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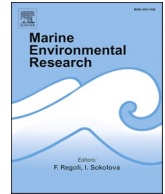
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Isotopic niche size variability in an ecosystem engineer along a disturbance gradient in a South African lagoon

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ABSTRACT

A key challenge for natural resource management is how to detect effects of environmental stress on individuals and populations before declines in abundance occur. Variability in carbon and nitrogen isotope composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) among consumers can provide information on the population trophic niche and how it may change in response to environmental stress. We measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in primary producers and in an ecosystem engineer, the bioturbating sandprawn *Kraussillichirus kraussi*, in Langebaan Lagoon, South Africa, along a human disturbance gradient. Diet partitioning mixing models were coupled with isotope niche analyses and individual body condition data to investigate shifts in resource utilisation and diet plasticity from minimally to highly disturbed sites. The $\delta^{15}\text{N}$ values of seagrass, *Zostera capensis* indicated a nutrient gradient, with the highest $\delta^{15}\text{N}$ values at highly disturbed sites indicating either anthropogenic or marine nitrogen inputs. A decreasing $\delta^{15}\text{N}$ signal with distance from human disturbance/mouth of lagoon was however not evident for sandprawns nor their presumed dietary sources (phytoplankton, microphytobenthos or sediment organic matter), likely because of faster isotope turnover time compared to seagrass and/or differential fractionation for sandprawns among the sites. Sandprawn isotope niche sizes varied among sites, with no trend along the disturbance gradient. The smallest niche coincided with uniform feeding on microphytobenthos according to mixing models. On an individual level, deviating isotope values from population means were correlated to better body condition, suggesting that a divergent feeding strategy is beneficial. Our results support a generalist feeding behavior of the sandprawns with no evidence of reduced physiological status at the site with most human disturbance.

1. Introduction

Coastal ecosystems are among the world's most productive systems and provide diverse and critical socio-ecological services. However, human activities such as resource harvesting, habitat destruction and nutrient enrichment degrade many of the services provided by these ecosystems (Lotze et al., 2006; Barbier et al., 2011; Duarte et al., 2013; Mead et al., 2013). Estuaries and lagoons are often subjected to multiple human stressors, due to their extensive recreational use and proximity to human development (Mead et al., 2013; Lucrezi et al., 2016).

Detecting changes in the environmental status and health of marine ecosystems requires an in-depth understanding of their structure and

functions. The study of marine food webs is a growing field of research, however current understanding of food web structures is limited, particularly for omnivores and deposit-feeders, where traditional gut content analyses are difficult to carry out and interpret and provide only a limited window on resources that support consumers.

Stable isotope ratios of carbon ($^{13}\text{C}:^{12}\text{C}$) and nitrogen ($^{15}\text{N}:^{14}\text{N}$), expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, can be used as indicators of carbon and nitrogen flows within food webs, to distinguish between sources of organic matter and to estimate the trophic position of organisms (Peterson and Fry 1987; Glibert et al., 2018 and references therein). Furthermore, by quantifying variation in isotope composition among individuals in a population, the so-called isotope niche, a proxy for the

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trophic niche of a population can be assessed (Layman et al., 2007; Newsome et al., 2007; Jackson et al. 2011). A small niche size may indicate uniform feeding on an abundant food source among individuals in a population, while a large niche indicates greater dietary diversity (Karlson et al., 2014). Comparing isotope niches for key-species along an expected disturbance gradient can provide valuable insights on shifts in diet. For example, when preferred food items are in short supply, individuals might broaden their diet to suboptimal food resources resulting in niche expansion (Svanbäck and Bolnick 2007). However, isotope composition of a consumer is not entirely reflective of diet but also physiological processes related to growth rate and physiological status, e.g. slow growth and stress may result in inflated $\delta^{15}\text{N}$ values in consumers (Martinez del Rio et al., 2009; Ek et al., 2015). Inter-individual variability in metabolic capacity to withstand food limitation and/or

environmental stress can manifest as increased variability in isotope fractionation and thus increased isotopic niche size (Gorokhova 2018; Karlson et al., 2018). Hence, a large niche size could indicate deteriorated health status of a population, which is potentially useful from an environmental assessment perspective (Karlson et al., 2018).

In the present study, we use stable isotopes to assess the environmental status of a locally important coastal ecosystem on the west coast of South Africa – Langebaan Lagoon, a tidal embayment that is permanently open to the Atlantic Ocean (Fig. 1). The system is a priority conservation area in South Africa since it is one of few coastal habitats that still supports large stands of seagrass (*Zostera capensis*; Pillay et al., 2010). The lagoon is managed through the designation of three zones with decreasing human presence from the northern parts of the lagoon, where bait collection (extraction of endobenthic organisms) is allowed,

