



Spatio-temporal variation of sediment properties reveals missing trophic links for deposit-feeding crabs in sandy shore food webs

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ABSTRACT: Quantifying trophic relationships among basal food sources and primary consumers is essential to our understanding of food web structure and dynamics, but is challenging in soft shore systems where the variety of potential food sources often masks the actual pathways of energy flow. To elucidate trophic relationships among basal food sources and primary consumers, we assessed the diet composition of a deposit-feeding crab, *Scopimera intermedia*, an abundant primary consumer inhabiting tropical shores, using direct enumeration and stable isotope techniques. Stable isotope analyses revealed that meiofauna accounted for the majority of the crab's diet (nematodes reaching 43% in median proportion) compared to, at most, 11% contributed by microphytobenthos (MPB). Although the abundances of MPB and meiofauna varied, meiofauna dominated over MPB in the crab's diet at different sites and seasons. Such an important role of meiofauna in consumer diets contrasts with previous studies on sediment food webs, where MPB has often been proposed as the most plausible primary food source. The relative roles of meiofauna and MPB as food sources are, however, likely to be mediated by local physical environments. Sediment particle size, for example, is more coarse higher on the shore, where the larger interstitial spaces enable colonization of meiofauna but will limit large, motile MPB due to increased photostress. The trophic importance of commonly assumed primary food sources may thus be modified by environmental physical stress and, as a result, the role of intermediate trophic links in modulating food web dynamics should not be neglected.

KEY WORDS: Sediment food web · Stable isotopes · *Scopimera intermedia* · Particle size · Microphytobenthos

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1. INTRODUCTION

Quantifying species' diets is critical to our understanding of food webs and ecosystem function (Pimm 2002, Duffy et al. 2007). Variations in diets not only imply different interaction strengths among species, but also depict trophic pathways and efficiency of energy flow in ecosystems (Paine 1980, Hairston & Hairston 1993). At the individual level, optimal foraging decisions determine individual diet breadths

(MacArthur & Pianka 1966), which collectively drive food web complexity patterns (Beckerman et al. 2006) under varying physical/environmental constraints (deVries 2017). Elucidating spatio-temporal variations in species diets, therefore, is key to our understanding of species interactions and ecosystem functions. On intertidal soft shores, a variety of microscopic and meiofaunal organisms constitute the base of sediment food webs. These organisms include meiofauna (e.g. nematodes, copepods, oligo-

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chaetes etc.), microphytobenthos (MPB; autotrophs including diatoms, cyanobacteria, euglenids etc.; MacIntyre et al. 1996), bacteria and their organic secretions (Decho & Lopez 1993, Coull 1999, Meziane et al. 2002). Macroscopic materials (e.g. living/decaying macroalgae, vascular plant detritus), on the other hand, make up most of the remaining sediment organic matter pool (Rice 1982, Lotze & Worm 2000, Adin & Riera 2003). These complex arrays of living and non-living organic materials can contribute variable amounts of energy to higher trophic levels dependent on whether they are selected or avoided by deposit-feeders in benthic sediment food webs (Hsieh et al. 2002).

Deposit-feeders (e.g. crustaceans, gastropods and polychaetes) exhibit diet selection via various means, including particle size classes, chemical stimulants, nutritional value or choosing particular groups of organisms such as nematodes or copepods (Robertson & Newell 1982, Jumars 1993). Such selections are facilitated by specific chemoreceptors (Robertson et al. 1981), feeding apparatus morphology (Ono 1965, Lim & Kalpana 2011) and/or flexibility in deposit-feeders' foraging movements (Hui & Williams 2017). MPB, in particular, has been considered an important and nutritious food source for the majority of deposit-feeders on both temperate and tropical sediment shores (MacIntyre et al. 1996, Middelburg et al. 2000, Yang et al. 2003, Vermeiren et al. 2015). Availability of MPB, however, varies spatially and temporally according to the interaction between physical and biological factors. These include particle size, shore height and competitive interactions within or between deposit-feeding species (Levinton 1972, Jesus et al. 2009). Meiofauna represent another nutrient source for deposit-feeders (Coull 1999, Lee 2007), but their trophic importance is variable depending on the species identity of, and selective digestion by, deposit-feeders (MacIntyre 1969, Dye & Lasiak 1986, Coull 1990, Abdullah & Lee 2016). As such, the importance of various interstitial components as food sources to higher trophic levels on sediment shores appears variable depending on local environments.

Quantifying the diets of individual deposit-feeding species at appropriate spatial and temporal scales can reveal the contributions of different energy pathways in supporting the productivity of intertidal sediments under specific environmental conditions. To achieve this goal, the present study quantified spatio-temporal variation in MPB and meiofauna on tropical, high shore sediments and estimated their relative contributions to the diet of the sand-bubbler

crab *Scopimera intermedia*. Crabs in the genus *Scopimera* are common deposit-feeders on tropical sandy shores, burrowing at higher tidal heights than the confamilial *Dotilla* (Allen et al. 2010, Hui & Wong 2019), and they are abundant in high shore sediments on local sandflats (Hui 2017). To survive the strong thermal stress, desiccation and low food availability found in these habitats, *S. intermedia* possesses a number of behavioural adaptations to efficiently maintain water balance and optimize food acquisition (Hui & Williams 2017, Hui et al. 2019). The diet of *S. intermedia* thus represents one of the major trophic pathways on tropical high shore habitats characterized by high temperatures, coarse particle size and low water content. The crab extracts labile components from sediments via flotation feeding and discards un-ingested sediments as pellets, allowing direct estimation of the ingestion of sediment food sources. Using both direct measurements and stable isotope techniques, we tested whether MPB is the dominant food source of the crabs, as traditionally assumed, and to what extent meiofauna contribute to the crab's diet under the dynamic and extreme physical conditions on tropical high shore sediments.

