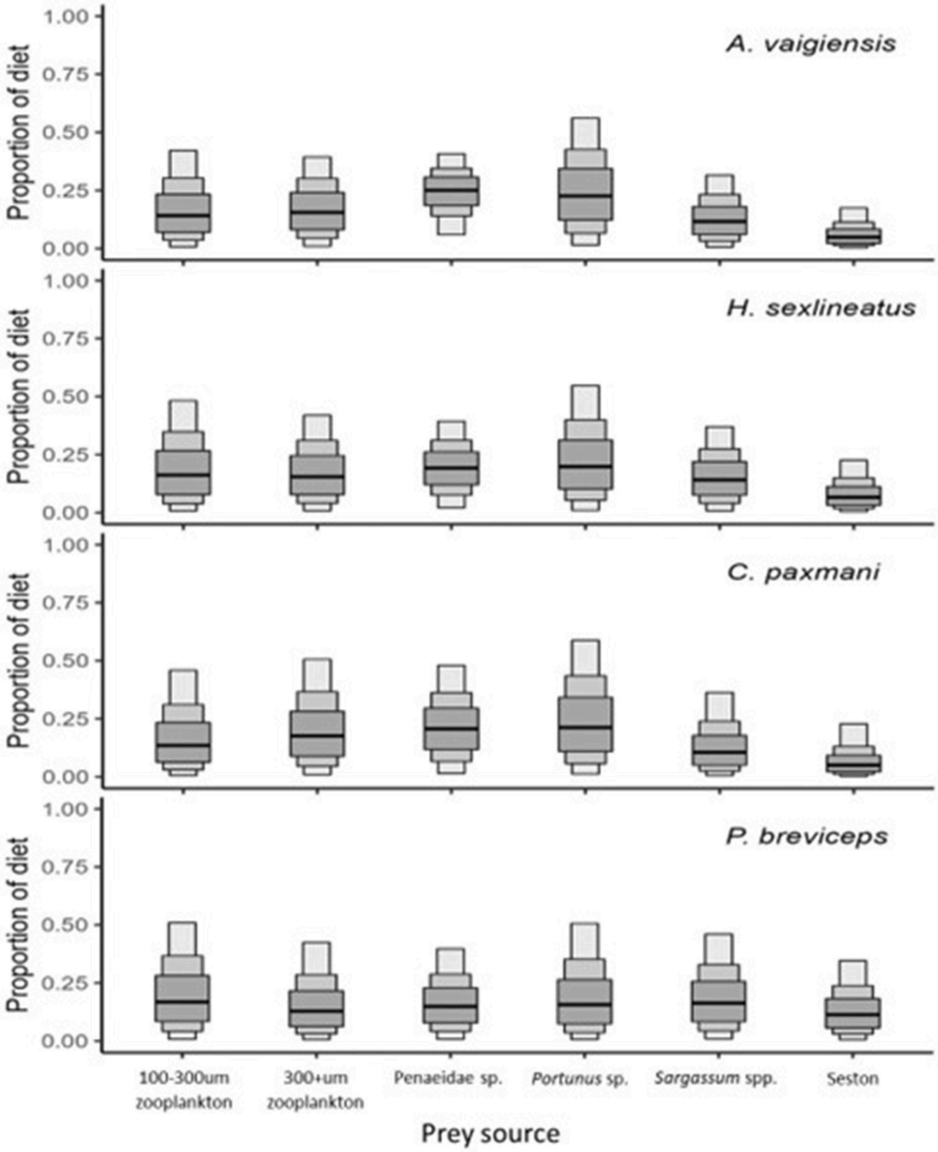

Fig. 2. MixSIAR model results comparing the contribution of potential prey sources to the diet of the most abundant fishes associated with Sargassum rafts. Grey boxed areas represent 50%, 75% and 95% confidence intervals, darkest to lightest respectively. Black centre lines indicate medians.

than primary producers. Hence, *Sargassum* spp. provide nutrition for herbivores when attached to the benthos (Doropoulos et al., 2013; Michael et al., 2013) and indirectly to juvenile fishes when floating. Drifting *Sargassum* spp. have been recently recognised as a significant dietary source to whale sharks at Ningaloo Reef (Meekan et al., 2022) but here we demonstrate that the organic matter it produces is also important for the abundant and diverse juvenile bony fishes that associate with *Sargassum* rafts in this region. Whilst benthic macroalgae that accumulates as wrack within surf zones and on nutrient-poor beaches is recognised as providing trophic subsidies to those ecosystems (e.g., Crawley et al., 2009; Hyndes et al., 2022) here we show that *Sargassum* spp. also provide a trophic subsidy to pelagic environments.