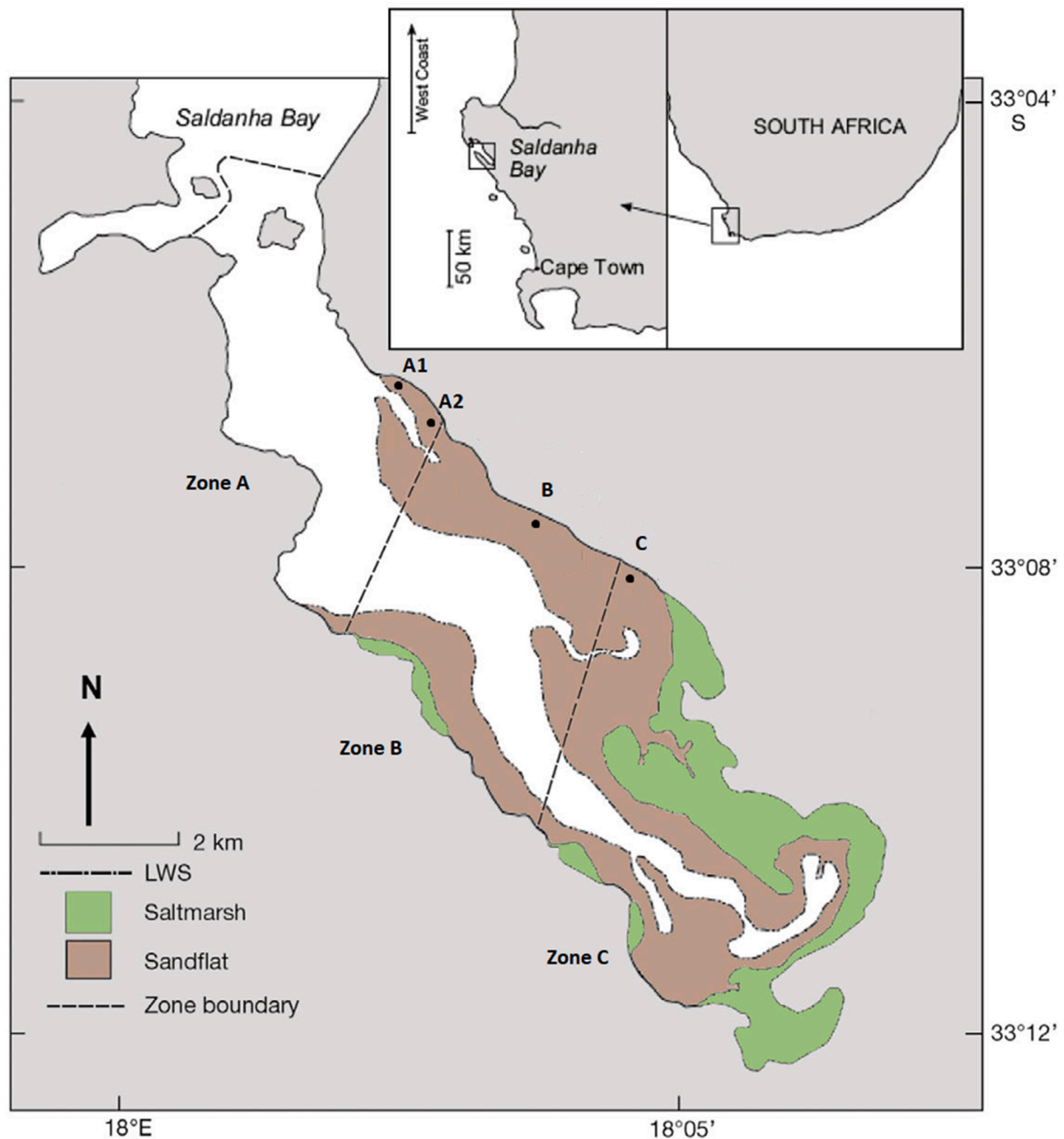


Fig. 1. Langebaan Lagoon with the four sampling sites; site A1 ($33^{\circ}6'47,2\text{ S}$; $18^{\circ}2'36,8\text{ E}$), site A2 ($33^{\circ}7'19,1\text{ S}$; $18^{\circ}3'10,9\text{ E}$), site B ($33^{\circ}7'59,7''\text{ S}$; $18^{\circ}4'6,2''\text{ E}$) and site C ($33^{\circ}8'40,2\text{ S}$; $18^{\circ}5'23,9\text{ E}$). In zone A and B human presence is allowed, site A1 is located on the popular Shark beach. In zone B, bait fishing is not allowed and in zone C human access is prohibited. All samples sites were located on bare sandflats.

to the southern part where human presence is prohibited (see methods for additional details). Langebaan Lagoon has no riverine input resulting in a negligible salinity gradient, while temperature variation is low, particularly in the intertidal zone. These features are ideal for studying the effects of human disturbance on the trophic ecology of a key species as the stable physicochemical conditions is not expected to alter isotopic signatures of basal organic matter sources.

The intertidal sandflats of Langebaan lagoon are dominated by the sandprawn *Kraussilichirus* (formerly *Callichirus*, *Callianassa*) *kraussi*, an important ecosystem engineer due to their bioturbation effects (Pillay and Branch 2011). Through the burrowing activities of sandprawns, mounds of sediment are deposited on the sediment surface at high rates (Branch and Pringle 1987). This activity along with mixing of sediment (both vertical and horizontal) have important structuring effects on soft-sediment communities (Siebert and Branch 2005; Pillay et al., 2007; Pillay and Branch 2011). Sandprawns are harvested from the sediment in designated areas using hand-held suction pumps and several studies have assessed the ecological impacts of this disturbance (Wynberg and Branch 1991, 1994, 1997). This is consistent with global approaches, where bait collecting and associated trampling have led to concerns about ecosystem effects on soft sediment habitats (Hailstone and Stephenson 1961; Contessa and Bird 2004). Callianassid prawns (such as *K. kraussi*) are classified as deposit-feeders, however little is known about the relative contribution of food sources assimilated by these bio-engineers (Antonio and Richoux 2014; Ziebis et al., 1996). Additionally, plasticity in feeding behaviors complicates understanding of their feeding ecology (Nickell and Atkinson 1995), especially in the context of disturbance associated with bait collecting and physiological stress. Given that sediment oxygenation is typically reduced following bait collection and trampling due to compaction (Wynberg and Branch 1994; Contessa and Bird 2004), metabolic losses and reduced body condition of sandprawns are plausible at sites intensely disturbed by harvesting. Moreover, in the short term, organic matter declines associated with bait collection (Wynberg and Branch 1994) could result in dietary shifts and potentially feeding stress for sandprawns. In the long-term, reduction in rates of bioturbation by sandprawns can lead to increased sedimentary organic matter and microalgal biomass following heavy harvesting (Wynberg and Branch 1994). Thus, disturbance from bait collection and trampling can generate either positive or negative effects on sandprawn body condition and alter feeding behavior depending on the strength of these processes.

We sampled sandprawns and potential food sources along the disturbance (bait collection and trampling) gradient in Langebaan Lagoon, for which we characterised stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and assessed the sandprawn body condition. By using isotope mixing models and isotope niche analyses in relation to the sandprawn body condition, shifts in resource utilisation and diet plasticity from less- to highly disturbed sites were quantified. We expected that the isotope (trophic) niche size would change along the disturbance gradient and that generalist feeding (i.e. a large niche) would be linked to better body condition of sandprawns.

2. Material and methods

2.1. Study site

Langebaan Lagoon (located between 33°11'27" S; 18°07'37" E and 33°03'54" S; 17°58'07" E, Fig. 1) is a marine-dominated system, with a tidal range of approximately 1.8 m and a subtidal region generally no deeper than 4 m. There is no riverine input into the lagoon, resulting in salinity being marine (35‰) across the system (Shannon and Stander 1977). The lagoon was declared a national park in 1985 and is registered as a wetland of international importance in terms of the Ramsar Convention (Pillay et al., 2010). The system is divided into three management zones with varying human activities (Fig. 1). Zone A is near an active shipping port (Saldanha Bay) and is subjected to extractive

activities such as bait collection along with recreational angling and surfing (site A1 is located on Shark beach). Bait harvesting is undertaken mainly by hand-operated suction pumps, with sandprawns (*Kraussilichirus kraussi*) being targeted. Zone B permits limited recreational activities but no extractive bait collection, while zone C is a sanctuary where entry without a valid permit is prohibited (Pillay et al., 2010). These three zones therefore constitute a gradient of human presence (and physical disturbance) in the lagoon. Seagrass cover has decreased in the regions of the lagoon where humans are present, especially in zone A (Pillay et al., 2010). Anthropogenic sources of nutrient input are expected to be reflected in higher $\delta^{15}\text{N}$ values in seagrass (cf. Jones et al., 2018) at sites in zone A compared to zone C.