2. MATERIALS AND METHODS

2.1. Study sites

Diets of *Scopimera intermedia* were investigated at 2 sediment shores in Tolo Harbour, Hong Kong, during 2014–2016: Starfish Bay (SFB; 22° 25' 55" N, 114° 14' 41" E) and Three Fathoms Cove (TFC; 22° 25' 43" N, 114° 16' 13" E). These 2 shores were selected as they support abundant populations of *S. intermedia* (reaching ~ 70 ind. m⁻² along the mid to high tidal heights), and the seasonal feeding patterns of the crabs are well documented (Hui 2017), facilitating interpretation of food web dynamics. Study areas at both sites were characterized by a median particle size of 0.77 ± 0.48 mm (mean ± SD) and sediment water content of 17 ± 4% during the study period (Hui 2017). In Hong Kong's strongly monsoonal system (Kaehler & Williams 1996), 2 distinct principal and associated transition seasons can be defined based on temperatures measured in the crabs' habitat: the cool and dry seasons (air temperature at 0.5 cm above the sediments ≤ 25°C, from Jan–Mar) and hot and wet seasons (≥ 30°C, from May or June to Sep or Oct), and cool–hot transition (months between cool and hot seasons) and hot–cool

transition (months between hot and cool seasons). During these 4 seasons, sediment/crab samples were collected along ~ 1.7 m + chart datum (CD) at both SFB and TFC, where the crabs were the most abundant (reaching ~ 70 ind. m^{-2}) to assess their effects on the dynamics of potential food items (i.e. MPB and meiofauna; see detailed sampling schemes below). The crabs are deposit-feeders that feed on surface sediments during diurnal low tide periods and, since feeding activities of the crabs have been shown to vary seasonally (Hui 2017), diet analyses were conducted in both hot and cool seasons during the study period.

2.2. Spatial and temporal variations in sediment MPB and meiofauna, and the ingestion efficiency of *S. intermedia*

Sediment chlorophyll *a* (chl *a*) content was adopted to represent MPB biomass (MacIntyre et al. 1996). To quantify the spatial and temporal variations in sediment chl *a* content, 2–5 surveys were conducted at both sites during each of the 4 seasons from May 2014 to May 2016. In each survey, 5 quadrats (25×25 cm²) were randomly selected along a 10 m transect. In each quadrat, surface sediment samples were taken, using a syringe core (19 mm diam., 2 mm depth), at 5 random locations within the quadrat. These 5 within-quadrat samples were averaged to estimate the sediment chl *a* content of one replicate (quadrat: $\Sigma n = 2$ [sites] $\times 4$ [seasons] $\times 2$ [yr] $\times 2$ –5 [surveys] $\times 5$ [replicates] = 250). During feeding, the crabs scrape sediments into their mouthparts with their chelae, extract food using maxillipeds and discard unwanted sediments as distinct food pellets. These pellets are roughly spherical (~ 3 mm diam.; T. Y. Hui unpubl. data) and are deposited by the crabs in a radiating pattern from the burrow entrance (see Hui & Williams 2017). The food pellets are readily distinguishable from sediment pellets (produced due to burrow maintenance), which are much larger in size and not deposited along foraging tracks. Food pellets produced by the crabs were collected in tandem at 4 of the surveys during 2014–2015 to assess the crabs' ingestion efficiency ($n = 8$ –10 survey⁻¹). To collect food pellets, a parafilm sheet (~ 5 cm²) was fixed along the most recent foraging track of the crab. Processed sediments (food pellets) were deposited onto the sheet near the crab without contacting the background, unprocessed sediments. The parafilm sheets were retrieved ~ 15 min after placement and the food pellets transferred to sampling tubes.

All sediment samples were transported to the laboratory within 2 h in an icebox, freeze-dried overnight, weighed (± 0.001 g), and extracted for chl *a* using 90% acetone at -20°C for 24 h. The samples were then centrifuged (3500 rpm [$2374 \times g$], 5 min), and the supernatant assayed spectrophotometrically for chl *a* content, while the residual sediments were retrieved for particle size analyses. Absorbance of the supernatant was measured at 665 and 750 nm, both before and after acidification (2 drops of 0.1 M HCl) to correct for phaeopigment absorption (Lorenzen 1967, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m654p079_supp.pdf for phaeopigment contents). Retrieved sediments of the 5 within-quadrat samples were pooled, oven-dried, weighed (± 0.001 g) and wet-sieved to determine the median particle size (bulk particle size including both mineral and organic fractions remaining after chl *a* extraction; 6 sieve sizes were used: 2000, 1000, 500, 250, 125 and 63 μm). Calculations of median particle size were performed using the program SEDSIZE (Bale & Kenny 2005).

To investigate sediment meiofaunal assemblages, 2–5 surveys were conducted at both sites within each of the 4 seasons during 2015–2016. In each survey, surface sediment and food pellet samples were collected and transported to the laboratory within 2 h ($n = 8$ –9, $\Sigma n = 412$). Food pellets were collected using the parafilm approach (see the MPB collection methods in Section 2.2). Whilst there is the possibility that some meiofauna might escape from the collected pellets onto the parafilm, thus overestimating ingestion efficiency of the crabs, the negative phototaxis of many meiofauna taxa (nematodes, harpacticoids, oligochaetes and polychaetes; Clark 1956, Burr 1979, Palmer 1984, see also the review in Giere & Pfannkuche 1982) suggests that they are likely to remain inside the pellets. Samples were then fixed and stained using 4% formaldehyde in 33 psu artificial seawater with ~ 3 g ml^{-1} Rose Bengal for > 24 h. Fixed samples were then elutriated using tap water 6 times from a 50 ml centrifuge tube, and elutriated materials were retained by a 63 μm mesh. Retained materials were then examined under a light microscope (100 \times), with meiofauna sorted to major taxa (nematodes, copepods [adult and nauplius], oligochaetes, polychaetes, tardigrades, kinorhynchans, cnidarians, chironomids, amphipods, ostracods and foraminiferans) and counted. Sorted samples were then pooled with the original sediments, oven-dried and weighed (± 0.001 g) to estimate the sample dry mass (therefore excluding portions ≤ 63 μm which account for $< 1\%$ of dry mass).

2.3. Stable isotope analyses of the contributions of various interstitial components to the diets of *S. intermedia*

To quantify assimilations of different interstitial components by *S. intermedia*, stable isotopes (^{13}C and ^{15}N) of the crabs and different potential food sources from both sites were analyzed during Dec 2015–Feb 2016 (predominantly the cool season) and Jun–Aug 2016 (the hot season). To investigate contributions of various sources of organic matter, crab, plant, macroalgae, seawater and sediment samples were collected during these periods and transported to the laboratory within 2 h of collection. In total, 2–3 surveys were conducted per site in each of the cool and hot seasons, providing 1–12 replicate measurements of the crabs and various food sources per site and season (see details of sample sizes below).