Our findings suggest that juvenile pelagic fishes at Ningaloo Reef ultimately acquire a greater proportion of their diet from *Sargassum* than those in the Gulf of Mexico, where *Sargassum* spp. and POM each contributed approximately 50% of organic matter to some juvenile pelagic fishes associated with *Sargassum* rafts (Wells and Rooker, 2009). However, Wells and Rooker (2009) focused on larval and juvenile apex predatory species such as blue marlin (*Makaira nigricans*) and sword fish (*Xiphias gladius*). When a greater diversity of fishes (22 species) associating with *Sargassum* rafts was sampled, the contribution of *Sargassum* spp. ranged from 0% to 60.5% and the fish species that obtained >35% of organic matter from *Sargassum* spp. were mostly higher order consumers, such as tuna (*Thunnus albacares & T. atlanticus*) and wahoo (*Acanthocybium solandri*), although *Balistes capriscus* (Balistidae) was a notable exception (Rooker et al., 2006). Indeed, in direct contrast to our findings, in the Gulf of Mexico, organic matter from *Sargassum* spp. did not contribute substantially to the diets of *H. histrio,* juvenile *A. saxatilis* or some juvenile Monacanthidae species (e.g., *Aluterus heudeloti & Monacanthus hispidus*) (Rooker et al., 2006). Hence, at Ningaloo Reef, *Sargassum* spp. appears to contribute to the diets of a greater diversity of pelagic fishes than in the Gulf of Mexico where *Sargassum* spp. primarily supports juvenile apex pelagic fishes.

Very limited information is available about the types of prey ingested by the juvenile fish species we sampled. *A. vaigiensis* sampled around macroalgal rafts in Japan mostly ingested copepods and diplostracans, whilst the gut contents of *H. histrio* contained mostly fish larvae and pelagic crustaceans, including amphipods and larval crabs (Ida et al., 1967b). The mixing models used in the current study were consistent with *H. histro* consuming large amounts of fish, and *A. vaigiensis*,

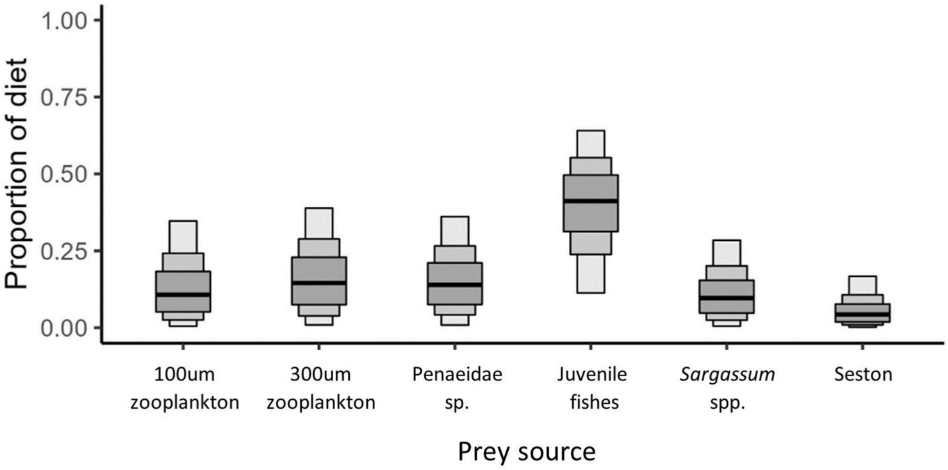

Fig. 3. MixSIAR model results comparing the contribution of potential prey sources including juvenile fishes (*Abudefduf vaigiensis*, *Helotes sexlineatus*, *Colurodontis paxmani*, *Petroscirtes breviceps* & *Syphraena barracuda*) to the diet of *Histrio histrio*. Grey boxed areas represent 50%, 75% and 95% confidence intervals, darkest to lightest respectively. Black centre lines indicate medians.