2.2. Sampling of sandprawns

Sandprawns were sampled at four sites along the disturbance gradient in Langebaan Lagoon (Fig. 1). Both adults and juvenile sandprawns were collected at each site, from mid-shore intertidal sandflats, using a stainless-steel suction pump, with a minimum of 20 individuals collected per site. Sampling of the four sites was conducted during southern hemisphere autumn 2019 at low tide (site A1 and A2 on April 14th, and site A1 (again), B and C on May 3rd). In addition to the 2019 sampling, sandprawns (and seagrass, see below) were also sampled from site A1 and zone C ($n = 3$ in both cases) in January 2018 (southern hemisphere summer) and results are presented here to demonstrate seasonal consistency. All sandprawns were snap-frozen ($-20\text{ }^{\circ}\text{C}$) until further processing in the laboratory.

2.3. Sampling of primary producers and potential food sources

Potential food sources of sandprawns (particulate organic matter (POM), microphytobenthos (MPB) and sediment organic matter (SOM)) were sampled simultaneously during prawn sampling at sites A1, A2, B and C in 2019. In addition, seagrass (*Zostera capensis*) and macroalgae were sampled from the sites since they contribute to detrital organic matter (OM) pools that influence sediment OM composition. Moreover, seagrass has been shown to be an indicator of long-term nutrient status of coastal ecosystems (Jones et al., 2018). The dominant vegetation differed among the sites, with seagrass abundant at site A2 while nearly absent at A1, where agar weed (*Gracilaria gracilis*) instead dominated. *Z. capensis* was also sampled in January 2018 from site A1 and C. All samples of plants/algae were snap-frozen ($-20\text{ }^{\circ}\text{C}$) immediately after sampling. Seagrass and macroalgae were rinsed in prefiltered seawater, and seagrass epiphytes were scraped off the leaves before oven drying. For a detailed description of the macroalgae and seagrass sampled, see supplementary material.

Seawater was collected from the upper 0.5 m layer of the water column at each site for POM determination. Water samples were sieved ($106\text{ }\mu\text{m}$) to remove zooplankton, and filtered through pre-combusted ($4\text{ h} - 450\text{ }^{\circ}\text{C}$) glassfibre filters ($0.7\text{ }\mu\text{m}$ pore size; 47 mm \varnothing) using a vacuum pump. Intertidal surface sediment (uppermost 1 cm) was collected during low tide at each site (A1, A2, B and C) and stored at $-20\text{ }^{\circ}\text{C}$ until analyses (SOM) or extraction for MPB. MPB was extracted from sediment following the method of Liénart et al. (2017): a density gradient created by a solution of sodium polytungstate (2 g ml^{-1}) and prefiltered seawater from Langebaan Lagoon (filtered through $0.7\text{ }\mu\text{m}$ with a density of approx. 1 g ml^{-1}), was used to separate the MPB from the sediment by centrifugation. The MPB was then isolated in prefiltered seawater and filtered through pre-combusted ($4\text{ h} - 450\text{ }^{\circ}\text{C}$) glassfibre filters ($0.7\text{ }\mu\text{m}$ pore size; 47 mm \varnothing).

Filters of POM ($n = 4$ per site) and MPB ($n = 4$ per site), and aluminium cups containing SOM ($n = 5$ per site) and macrophytes ($n = 5$ per site) were oven dried at $60\text{ }^{\circ}\text{C}$ for 24 h and stored in a desiccator until analysis.

2.4. Body condition and sex determination of sandprawns

Total length was measured from the rostral tip to the end of the telson with a digital calliper and dry weight was determined for each sandprawn (oven dried at 60 °C for 48 h). The prawns were sexed, and specimens less than 30 mm that were difficult to sex were classified as unsexed juveniles. In zone C, 61% of the female sandprawns were ovigerous, for these the eggs were removed before weighing and statistical comparisons (t-tests) were made between ovigerous and non-ovigerous females with respect to body condition and isotope composition. Ovigerous females were not encountered at any of the other sites during sampling.

Length and body mass relationships were visualized (Béguet et al., 2011; Blanco-Martinez et al., 2020), however the differential sampling dates precluded statistical analysis to be performed. To assess body condition of adult sandprawns for use in correlative analyses with isotope composition, a weight:length (mg:mm) ratio was obtained for each prawn sampled on the same date (May, site A1, B and C).

2.5. Stable isotope analyses

All samples of sandprawns and potential food sources were weighed individually into tin cups for stable isotope (SI) and elemental composition analyses. Muscle tissue of individual sandprawns (total n = 107, per site: A1 (n = 26), A2 (n = 23), B (n = 31) and C (n = 29) were extracted from the prawns' abdomen and dried directly in the tin cups. Macrophytes were powdered using a ball mill, while POM and MPB were scraped off filters. Pre-dried SOM was analysed untreated (for nitrogen isotope analyses) and acid-treated (1 M HCl) to remove inorganic carbon (i.e. for carbon isotope analyses), before being oven dried again (60 °C for 48 h).

All samples were analysed at the Mass Spectrometry Laboratory, Center for Physical Sciences and Technology, Vilnius, Lithuania. The relative abundance of bulk stable carbon and nitrogen isotopes were measured simultaneously using a Flash EA 1112 Series Elemental Analyzer connected via a ConFlo III to a DeltaV Advantage Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany).

The isotope ratios are expressed in the delta notation by the following equation:

$$\delta(\text{‰}) = \left(\frac{R_{\text{sample}} - R_{\text{std}}}{R_{\text{std}}} \right) \times 1000$$

where R is the ratio between the heavy and light isotopes; $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$. The stable isotope ratio is defined as the deviation in ‰ from the international reference standards Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$. Samples were run in continuous flow with an overall analytical precision under 0.10‰ for $\delta^{13}\text{C}$ and 0.15‰ for $\delta^{15}\text{N}$. The $\delta^{13}\text{C}$ values of the sandprawns were corrected for C:N ratio (a proxy for lipid content) according to the equation in Post et al. (2007) since the average C:N was 3.8 ± 0.3 (the recommended threshold for normalisation is 3.5) for both juvenile and adult sandprawns at each site (this shifted the $\delta^{13}\text{C}$ values by $0.5 \pm 0.3\text{‰}$).

2.6. Data analyses and statistics

To assess background levels of $\delta^{15}\text{N}$, fresh seagrass leaves were compared between the sampling sites along the disturbance gradient, since seagrass assimilates nutrients over the long-term and reflects integrated conditions (isotope turnover rate is several weeks to months, Lepoint et al., 2004; Jones et al., 2018).