For crab sample preparations, collected crabs were frozen, sexed and subsequently dissected. Claw muscles were extracted from the left or right claw haphazardly and transferred directly to a tin capsule without homogenization, as muscles from the entire claw were used (including both males and females, $n = 9–11$, $\Sigma n = 40$). Living plants (above-ground stems and leaves of C4 grasses *Sporobolus vaginicus* and *Paspalum vaginatum*), detrital plant (deposited and decaying leaves of *Hibiscus tiliaceus*) and macroalgae samples (*Enteromorpha* spp.) were rinsed to remove adhering debris, oven-dried at 45°C and subsequently homogenized using a bead mill homogenizer (Bioprep-24 Homogenizer; Allsheng). Homogenized samples were transferred to a tin capsule directly (including the grass, *Hibiscus* and macroalgae, $n = 6–12$, $\Sigma n = 65$). Macroalgae were collected only during the cool season, since they are ephemeral and absent on the shore during the hot season in Hong Kong (Williams et al. 2019). Plant and macroalgal materials were collected as proxies for their organic matter being deposited onto the sediments (Haines 1976), since the crabs are strict deposit-feeders, feeding only on sediments and not directly on these plants and macroalgae.

For particulate organic matter (POM) preparations, seawater samples (~3 l each) were collected and filtered on ashed GF/F glass microfiber filters in the laboratory; the loaded filters were dried in an oven at 45°C. Material was then carefully scraped from the dried filters and transferred to both tin (nitrogen analysis) and silver (carbon analysis, see below) capsules ($n = 6–8$, $\Sigma n = 26$). For fine sediment organic matter (SOM), portions of sediments $\leq 63 \mu\text{m}$ were elutriated using tap water and collected by centrifuge tubes ($n = 6–9$, $\Sigma n = 27$). Tap water has negligible carbon

($< 1 \times 10^{-7} \text{ g ml}^{-1}$) and nitrogen (0 g ml^{-1}) contents with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ below detection limits (T. Y. Hui unpubl. data). Elutriated sediments were centrifuged (3500 rpm [$2374 \times g$], 5 min) and the supernatant water discarded. Residual sediments were then oven-dried at 45°C until being transferred to both tin and silver capsules. Filters and sediments in the silver capsules were acidified by adding 10% HCl to remove inorganic carbonates for stable carbon isotope measurements. Filters and sediments in the tin capsules were not acidified and were used for stable nitrogen isotope measurements. Remaining scraped filters and sediments were ashed in a furnace at 500°C for 4 h to determine their organic matter contents.

Both MPB and meiofauna were extracted from collected sediments for stable isotope analyses. To extract MPB, ~150 ml of sediments were first elutriated by tap water and portions $\leq 63 \mu\text{m}$ collected by sieving and centrifugation (3500 rpm, 5 min, $n = 6$, $\Sigma n = 24$). Ludox TM-50 (colloidal silica) (15 ml), diluted to a specific gravity of 1.20 g ml^{-1} , was added and the blend mixed on a vortex. The mixtures were then centrifuged (3500 rpm, 5 min) and the top green layer extracted using a pipette. Extracted materials were topped with tap water to 50 ml, re-centrifuged, and the supernatant water discarded. Ludox TM-50 (10 ml), diluted to a specific gravity of 1.12 g ml^{-1} , was then added to the centrifuged pellets, mixed on a vortex, centrifuged, and the green top layer extracted (to minimize inclusion of heavier sediment debris remaining after the first extraction). Extracted materials were washed with tap water 3 times (each centrifuged at 3500 rpm for 5 min) to remove Ludox; the washed extracts were pipetted into a tin capsule and oven-dried at 45°C. To extract meiofauna in quantities sufficient for stable isotope analyses, ~400 ml of sediments were elutriated with tap water and washed on a $63 \mu\text{m}$ mesh. The retained sediments were floated by centrifuging (3500 rpm, 5 min) with Ludox TM-50 diluted to 1.20 g ml^{-1} . Supernatants were washed onto a $63 \mu\text{m}$ mesh, rinsed with tap water and stored at -18°C until sorting. Meiofauna were sorted to major taxa (see above) and hand-picked using an insect-pin from the rinsed materials into a tin capsule under a stereomicroscope ($n = 1–6$ capsules for each meiofauna taxon; $\Sigma n = 67$ capsules). Nematodes (~200 ind. capsule $^{-1}$), oligochaetes (~100 ind. capsule $^{-1}$), polychaetes (~10 ind. capsule $^{-1}$) and chironomids (~10 ind. capsule $^{-1}$) were collected. For amphipods, individuals were picked into both tin and silver capsules for measurements of stable nitrogen and carbon isotopes respectively (~5 ind. capsule $^{-1}$). Copepods were too small to be

hand-picked and were collected in bulk by sieving the rinsed materials through a 500 μm mesh to remove large debris and floated by centrifuging with 1.20 g ml^{-1} Ludox TM-50. Supernatants were washed on a 63 μm mesh, rinsed with tap water and transferred to both tin and silver capsules using a pipette. To determine the meiofaunal composition of such bulk samples (referred to as small meiofauna, in which copepods constituted $78 \pm 22\%$), 3 subsamples each of 0.1 ml were taken, fixed with 4% formaldehyde in 33 psu artificial seawater with $\sim 3 \text{ g ml}^{-1}$ Rose Bengal and sorted under a light microscope (100 \times). Amphipods and copepods in the silver capsules were acidified by adding 10% HCl to remove inorganic carbonates for stable carbon isotope measurements, while those in the tin capsules were not acidified and were used for stable nitrogen isotope measurements.

All samples in tin and silver capsules were oven-dried (45°C), weighed by a microbalance ($\pm 0.001 \text{ mg}$) and encapsulated. Encapsulated samples were analyzed using an elemental analyzer (Eurovector EA3028) coupled to a stable isotope ratio mass spectrometer in continuous flow mode (Nu Instruments, Perspective Series) at the Department of Earth Sciences, The University of Hong Kong. Isotope values are expressed as δX , which is calculated by comparing the relative abundance of an isotope of the samples to that of a standard (carbon: Peedee Belemnite; nitrogen: atmospheric nitrogen): $\delta X = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000$, where X is the isotope (either carbon or nitrogen), R_{sample} is the ratio of the abundance of heavy to light isotopes in the sample ($^{13}\text{C}/^{12}\text{C}$ for carbon and $^{15}\text{N}/^{14}\text{N}$ for nitrogen) and R_{standard} is that of the standards; δX is expressed in permil (‰). To account for concentration effects in calculating the relative contributions of different food sources to the crabs' diets (Fry 2006), percentage nitrogen and percentage carbon were also measured from each sample.