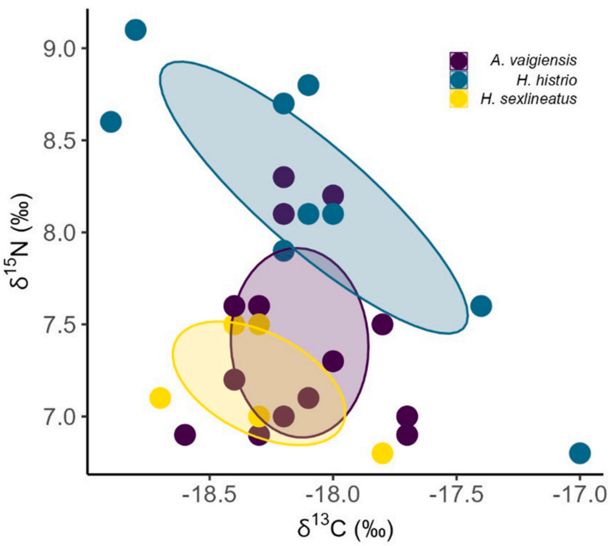

Fig. 4. Stable isotope biplot illustrating the isotopic niche occupied by the three most abundant fish species associated with *Sargassum* rafts. Symbols represent values for individual fish and ellipses represent 40% of the isotopic niche area occupied by a species (Jackson et al., 2011).

H. sexlineatus, *C. paxmani,* and *P. breviceps* having generalist diets consisting of mixtures of zooplankton and macroinvertebrates and small amounts of primary producers. The generalist diets of most of the species we sampled may reflect the ephemeral nature of the *Sargassum* raft habitat (Yatsuya, 2007) and that rafts may be advected considerable distances by wind and waves (Hees et al., 2019). Environmental variability can constrain foraging opportunities (Pimm and Kitching, 1987), thus the generalist foraging nature of most fishes associated with *Sargassum* rafts at Ningaloo Reef probably reflects the requirement to utilise a variety of foraging opportunities for survival (Rooker et al., 2006).

Whilst most fishes sampled had generalist diets, the contribution of direct sources varied between species and was reflected in their trophic level and niche estimates. *H. histrio* occupied the largest isotopic niche, indicating it had the broadest diet. The minimal overlap between the SEA of *H. histrio* and *A. vaigiensis* or *H. sexlineatus* and its higher trophic level, is consistent with *H. histrio* being predominantly piscivorous and having a diet distinct from the other fishes sampled. The 50% overlap in the SEA of *A. vaigiensis* and *H. sexlineatus* and their lower trophic levels reflects their shared diet and a potentially greater reliance on primary producers or the algae-associated invertebrates they consumed.

Only small (<1 m^2) rafts were sampled in our study, but even small rafts can support large numbers of juvenile fishes. Indeed, more than 80 fishes were observed around a single floating alga (Pitt KA pers. obs). Much larger rafts (e.g., exceeding 100 m^2) also form in this region and attract larger animals, including adult squid (Pitt KA, pers. obs.). Although *Sargassum* rafts support a diverse community of fishes and invertebrates, the dynamics of this important habitat within the Ningaloo Coast World Heritage Area have never been studied. We suspect that rafts may be most prevalent during Autumn and Winter because this period coincides with the decline of benthic *Sargassum* spp. on Ningaloo Reef (Fulton et al., 2014). Thus, the peak abundance of raft habitat may lag the Summer peak in recruitment of coral reef fishes (McIlwain, 2003). A much more extensive investigation of the temporal and spatial dynamics of *Sargassum* rafts and the organisms that inhabit them, the relationship between the distribution and abundance of rafts and recruitment of coastal fishes, and the potential of rafts to transport fishes by drifting over considerable distances, is warranted.

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CRediT authorship contribution statement

Samuel Q. Mazoudier: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Michael J. Kingsford:** Supervision, Methodology, Investigation, Conceptualization, Funding acquisition, Writing - review & editing. **Jessica K. Strickland:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Kylie A. Pitt:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Sam Mazoudier reports financial support was provided by Griffith University. Kylie Pitt reports equipment, drugs, or supplies and travel were provided by The Minderoo Foundation. Michael Kingsford reports equipment, drugs, or supplies and travel were provided by The Minderoo Foundation. Jessica Strickland reports financial support and equipment, drugs, or supplies were provided by The Minderoo Foundation. Sam Mazoudier reports equipment, drugs, or supplies was provided by The Minderoo Foundation.

Data availability

Data will be made available on request.

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