To test if mean $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and body condition differed among female, male and juvenile sandprawns, one-way ANOVA tests were performed for each site (A1, A2, B and C; A1 was sampled on the two different occasions, April vs May 2019) followed by pairwise Tukey's post-hoc test. A t-test was used to test for potential difference in the same

variables between ovigerous and non-ovigerous females at site C. No differences were found in the values of either $\delta^{15}\text{N}$ (t-test: $t_8 = -1.02$; $p = 0.33$) or $\delta^{13}\text{C}$ (t-test: $t_8 = 1.83$; $p = 0.11$) of female sandprawns sampled at the same site (A1) in April and May, hence isotope composition could be compared between the different sampling occasions and sites and used in later niche analyses. ANOVA was used to test if $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (one test for each isotope) differed among the sites in adult individuals. Normality and homogeneity of variance required for parametric testing were assessed using the Shapiro-Wilk and Levene's tests, respectively (α set at 0.05). When the distribution was normal within the groups, but the variance was not homogenous among the groups; Welch's F-test was used followed by Games-Howell post-hoc test.

For each site, the populations' isotope niches of adult sandprawns (too few individuals per site for juveniles) were calculated using the SIBER-package (Stable Isotopes Bayesian Ellipses in R) developed by Jackson et al. (2011). We used the Standard Ellipse Area (SEA), which provides a more robust measure of the isotope niche size (the core aspect of the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot space, comparable to SD in univariate cases) in a population. Differences in Standard Ellipse Area among sites was estimated using Bayesian inference (hereafter SEA_B, expressed in ‰²) as described by Jackson et al. (2011).

To explore potential drivers behind adult and juvenile sandprawn isotope composition along the disturbance gradient, Pearson's correlations were performed for their respective mean values and the site-specific POM, MPB and SOM $\delta^{15}\text{N}$ (or $\delta^{13}\text{C}$) as well as *Zostera* $\delta^{15}\text{N}$ (the latter reflecting a more integrated nitrogen isotope baseline although not expected as a dietary source for sandprawns). To assess the diet plasticity of the sandprawns among the four sampling sites in Langebaan lagoon, Mix Stable Isotope Analysis in R (MixSIAR-package; 'normal' run, a 'generalist' prior; Stock et al., 2018) models were performed separately for each site on dual stable isotope data, with female, male and juvenile prawns as fixed categorical factors. As a compromise between the number of sources to include in the model (number of tracers + 1) and a realistic diet for these deposit-feeders, the three most important food sources (Antonio and Richoux 2014) sampled at each site were included in the site-specific models; MPB, POM and SOM. Trophic enrichment factors (TEF) of 0.40 ± 0.18 for $\delta^{13}\text{C}$ and 2.30 ± 0.28 for $\delta^{15}\text{N}$ were used in the models, according to the recommendations of McCutchan et al. (2003) for ammonotelic organisms. Model output was evaluated using the Gelman-Rubin and Geweke convergence diagnostics as recommended in the package guidelines. To check the robustness of the model outputs, we also performed models with alternative TEF estimates since diet model results are strongly influenced by the choice of TEF factors (e.g. Bond and Diamond 2011); i) site and source-specific TEF values calculated according to Caut et al. (2009) equation for invertebrates (see Table S1), and ii) based on our own data as the mean $\delta^{15}\text{N}$ (or $\delta^{13}\text{C}$) prawn values (adults and juveniles separately) minus the mean $\delta^{15}\text{N}$ (or $\delta^{13}\text{C}$) for all sources for each site (Table S1). To test whether our empirical TEF-proxies (for each site, averaged across sources) were influenced by the site-specific SOM nitrogen content (%) (c.f. Karlson et al., 2015), a simple linear regression was performed.

Finally, to test whether variability in individual isotope composition in prawns (sampled on the same date to avoid potential confounding effects i.e. adult females in May from sites A1, B and C, see results 3.4) was positively or negatively related to the body condition, we used Pearson's product moment correlations (e.g. deteriorated body condition could be a consequence of diet assessed from isotope composition but also a driver behind altered isotope fractionation *sensu* Karlson et al., 2018). The effect of different isotope baselines among sites was first removed by calculating anomalies of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Euclidean Distances (ED) in the isotope space for the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to the centroid value of each site was calculated using the following equation (where *a* denotes anomalies):

$$ED = \sqrt{((\delta^{13}\text{C}a)^2 + (\delta^{15}\text{N}a)^2)}$$

All statistical analyses were performed using RStudio, version 3.6.1 (released 2019-07-05).

3. Results

3.1. Gradient in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and N content in food sources

Seagrass, *Zostera capensis*, had greater $\delta^{15}\text{N}$ values in zone A, compared to the less human impacted sites in zone B and C (11.5 vs 7.7‰, Fig. 2). Data from January 2018 support this gradient: *Z. capensis* $\delta^{15}\text{N}$ values at site A1 (12.9 ± 1.6‰) were also higher than in zone C (6.6 ± 2.1‰). Differences in epiphytic growth was visually observed on the sampled seagrass at the different sites; both sites in zone A had an epilithic algal matrix covering most of the seagrass blades, whereas epiphytes were practically absent at zone B and C (i.e. not enough material to perform isotope analyses of epiphytes). The $\delta^{15}\text{N}$ values of SOM and MPB were instead greatest at site A2, followed by site B (highest values for POM) and relatively low values at site A1 and C (Fig. 2). The sediment N% content was also highest at site A2 (0.021%) and lowest at site B (<0.01%) with intermediate values at A1 (0.010%) and C (0.017%). The ^{13}C values were more depleted for POM and more enriched for *Zostera* while intermediate for SOM and MPB over the gradient. POM and *Zostera* $\delta^{13}\text{C}$ values were significantly negatively correlated over the gradient (Pearson's $r = -0.98$, $p < 0.02$). In summer 2018, the *Zostera* $\delta^{13}\text{C}$ values were more enriched at site A1 compared to C; -9.3‰ and -13.1‰ respectively (±SD of 0.2). None of the three potential diet sources nor *Zostera* had a significant correlation between their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across the gradient in 2019 (r ranging -0.7 to 0.4, $p > 0.2$). Biplots of isotope composition in additional macrophytes and macroalgae (not included as food sources, but likely contributing to SOM isotope composition, see methods) are shown in Fig. S1.