2.4. Statistical analyses

Variations in sediment chl a content were tested between sites and seasons using generalized linear models (GzLM) with gamma error distributions (explanatory variables: sites [fixed, 2 levels], seasons [fixed, 4 levels] and median particle size [fixed, covariate]). Gamma distribution was used since sediment chl a content is a continuous and strictly positive quantity where sample standard deviation scales positively with the mean (see Philippart et al. 2010). Spatio-temporal variation in sediment particle size was tested using a general linear model with median particle size

as the response, and site, season and their interaction as the explanatory variables. Ingestion efficiency of chl a was calculated by dividing the difference in the mean chl a content between unprocessed sediments and food pellets by the mean chl a content of unprocessed sediments. Potential statistical significances of crabs' ingestion were investigated by comparing chl a contents of unprocessed sediments and food pellets produced by the crabs (explanatory variables: sediment types [fixed, 2 levels], sites [fixed, 2 levels], season [fixed, 4 levels]) using a GzLM with gamma error distribution. Likewise, the ingestion efficiency of different meiofauna taxa was calculated by dividing the difference in mean meiofauna densities between unprocessed sediments and food pellets by the mean meiofauna density of unprocessed sediments. Variations in meiofaunal community were investigated using multivariate GzLMs via the package 'mvabund' in R (Wang et al. 2012). This approach simultaneously fitted GzLMs (negative binomial errors with log link function) to model variations in the abundance of each meiofaunal taxon against sediment types (unprocessed sediments vs. food pellets, fixed, 2 levels), sites (fixed, 2 levels), season (fixed, 4 levels) and all their interactions, where sediment sample mass was used as an offset variable. These taxon-specific responses were then resampled, based on the residuals from GzLMs of individual meiofaunal taxon, to generate statistical inferences at the community level (Warton et al. 2017). A negative binomial error distribution was used to account for overdispersion in meiofaunal counts.

Relative contributions of different interstitial components to the crabs' diets were analyzed using their stable isotope signatures via the package 'MixSiar' in R (Stock & Semmens 2016). Only food sources with more than one measurement per season were used to incorporate empirical measures of signal variations. Detrital *Hibiscus* were excluded from the analyses since they were isotopically too distinct (average $\delta^{13}\text{C} = -31\%$, average $\delta^{15}\text{N} = 1\%$) from the majority of sediment food web components (average $\delta^{13}\text{C}$ ranged from ~ -21 to -13% , average $\delta^{15}\text{N}$ ranged from ~ -6 – 18%) and, therefore, were unlikely to be an important diet component for the crabs. 'MixSiar' produces posterior estimates of percentage contributions of each specified food component using a Bayesian method, with a Dirichlet distribution of equal contribution by each food source as the prior. The Bayesian method produced the probability distribution of the respective contribution of each food source, using a Monte Carlo Markov chain (iterations = 100 000, burn-in length of 50 000, thinning by 50, implemented using a Gibbs sampler JAGS) and given

the prior distribution and sample data. In cases where the sample size for carbon and nitrogen stable isotope measurements of a food source differed (difference in n ranged from 0–3), the average sample size was used. Carbon and nitrogen concentrations of different food sources were incorporated to account for concentration effects: those from crabs, plants, MPB and meiofauna were input without correcting their organic contents as they are primarily organic materials, while those from POM (scraped filters) and SOM were corrected by their organic matter contents, which averaged ~10%. Trophic enrichment factors (TEFs) from various food sources to the crabs were estimated from the literature (Table S2). Results from controlled diet studies of marine or intertidal crabs (using $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) were collected and regressed against isotope signatures of their diets ($n = 12$; see Fig. S1 for details). The regression relationships were then used to calculate food-source-specific TEFs in the current study (see Hussey et al. 2014), which ranged from 0–5.4‰ for $\Delta\delta^{15}\text{N}$ and –3.4 to 5.9‰ for $\Delta\delta^{13}\text{C}$.

3. RESULTS

Scopimera intermedia ingested $23 \pm 10\%$ (mean \pm SD over the 4 surveys; see Fig. S2 for complete description) of MPB available in the sediments, and the chl *a* content of their food pellets was reduced compared to unprocessed sediments ($t_{150} = 0.48$, $p < 0.001$). Sediment chl *a* did not vary between sites or seasons, but decreased with sediment particle size which explained the majority of chl *a* variation (Fig. 1, Table 1). Sediment particle size was more coarse during the cool season ($F_{3,240} = 10.0$, $p < 0.001$) and varied between sites according to seasons ($F_{3,240} = 5.3$, $p < 0.01$): during the cool season sediments in SFB were 40% more coarse than at TFC, but only 27% more coarse during the hot season (Fig. 1).

Meiofauna were also ingested by the crab, with densities of major meiofaunal groups (nematodes, copepods, oligochaetes and polychaetes) in food pellets being 68–100% less than unprocessed sediments

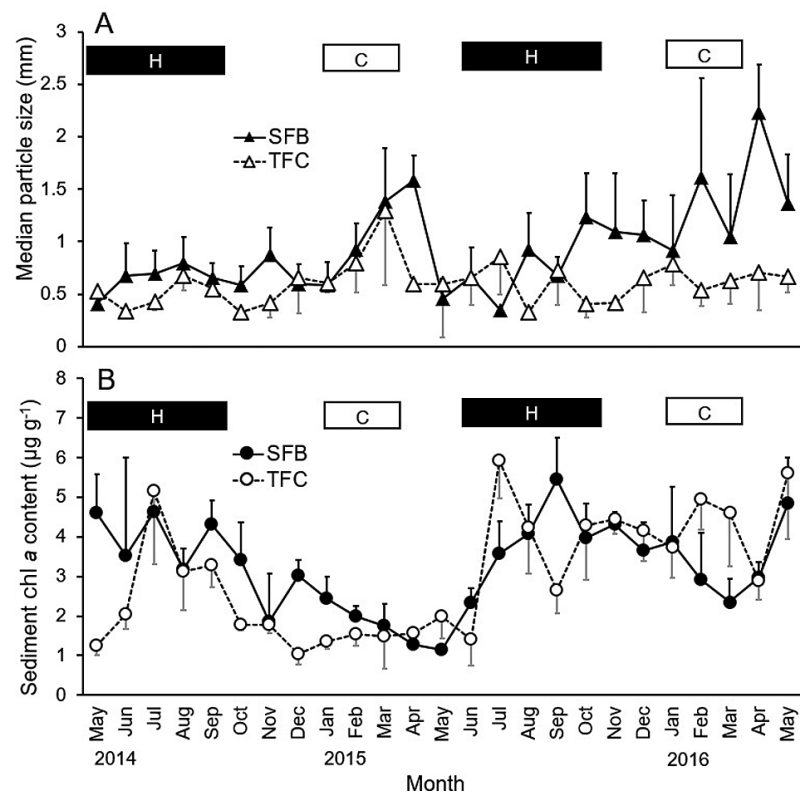


Fig. 1. Spatio-temporal variations in (A) sediment median particle size and (B) mean chl *a* content during 2014–2016 in Starfish Bay (SFB) and Three Fathoms Cove (TFC), along a ~10 m transect at ~1.7 m + chart datum at each site where *Scopimera intermedia* burrows were located. $n = 3$ –5 for each mean value. Vertical bars: ± 1 SD (black: SFB; grey: TFC). H and C: hot and cool seasons, with transition periods between (see Section 2.1 for explanation)

Table 1. Analysis of deviance from the generalized linear model (gamma error distribution) investigating spatio-temporal variation in sediment chl *a* at Starfish Bay and Three Fathoms Cove during the cool, hot, cool-hot transition and hot-cool transition seasons. Explanatory variables included sites, season, particle size and the interaction between season and particle size. The significant interaction was further analyzed by testing the coefficients (the change in chl *a* [log-link] per unit increase in particle size) within each hot, hot-cool transition, cool and cool-hot transition seasons

Source	χ^2	df	p
Site	2.02	1	0.15
Season	7.11	3	0.07
Particle size	18.68	1	<0.001
Season \times particle size	11.19	3	0.01
Season \times particle size interaction			
Season	Coefficient	p	
Hot	–0.13	0.39	
Hot-cool transition	–0.05	0.81	
Cool	–0.48	<0.001	
Cool-hot transition	0.16	0.41	

Table 2. Analysis of deviance from the multivariate generalized linear model (GzLM, with negative binomial error distribution) investigating the spatio-temporal variation in tidal sediment meiofauna community at Starfish Bay and Three Fathoms Cove during the cool, hot, cool-hot transition and hot-cool transition seasons. A GzLM was fitted to each individual meiofaunal taxon with explanatory variables including sediment type (unprocessed sediments and food pellets), site, season and interactions between sediment type, site and season. Sediment sample mass was used as an offset variable. **Bold** numbers indicate significant effects ($p < 0.05$); zeros indicate small deviances (< 0.05). Statistical inferences at the community level were achieved using resampling procedures (see Section 2.4). 'Others' includes unsorted taxa (e.g. insects) and sorted taxa contributing $< 1\%$ of total meiofaunal abundance in unprocessed sediments

Taxon	Type	Site	Season	Site × season	Type × site	Type × season	Type × site × season
Source deviance (individual meiofaunal taxon)							
Nematoda	150.3	43.4	26.7	58.9	0.1	2.9	3.4
Copepoda (adult)	27.7	104.6	39.6	55.4	1.6	5.7	5.9
Copepoda (nauplii)	29.4	101.6	82.7	60.5	0.2	0.6	5.9
Oligochaeta	34.4	11.1	2.1	14.6	0.7	1.4	0
Polychaeta	21.0	1.0	15.9	0.8	0	0	0
Tardigrada	45.8	137.5	6.4	0	0	6.1	0
Ostracoda	9.6	3.3	16.1	25.0	0.7	0.4	5.1
Foraminifera	3.8	4.8	5.8	44.1	0	2.4	10.8
Cnidaria	0.6	77.2	53.6	21.6	0	2.5	5.4
Others	49.9	12.0	12.2	8.6	2.4	0.9	1.9
Source		Deviance	df	p			
Source deviance (community level)							
Type		372.4	1	< 0.001			
Site		496.4	1	< 0.001			
Season		261.2	3	< 0.001			
Site × season		289.5	3	< 0.001			
Type × site		5.6	1	0.72			
Type × season		22.9	3	0.77			
Type × site × season		38.4	3	0.06			

(Table 2, Figs. 2 & S3). In particular, the crab ingested $86 \pm 13\%$ (mean \pm SD) of nematodes and $74 \pm 19\%$ of copepods from the sediments, and oligochaetes and polychaetes were reduced by almost 100%, as none were found in the crabs' food pellets except in one sample from TFC (Fig. 2). The meiofauna community was spatially and temporally variable, with more nematodes and copepods at SFB compared to TFC (Fig. 2) and, in general, more in the sediments during the hot and hot-cool transition periods compared to the cool season (Fig. S3).

During the cool season, the crabs did not differ in $\delta^{13}\text{C}$ between TFC and SFB (Welch's $t_{11.2} = 0.3$, $p = 0.76$), but the crabs from TFC were more depleted in $\delta^{13}\text{C}$ than SFB during the hot season (Welch's $t_{13.1} = 5.5$, $p < 0.001$; Fig. 3). The crabs were more enriched in $\delta^{15}\text{N}$ in TFC than SFB across both seasons ($t_{36} = 3.4$, $p < 0.01$; Fig. 3). MPB and SOM ($< 63 \mu\text{m}$) had similar $\delta^{13}\text{C}$ ($t_{49} = 1.7$, $p = 0.10$) and $\delta^{15}\text{N}$ ($t_{42} = 0.3$, $p = 0.76$) across sites and seasons, indicating that the majority of the SOM pool was contributed by MPB. The

Bayesian mixing model, however, revealed nematodes contributed a higher proportion of the crabs' diet (ranging from 18–43% in median proportion) than other organic components such as MPB or POM (Fig. 4), which only constituted 3–11 and 4–10%, respectively. Other meiofaunal taxa such as polychaetes and oligochaetes also constituted 10–17%, which were comparable to the C4 grasses (*Sporobolus* and *Paspalum*) which contributed 6–22%. The ephemeral macroalgae *Enteromorpha* spp. contributed $< 10\%$ to the crabs' diet.