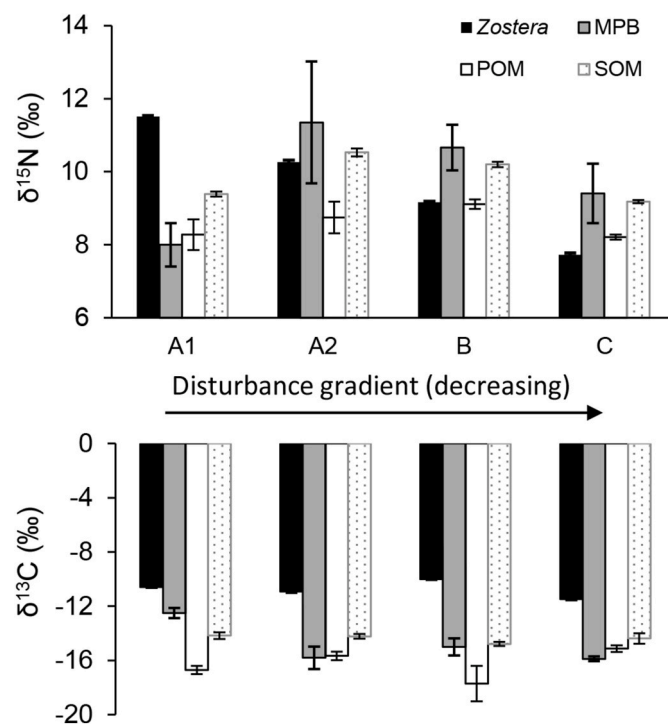


Fig. 2. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (±SE, $n = 4-6$ for each site) of fresh seagrass leaves (*Zostera capensis*), microphytobenthos on the sediment surface (MPB), particulate organic matter in the water (POM) and surface sediment (SOM) from the four sampling sites in Langebaan lagoon (A1 is the most disturbed site and C the most pristine).

3.2. Sandprawn isotope composition and niche size

Spatial differences in the $\delta^{15}\text{N}$ of adult sandprawns were significant (Welch's F-test: $F_{3, 39,1} = 45.52$; $p < 0.001$, Games-Howell post-hoc test: $p < 0.01$ for pairwise comparisons between all sites, except for A1 versus C where $p = 0.96$), with greatest $\delta^{15}\text{N}$ values recorded at site B, and lower values recorded at sites A1 and C (Fig. 3). Juveniles also showed similar spatial differences in $\delta^{15}\text{N}$; adult and juveniles mean $\delta^{15}\text{N}$ values correlated significantly with each other along the gradient (Pearson's correlation: $r = 0.96$, $p = 0.04$). Sandprawn $\delta^{15}\text{N}$ values correlated significantly with POM $\delta^{15}\text{N}$ (Pearson's correlation: $r = 0.99$ and $p < 0.02$ for adults, and $r = 0.98$ and $p < 0.03$ for juveniles) but not to any of the other food sources or to the *Zostera* $\delta^{15}\text{N}$ values.

The adult sandprawns also differed significantly in their $\delta^{13}\text{C}$ values among the sites (Welch's F-test: $F_{3, 36,2} = 10.38$; $p < 0.001$) with prawns at site C significantly more enriched in ^{13}C compared to conspecifics at sites A1, A2 and B (Games-Howell post-hoc test, $p < 0.01$ for all three comparisons, Fig. 3). Juvenile and adult sandprawns had a similar trend along the gradient ($r = 0.78$, $p > 0.2$). Prawn $\delta^{13}\text{C}$ values were not significantly correlated to any of the food sources' $\delta^{13}\text{C}$ values along the gradient ($p > 0.5$). In summer 2018, prawn isotope composition was generally more enriched in ^{13}C compared to 2019 but the trend among sites remained; at sites A1 and C $\delta^{13}\text{C}$ values were -12.7 ± 0.8 and -10.7 ± 0.1 ‰, respectively ($\delta^{15}\text{N}$; 12.4 ± 3.0 and 11.0 ± 3.4 ‰).

There were no significant differences in the isotope composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) between males and females at any of the sites (Table S2). However, juvenile and adult prawns differed significantly in their isotope composition within the sites (more depleted values for juveniles, Fig. 3, Table S2 but with similar spatial trend as for adults). At site C, there was no significant difference between ovigerous and non-

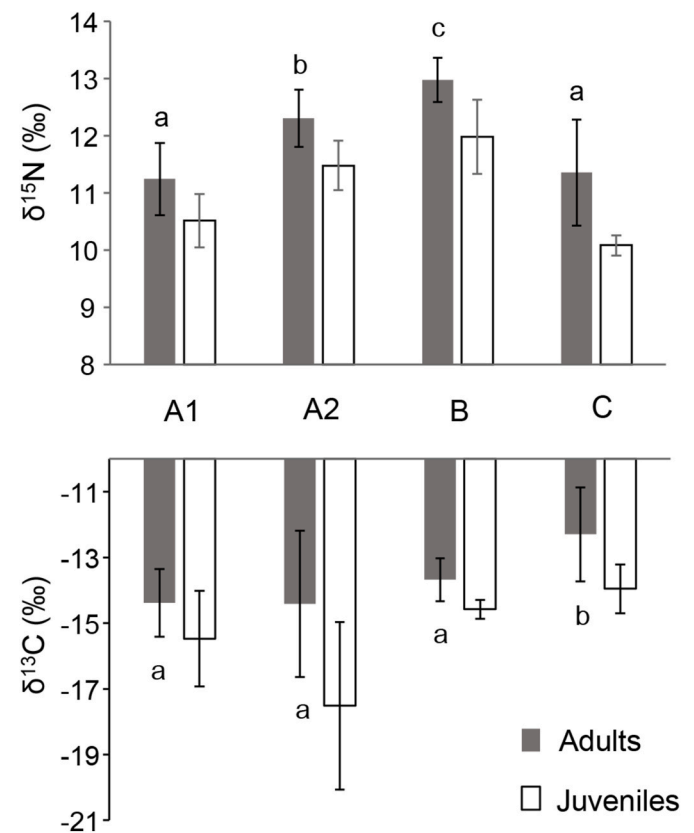


Fig. 3. Mean values (±SD) of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of adult ($n = 16-24$ for each site, grey bars) and juvenile ($n = 5-7$ for each site, white bars) sandprawns from site A1, A2, B and C in Langebaan lagoon. Common letters (adults only) denote no significant difference, this indicator is valid for both groups.

ovigerous females, even though ovigerous females were generally more enriched in ^{13}C ($\delta^{15}\text{N}$; $t_{11} = 0.07$, $p > 0.90$, $\delta^{13}\text{C}$; $t_{11} = 1.80$, $p < 0.07$).

The isotope niche of the adult sandprawns was distinctive between the four sites, with hardly any overlap of the Standard Ellipse Areas among sites (SEA, Fig. 4a). At site B, the Bayesian estimate standard Ellipse Area (SEA_B) was considerably smaller than at the other sites while site C had the largest SEA_B (Fig. 4b). The same separation among sites remained if juveniles ($n = 5\text{--}7$ per site) were included in the niche analyses (data not shown).