4. DISCUSSION

4.1. Meiofauna as the dominant dietary sources for high shore deposit-feeders

Despite previous assumptions that MPB is the dominant food source for deposit-feeders on sediment shores (Decho & Lopez 1993, Middelburg et al. 2000), both stable isotope analyses and direct enumeration

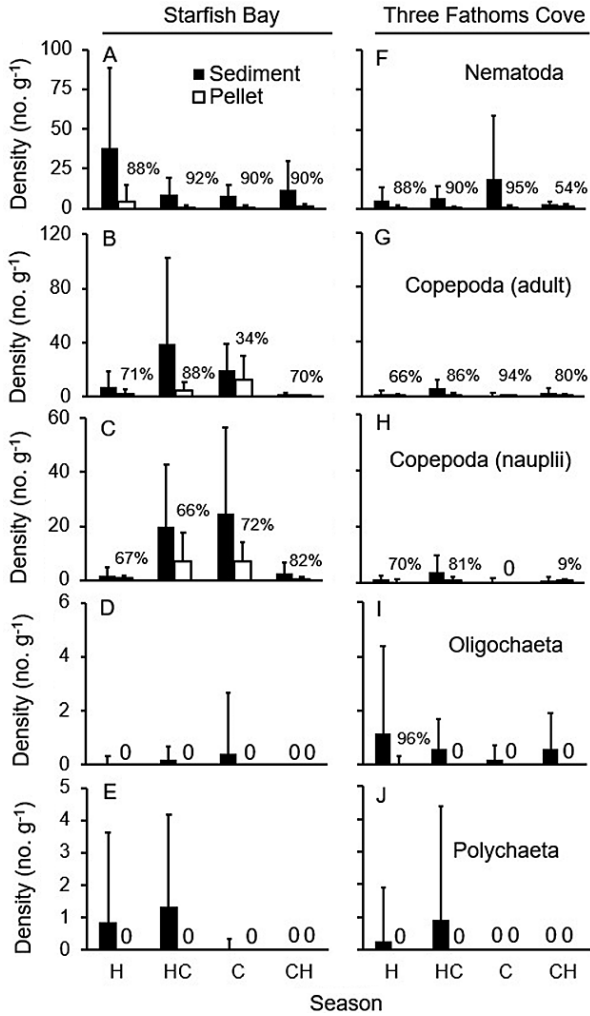


Fig. 2. Spatio-temporal variations in the ingestion of common meiofauna groups by *Scopimera intermedia* in Starfish Bay and Three Fathoms Cove as determined by the difference between unprocessed sediments and discarded pellets after crab feeding. (A,F) Nematoda; (B,G) Copepoda (adult); (C,H) Copepoda (nauplii); (D,I) Oligochaeta; (E,J) Polychaeta. H and C: hot and cool seasons; HC and CH: Hot-cool and cool-hot transition periods (see Section 2.1 for definition). Numbers represent the ingestion efficiencies of the crabs in each season, and zeros indicate that no target meiofaunal taxa were found in the samples (= not present in the sediments/100% ingestion efficiency). n = 16–44 in each site and season; error bars: +1 SD. See Fig. S3 for all meiofauna groups

showed that *Scopimera intermedia* predominantly consumed meiofauna over other potential food sources across sites and seasons. As nitrogen is poorly retained on sandy shores even under conditions of high exogenous nitrogen inputs (McLachlan & McGwynne 1986), nitrogen-rich meiofauna, such as nematodes and copepods, represent important food sources for macroinvertebrates as highly concentrated, discrete packages of energy as compared to the smaller MPB (Sikora et al. 1977). This is particularly evident during the hot season in SFB, where nematodes were more abundant than in the cool season and thus contributed more to the crab's diet. Nematodes and copepods are also able to biosynthesize polyunsaturated fatty acids (De Troch et al. 2012), facilitating the intake of various lipids important for maintenance and reproduction in crabs (Mourete et

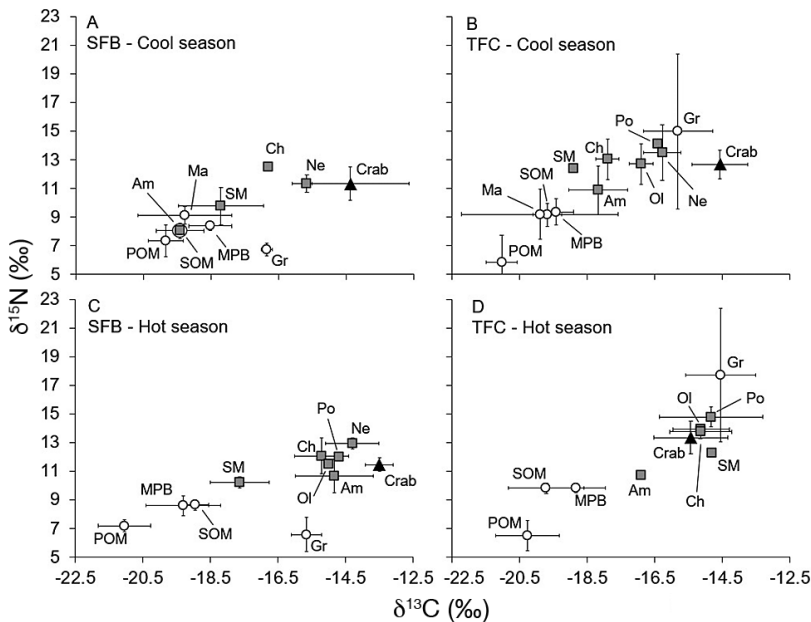


Fig. 3. Carbon and nitrogen stable isotope biplots of sediment food webs in Starfish Bay (SFB) and Three Fathoms Cove (TFC) during the (A,B) cool and (C,D) hot seasons. Error bars: ±SD; n = 9–11 for crab muscle measurements, n = 1–12 for potential food source measurements. POM: particulate organic matter; SOM: sediment organic matter; MPB: microphytobenthos; Gr: grass; Ma: macroalgae; SM: small meiofauna (where copepods constituted ~78%); Am: amphipods; Ch: chironomids; Ol: oligochaetes; Po: polychaetes; Ne: nematodes; Crab: *Scopimera intermedia* muscle. White circles: basal food sources (POM, SOM, MPB, Gr and Ma); grey squares: meiofauna (SM, Am, Ch, Ol, Po and Ne); black triangles: crabs

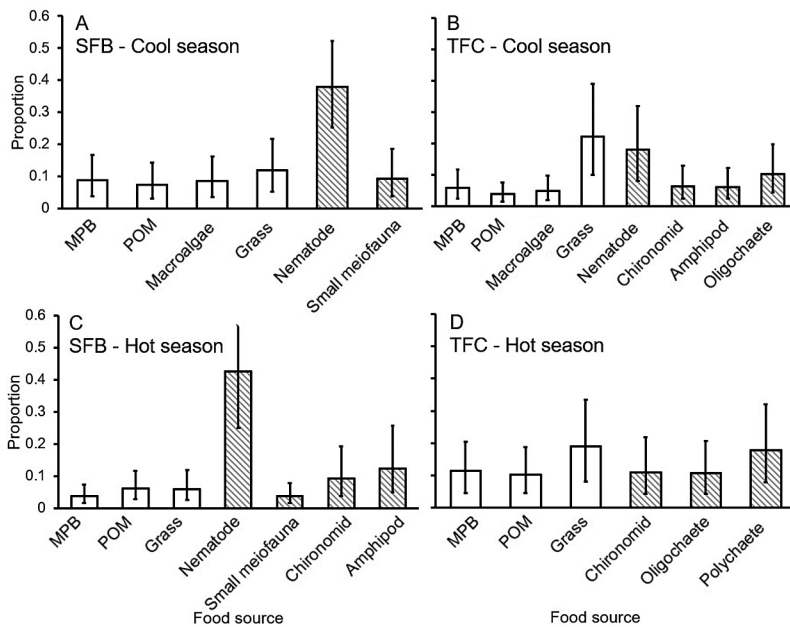


Fig. 4. Diet composition of *Scopimera intermedia* in (A,C) Starfish Bay (SFB) and (B,D) Three Fathoms Cove (TFC) during the hot and cool seasons, estimated using Bayesian methods in the 'MixSiar' package in R. Data are expressed in median dietary proportions (with error bars extending to the 25th and 75th percentiles). Hatched bars: proportion contributions of meiofauna groups; open bars: proportion contributions of various primary sources (MPB: microphytobenthos; POM: particulate organic matter)

al. 1994, Cuculescu et al. 1995). Though the densities of nematodes and copepods were similar in sediments and were ingested at comparable efficiencies by the crabs (87 and 74%), the high contribution of nematodes in the crabs' diets could result from the higher digestibility of nematodes compared to copepods (Coull 1990, Scholz et al. 1991), or the nematodes being larger in size compared to the copepods (which were too small to be hand-picked) measured in this study.

MPB, in contrast, dominated the fine SOM but only contributed at most 11% to the crab's diet. The slight increase of MPB in the crab's diet during the hot season in TFC (from 6 to 11% in median contribution) may be driven by the reduction in sediment particle size, which would promote higher MPB availability for the crabs. Vascular detritus, which was abundant from drift materials and senescent *Hibiscus* leaves, was also of minor importance to the sediment food web, since detritus primarily consists of non-labile and highly resistant compounds such as cellulose and lignin (Rice 1982), and sandy shore crabs possess less cellulase compared to crabs living in coastal vegetation habitats (Kawaida et al. 2013). The relative high contribution of C4 grasses to the crab's diet (~6–22%), however, suggests some detrital carbon was

assimilated and transferred to higher trophic levels (Alderson et al. 2013), likely due to the consistently high inputs by these supralittoral plants into nearby sediments.

4.2. Trophic energy flow structured by high shore sediment environments

The physical structure of high shore sediments appears to influence the contributions of different food items towards the crab's diet. Whilst the behaviour and morphology of food items determine their availability (e.g. nematodes escaping to deeper sediments to avoid being ingested; Coull 1990) and handling efficiency (e.g. large, motile diatoms are often more easily removed than non-motile, strongly adhesive species; Nicotri 1977, Connor & Edgar 1982), local physical environments regulate the abundance of food items and thus their availability to higher trophic levels. MPB communities on coarse, well-drained sediments are often composed of small, non-motile and adherent species capable of physiologically resisting elevated levels of photostress (Jesus et al. 2009). On the other hand, oxygen concentration in interstitial space is higher in coarse and well-drained sediments (McLachlan & Turner 1994), supporting higher biomass and diversity of more mobile meiofauna such as nematodes and copepods compared to fine, water-logged sediments (McLachlan 1977, Rodríguez et al. 2003). This difference in the relative availability of MPB and meiofauna might explain the unexpected low contribution of MPB to the diet of *S. intermedia*, which lives at the mid to high shore and feeds on medium to coarse sediments. The sediment particle size was more coarse during the cool season, probably driven by the stronger wave action, and thus reduced deposition of fine sediments during the cool compared to the hot season in Hong Kong (Williams et al. 2019). In both sites, chl *a* content decreased with increasing particle size, but this pattern was probably the opposite for meiofauna, as improved oxygen penetration in more coarse sediments would facilitate their migration towards the sediment surface (Giere 2009). The contribution of meiofauna to sediment food webs would thus become increas-

al. 1994, Cuculescu et al. 1995). Though the densities of nematodes and copepods were similar in sediments and were ingested at comparable efficiencies by the crabs (87 and 74%), the high contribution of nematodes in the crabs' diets could result from the higher digestibility of nematodes compared to copepods (Coull 1990, Scholz et al. 1991), or the nematodes being larger in size compared to the copepods (which were too small to be hand-picked) measured in this study.

ingly important when sediments are more coarse, such as towards the high shore and when wave action increases. In particular, nematodes have been shown to prefer well oxygenated interstitial spaces (Jansson 1967, Steyaert et al. 2005) and increase in diversity, although occur at lower abundance, in coarse compared to fine sediments (Heip et al. 1985). The trophic importance of nematodes in high shore sediments to deposit-feeders may, therefore, have been overlooked since meiofauna are not usually resolved using stable isotope techniques from bulk SOM in large-scale food web studies (Bergamino et al. 2011, Colombini et al. 2011, Tue et al. 2012), although Evrard et al. (2010) and Lee et al. (2011) suggested a strong carbon linkage from MPB to meiofaunal assemblages. Importantly, spatial variation over the tidal gradient has often been neglected in such studies, where a single mean value has been used to represent the SOM over much larger spatial scales relative to the ranges of individual species (e.g. Doi et al. 2005, Lebreton et al. 2011), masking the actual pathway of energy flow at any particular location.