3.3. Differences in sandprawn diet along the gradient

The proportions of the main food sources of the sandprawns' diet (POM, MPB and SOM) varied among the four sites based on the MixSIAR models (Fig. 5, Table S3). Biplots of all prawns (females, males and juveniles) with TEF-corrected (McCutchan et al., 2003) food sources are shown in Fig. S2. The estimates of the different food sources was sensitive to different TEF values used in the diet models. Adult prawns at site A2 had the most varied diet showing no clear dominance for any of the three potential food sources, while SOM was the dominant food source of adult prawns at site A1 and C, and MPB the dominant food source at site B (Fig. 5a). Adult TEFs based on empirical data from this study was similar to the estimates by McCutchan et al. (2003), as shown in Table S1, hence there was no need to rerun the model for adults. By contrast, model output based on adjusted TEF according to Caut et al. (2009) indicated that MPB was the dominant food source of adult

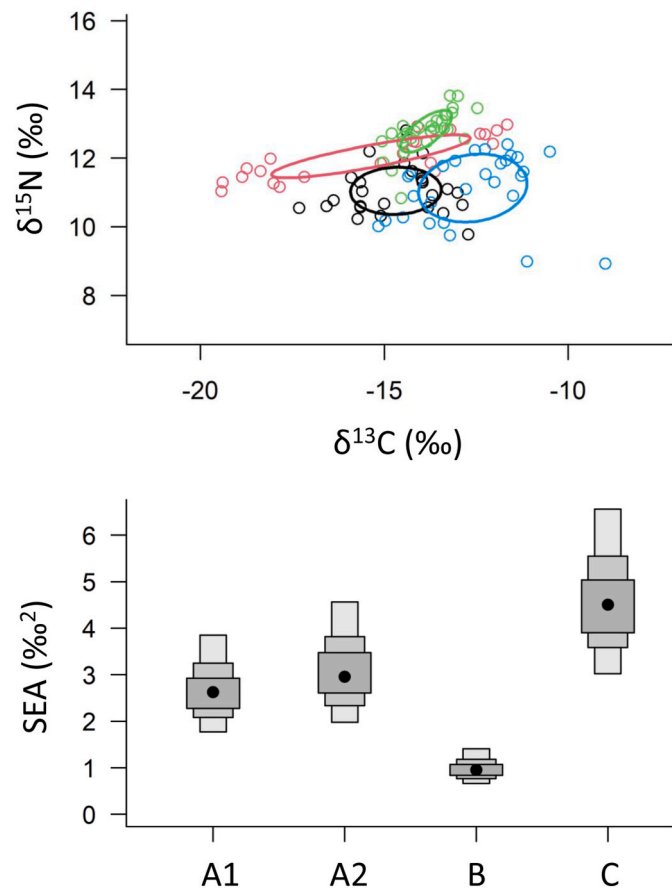


Fig. 4. (a) Stable isotope bi-plot illustrating the isotope niches of sandprawns from the four sites where solid lines enclose the Standard Ellipse Area (SEA) per site, and (b) density plots of Bayesian estimate Standard Ellipse Areas (SEA_B) from the same sites. Black dots indicate the modes of SEA_B and boxed areas Bayesian 50, 75 and 95% credible intervals. Colours in the upper figure represent sites: black = site A1, red = site A2, green=site B and blue = site C.

prawns at all sites except C, where SOM remained the dominant food source (Fig. 5c). Regarding juveniles, model output based on TEF from McCutchan et al. (2003) resulted in an overall larger contribution of POM in their diet compared to adults (Fig. 5b). Using Caut et al. (2009) estimates for juveniles resulted in generally decreasing POM and increasing MPB contributions (except at zone C, Fig. 5d). Finally, the models based on our empirical TEF estimates, meaning a lower TEF for ^{15}N in juveniles, resulted in a considerably smaller contribution of POM and a general increase of SOM to juveniles' diet compared to the other approaches (Fig. 5e).

3.4. Sandprawn body condition along the gradient

According to body-mass length relationships, sandprawns weight for a given length were smaller at site A2 compared to the other sites (Fig. 6), however the comparison was complicated by small sample size for some stations at different sampling times. Average length, body mass and body condition were all higher at A1 compared to A2 in April ($t_{12} = 2.56$, $p < 0.05$, $t_{12} = 3.21$, $p < 0.01$ and $t_{12} = 3.50$, $p < 0.01$, respectively).

Sandprawns at site A1 sampled in early May had lower values with regard to these physiological variables compared to the ones sampled in mid-April (body mass; $t_8 = 2.47$, $p < 0.04$; body condition: $t_8 = 2.67$, $p < 0.03$, body length; $t = 2.30$, $p = 0.050$). There were no significant differences in body condition for ovigerous compared to non-ovigerous females at site C for the small sample size ($t_{11} = 1.00$; $p = 0.34$). Hence, body condition between the sites could only be compared in prawns from the same sampling occasion (i.e. females sampled in May at site A1, B and C).

The correlation between the $\delta^{13}\text{Ca}$ and the body condition (in females sampled in May) was positive (Pearson's correlation: $r = 0.43$, $p < 0.03$) and similarly the correlation between $\delta^{13}\text{Ca}$ and body mass or length ($r = 0.44$, $p < 0.02$ in both cases). There was no significant correlation between the sandprawns' body condition and Euclidean distance (the univariate measure of isotopic composition, ED), nor with $\delta^{15}\text{Na}$ ($r < 0.3$, $p > 0.1$). If excluding the ovigerous females at site C, the significant positive correlation between body condition and $\delta^{13}\text{Ca}$ remained ($r =$ still 0.43) and $\delta^{15}\text{Na}$ was now also significantly correlated to body condition ($r = 0.42$, $p < 0.05$).

4. Discussion

This study demonstrates differences in isotope niche size and reproductive status of a key-species, the bioengineering sandprawn *Kraussillichirus kraussi*, among four sites in the Langebaan lagoon, South Africa. Overall, the large variability in the isotope niche size among sites (seven- and four-fold difference between site C and site A1 relative to site B), supported the results from diet partitioning models, with a smaller niche reflecting a more uniform diet and a larger niche reflecting a diet more evenly composed of the three potential food sources studied (sediment organic matter, microphytobenthos and particulate organic matter). On the individual level, greater diet diversity (deviating isotope values) was positively linked to body condition in adults, suggesting generalist feeding behavior is beneficial.