4.3. Evidence for meiofauna as an intermediate link in other food web studies

A review of sediment food webs involving Scopimerinae crabs, including *Scopimera* and *Ilyoplax* species, revealed large discrepancies of as much as +8‰ in $\delta^{13}\text{C}$ and +6‰ in $\delta^{15}\text{N}$ between the isotopic signals of the crabs and MPB, despite the fact that a direct trophic link between the two has often been assumed (Fig. 5). If MPB is the main diet of Scopimerinae crabs, such large discrepancies might result from selective retention of isotopically heavier compounds inside MPB (Keil & Fogel 2001), which will inflate the TEF (see Herbon & Nordhaus 2013). Such inflation, however, is unlikely to explain the large discrepancies in $\delta^{13}\text{C}$ between the crabs and the MPB (since $\delta^{13}\text{C}$ of MPB in these studies averaged at 20‰, TEF is predicted to be ~2‰; see Fig. S1). Selection of diatom size classes within the MPB (which vary ~3‰ in $\delta^{13}\text{C}$; Rzeznik-Orignac et al. 2008) is also unlikely to cause the observed shift in magnitude of $\delta^{13}\text{C}$. Alternatively, there could be unmeasured trophic links, such as bacteria/protozoa in the sediments (Dye & Lasiak 1986, Meziane et al. 2002) or symbiotic bacteria within the digestive tracts of the crabs, that increase the number of trophic levels and thus TEF between MPB and the crabs. Such intermediate trophic links between MPB and the crabs, how-

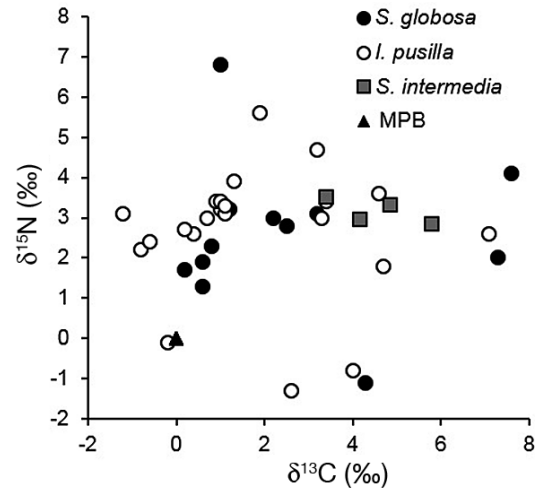


Fig. 5. Literature values of stable carbon and nitrogen isotope values of Scopimerinae crabs (*Scopimera globosa*, *S. intermedia* and *Ilyoplax pusilla*) relative to those of microphytobenthos (MPB) in literature records (circles) and the present study (squares). MPB values of each study were set to zero (triangle); therefore, the isotope values of crabs are expressed relative to MPB. Values were extracted from 11 studies from Japan and Korea: Doi et al. (2005), Yokoyama et al. (2005), Kang et al. (2007), Choy et al. (2008, 2009), Ishihi & Yokoyama (2010), Imamura et al. (2011), Kon et al. (2012), Kanaya et al. (2013), Park et al. (2015, 2016). If exact numbers were not available in the text, values were extracted from the graph using Engauge Digitizer (<http://markummitchell.github.io/engauge-digitizer/>)

ever, could be contributed substantially by meiofauna, which are known to be a major diet component in some deposit-feeding crabs living in similar environments (Lee 2007, Lee et al. 2011, Abdullah & Lee 2016).

4.4. Implications of meiofauna as a food source to the structure of sediment food webs and ecosystem management

Missing/unknown trophic links can substantially complicate the trophodynamics and temporal stability of food webs (Kristensen et al. 2010, Kuwae et al. 2012). Assuming sediment meiofauna obtain energy predominantly from MPB (Pinckney et al. 2003, Leduc et al. 2009), and *S. intermedia* is the dominant macrofaunal consumer in the area, then the interaction strengths in the food web will depend on the trophic interactions between MPB and meiofauna as well as the omnivory of the crabs (Pimm 2002). Whilst the presence of an omnivorous consumer increases the web's complexity (Pimm 2002), temporal varia-

tion in seasonal environments can modify these dynamics by elevation/suppression of temperature-dependent foraging traits (Petchey et al. 2010). When feeding activities of the crabs diminish during the cool season (Hui 2017), the food web reduces to a more simple version involving only meiofauna and MPB. The sediment food web thus alternates between an omnivorous web involving the crabs during the hot season and a direct producer–consumer web involving MPB and meiofauna with minimal crab feeding activities during the cool season. The omnivorous interactions during the hot season do not, however, necessarily suppress the overall abundance of lower trophic levels, as deposit-feeders often avoid feeding on sediment areas depleted of food (Levinton & Kelaher 2004, Hui & Williams 2017) thus allowing time for recovery, which is enhanced by the fast turnover rates of the meiofauna and MPB (see Gerlach 1971, Ribeiro & Iribarne 2011). The recovery of meiofauna is more pronounced in sandy than muddy areas following crab removal (Abdullah & Lee 2016), possibly due to the dominance of more mobile meiofaunal species which are adapted to highly disturbed sandy environments compared to the more stable muddy substrates (Schratzberger & Warwick 1998, Dernie et al. 2003). The recovery and availability of sediment food items, therefore, vary with the physical environment which governs species composition and dynamics at the microbial/meiofaunal levels, and ultimately determines the spatio-temporal structure of sediment food webs.

The dependence of food web structure on sediment particle size implies that small-scale variations in sediment qualities must be factored into ecosystem management strategies, particularly restoration of soft shores along coastlines which are being rapidly modified (Gittman et al. 2016, Williams et al. 2016). Deposit-feeding crabs often have feeding appendages which are specialized for a limited range of sediment sizes (Robertson & Newell 1982, Vogel 1984), and the composition of sediment size classes will, therefore, determine both the feeding efficiencies and ecological distributions of these crabs (Ono 1965, Hui & Wong 2019). In terms of monitoring ecosystem functioning, in addition to the routine use of sediment chl *a* as a proxy for primary production, the use of metrics such as total organic content which include meiofauna as an energy source should be adopted in assessing the overall energy available to consumers. The inclusion of total organic content will be particularly insightful in high shore areas where the importance of MPB to primary consumers is limited, as highlighted by the current study.

4.5. Conclusions

Diets of *S. intermedia* living on mid to high sediment shores were dominated by meiofauna, as revealed by both direct enumeration and stable isotope analyses. The dominance of meiofauna rather than MPB, as traditionally assumed for deposit-feeders, in the crabs' diets suggests that the physical high shore environment plays an important role in regulating the basal energy resources of sediment food webs. In high shore sediments with coarse particle size and high desiccation stress but good penetration of oxygen, meiofauna provide important carbon and nitrogen sources to deposit-feeders compared to MPB, which are more susceptible to excessive levels of photo and desiccation stress. Meiofauna, therefore, can function as a critical intermediate trophic link and are an underestimated source of energy for deposit-feeders on high sandy shores, especially in the tropics where physical stress limits primary productivity. Future assessments of sediment food web structures and dynamics across tidal heights and latitudes, therefore, need to accommodate these patterns when attempting to generalize about trophic patterns on these shores.

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