4.1. The effect of the nutrient gradient on isotope composition in biota

Our study focuses on the spatial variability in isotope composition of biota in a lagoon with little freshwater influence. The $\delta^{15}\text{N}$ signal of seagrass, *Zostera capensis*, indicates a nutrient gradient in the ecosystem. The higher $\delta^{15}\text{N}$ values found in zone A, which is in close proximity to Langebaan town and the shipping port in Saldanha Bay, likely reflects, at least to some extent, input of human-derived nutrients (Savage 2005), compared to the lower $\delta^{15}\text{N}$ seagrass values in zone C, the more protected area of the lagoon. Jones et al. (2018) showed that elevated values of $\delta^{15}\text{N}$ in *Zostera marina* were associated with anthropogenic

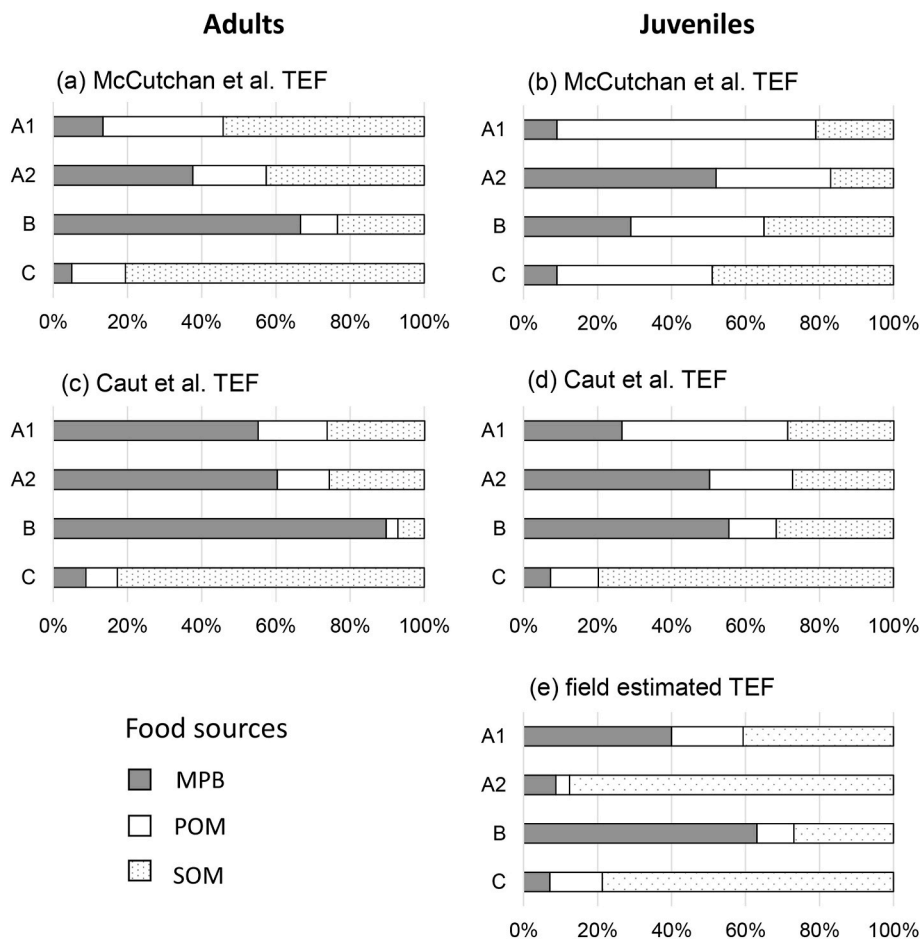


Fig. 5. Estimated food sources contribution to adult (a, c) and juvenile (b, d, e) sandprawns' diet according to the MixSIAR models run separately for each sampling site and with different trophic enrichment factors (TEFs) according to McCutchan et al. (2003) in (a, b) and according to Caut et al. (2009) in (c, d), and based on our empirical data in (e). TEF estimates for adults based on empirical data was nearly identical to the McCutchan estimate in (a) and hence is not shown. Complete Bayesian credible intervals for each source and category of sandprawns (females, males and juveniles) can be found in Table S3 (here female and male contributions are averaged for simplicity). MPB = microphytobenthos and POM = particulate organic matter in water, SOM = sedimentary organic matter.

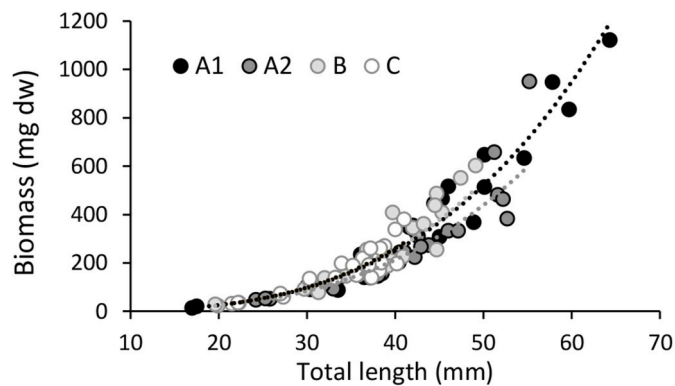


Fig. 6. Sandprawn length-weight relationship with power function trend line (dotted) for the four different sites (all sandprawns sampled including juveniles are shown here, each dot is one individual, see text for differences among sampling date and reproductive status).

influence in the UK, and this could be the same here. However we cannot discard the possibility that the higher $\delta^{15}\text{N}$ values in the northern parts of Langebaan Lagoon could be influenced by upwelling of nutrient-rich bottom water (also higher $\delta^{15}\text{N}$ value) from the Benguela current (Henry et al., 1977; Hill and McQuaid 2008). Tidal intrusion (via a narrow current in the main channel; 25 cm/s during flood and ebb tides) from the Atlantic Ocean likely transports some of the source anthropogenic and/or oceanic nutrients (Saldanha Bay/Atlantic Ocean) towards zone C (Shannon and Stander 1977), thus maintaining a declining nutrient gradient towards the southern end of the lagoon (zone C). In support of a

nutrient concentration gradient, an epilithic algal matrix covered most of the seagrass sampled in zone A, whereas this epiphytic growth was not found on seagrass in zone B and C during autumn 2019 and summer 2018, at least not in sufficient quantity for isotope analyses. Moreover, a stable nutrient gradient likely explains the decreasing trend of pelagic chlorophyll-*a* values from the mouth of the lagoon towards zone C (Qwabe 2019). In support of this, all diet models estimated a larger contribution of POM (planktonic organic matter) at site A1 and lowest at site C. The decreasing trend of $\delta^{15}\text{N}$ with distance from site A1 was however not reflected in $\delta^{15}\text{N}$ in pelagic microalgae (represented by POM in our study), in sedimentary organic matter (SOM), the microphytobenthic fraction of the sediment (MPB) nor the muscle tissues of sandprawns. Different isotope turnover times compared to *Z. capensis* can be one explanation. It is also worth pointing out that the highest sediment N content (%) was found at site A2 where the SOM and MPB had their highest $\delta^{15}\text{N}$, suggesting internal nutrient cycling in the sediment, and lowest at site B, the site where the least vegetation in proximity to the sampled sandflat was observed (pers obs, authors).

4.2. Sandprawn diet along the gradient

The muscle tissue of sandprawns, and other crustaceans, likely reflects the nutrient situation at week – month scales (e.g. Gorokhova and Hansson 1999), whereas *Zostera* integrates it over longer times (Leport et al., 2004). The significant correlation between prawn and POM $\delta^{15}\text{N}$, but not $\delta^{13}\text{C}$, further suggests a faster tissue turnover time for nitrogen than carbon in muscle tissue (Gorokhova and Hansson 1999). de Lecea et al. (2016) found that $\delta^{13}\text{C}$ in other decapods reflected the POM $\delta^{13}\text{C}$ from the previous season in a South African estuary. Nitrogen is the main limiting nutrient for marine invertebrates, especially deposit-feeders

(Tenore 1988). The higher TEF for $\delta^{15}\text{N}$ ($\Delta^{15}\text{N}$) observed with the lower N % in sediment (supplementary material) suggests a mismatch between dietary N availability and N requirements. Such a relationship between sediment N% and consumer $\Delta^{15}\text{N}$ has been observed for other marine invertebrates (Karlson et al., 2015) and can in addition to differential isotope turnover times, partly explain why sandprawn and *Zostera* $\delta^{15}\text{N}$ values are not changing in concert along the gradient. Individual body condition was however not negatively associated to $\delta^{15}\text{Na}$ (normalized for site-specific isotope baseline; c.f. Karlson et al., 2018), as would have been expected if compromised physiological status (from e.g. N imbalance) increased $\Delta^{15}\text{N}$ (c.f. Karlson et al., 2018). Instead, there was a positive correlation between individual body condition in adults and their respective $\delta^{13}\text{Ca}$ values (and positive with $\delta^{15}\text{Na}$ if excluding ovigerous females) which may rather indicate that dietary divergence among individuals in the population is beneficial for body condition. Interestingly, the smallest niche (site B) coincided with lowest sedimentary N content and a more uniform diet, dominated by MPB. The MPB might hence represent the most nutritious food source at this site. Antonio and Richoux (2014) used a combination of stable isotope and fatty acid analyses to demonstrate that the same species of sandprawn, in another estuary, feed mainly on phytoplankton, although when phytoplankton are scarce, they can rely on resuspended MPB. The MixSIAR models suggest a rather small overall contribution of POM to the diet of adult prawns in our study (ranging 12–20% depending on TEF values used, Fig. 5), although the contribution of POM to diet was largest at site A1 and lowest at zone C, similar to the pelagic chlorophyll-*a* gradient (mentioned above). It is likely that additional N, from human sources or marine inputs, benefit sandprawns (e.g. marine inputs discussed by Antonio and Richoux 2014) so that potential negative effects from disturbance (e.g. trampling) can be counteracted by greater food availability (e.g. from high POM production in zone A).

At site C, where sandprawns had the overall largest niche, SOM was the main food source according to diet models. SOM is a mix of detritus from multiple sources (i.e. settled organic matter from phytoplankton blooms, MPB, detritus of decaying macrophytes, smaller metazoans). Hence, the larger the contribution of the “SOM source” in diet models, the greater the potential for dietary diversity among individuals. Information on abundance of macrophytes and MPB could be used as priors in mixing models to improve results in future studies.

In our study, the contribution of POM was more important for juveniles than adults when using the estimates for TEF from McCutchan et al. (2003). When using our own lower estimates of TEF (e.g. 1.1 ± 0.7 for ^{15}N) in the diet partitioning models, there is no difference between juveniles and adults in POM contribution. It is well known that isotope mixing model outputs should be interpreted with caution since variation in TEF values used in the models influence the results strongly (e.g. Bond and Diamond 2011). Also, the prawns’ isotope composition is based on integrated values of their diet over the past weeks to months (e.g. Gorkhova and Hansson 1999) whereas the isotope composition of the POM and MPB used to run mixing models was a snapshot from the sampling time. All these factors (uncertain TEF estimates, different isotope turnover times for elements as well as food sources) contribute to the prawns not being inside the source polygon (as recommended in mixing model guidelines) at three of the four sites (see Fig. S2), despite the selected sources in our models being the most likely major components in prawns’ diet (Antonio and Richoux 2014).

4.3. Implications for environmental status

A comprehensive understanding of the impacts of point-source and non-point source nutrient inputs on estuarine trophodynamics requires both spatial and temporal sampling; however, the latter can be overcome by such differential growth patterns of biota as demonstrated here (c.f. van de Merwe et al., 2016). The nutrient gradient as indicated from $\delta^{15}\text{N}$ values in slow-growing seagrass (*Zostera*), was not detected in planktonic food sources, sediment nor sandprawns, likely due their

faster growth and hence isotope turnover time compared to *Zostera*. Additionally, variability in sandprawn $\Delta^{15}\text{N}$ among sites with different sedimentary N availability (see above) can also explain the absence of a nutrient gradient on non-*Zostera* food web components. The fact that sandprawns showed plasticity in their isotope niches among sites and that on the individual level, dietary divergence among adults was linked to better body condition, likely contributes to the numerical and distributional dominance of sandprawns in Langebaan lagoon (Nel and Branch 2013). A positive correlation between the mean body condition of sandprawns and the baseline nitrogen gradient, represented by *Zostera* $\delta^{15}\text{N}$, $r = 0.97$, $p < 0.05$ (females sampled in May) further indicates that higher nutrient loading is beneficial for sandprawns. Such correlations based on mean values over a few sites should naturally be interpreted with caution and future studies should aim for more thorough biometric data collection across Langebaan to assess population status in the lagoon and effects on reproductive status. High food availability may weaken the effect of density dependent growth and confer increased physiological resilience to sandprawns against disturbance by bait-collecting in zone A. Further studies designed to assess intra-specific competition (e.g. Blanco-Martinez et al., 2020) and to separate food availability from physical disturbance such as trampling are needed.

Previous studies have shown large-scale losses of seagrass cover in Langebaan lagoon over several decades (1960–2009), especially in zone A, where bait collection is allowed. It is likely that trampling and physical disturbance of the sediments are responsible for the decline of seagrass (Pillay et al., 2010) but not of sandprawns as no indications of deteriorated body condition at zone A was found in this study, rather the opposite). Siebert and Branch (2007) showed that sandprawns negatively affected transplanted plots of seagrass in Langebaan lagoon, and while the seagrass cover has decreased, sandprawn harvesting appears to be conducted sustainably, with no obvious effects on the sandprawn population (Nel and Branch 2014). In terms of environmental restoration, a reduction of sandprawn bait collection in zone A could protect existing seagrass beds (Pillay et al., 2010), but this is also critical for future restorative transplantation, to prevent sediment disturbance negatively impacting transplants.

To conclude, we found that variable isotope niches of sandprawns along the disturbance gradient likely reflects diet plasticity and that generalist feeding is beneficial for these sandprawns and contributes to their persistence.

Author statement

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2021.105541>.

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