Identifying potential pathways for turtle-derived nutrients cycling through beach ecosystems

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ABSTRACT: Resource fluxes between spatially separated ecosystems are ubiquitous and can strongly influence biotic communities and food web dynamics. These community effects should be most evident during resource pulses in oligotrophic systems, such as sandy beaches, which generally rely on allochthonous inputs. Here, we examined the role of sea turtles as vectors of nutrients from marine to coastal/terrestrial systems during the nesting season 'resource pulse', by exploring the utilization of turtle-derived nutrients by beach biota in South Africa. Nutrient uptake was tested by comparing the $\delta^{13}C$ and $\delta^{15}N$ isotopic values of representative taxa of 5 predicted supralittoral and intertidal pathways with that of turtle eggs. Turtle-derived nutrient uptake was confirmed only for supralittoral pathways (directly via ghost crabs and dune plants, indirectly via meiofauna), with limited evidence for intertidal pathways. The latter are expected to be secondary to the former given their spatial separation from nests and the exceptional rates of nutrient cycling through beaches; however, they may be more important on beaches where turtle densities are higher than in South Africa, and/or where hatching success is lower. Apart from turtle-derived nutrients that are exported to the ocean as hatchlings, the majority of nutrients from the turtle-egg resource pulse produce localized effects and are processed in the supralittoral. They are consumed by mobile vertebrate and invertebrate predators and scavengers, taken up by dune plants and decomposed by microbes and meiofauna. This highlights the ecological role of turtles as biotic transporters of nutrients and the value of beaches for ecosystem services.

KEY WORDS: Sea turtle eggs · Resource pulse · Sandy beach food webs · Nutrient pathways · Stable isotope analysis

INTRODUCTION

The flow of nutrients between both contiguous and spatially separated ecosystems is an important ecological process that underpins many food webs and ultimately, ecosystem functioning (Polis et al. 1997, Lundberg & Moberg 2003, Lastra et al. 2008, Bauer & Hoye 2014, McConkey & O'Farrill 2015, Doughty et al. 2016). The effects of nutrient-related processes are particularly pronounced when they take the form of resource pulses: short and intense episodes of increased resource availability (Yang et al. 2008), such as salmon migrations (Ben-David et al. 1998), sardine runs (Hutchings et al. 2010) and seabird guano (Erskine et al. 1998, Anderson & Polis 1999). These events characteristically alter food webs substantially at the individual (diet shifts), population (aggregative responses), community (changes in predator–prey relationships) and ecosystem levels (Yang et al. 2010). These effects should be most notable in nutrient-poor

systems, provided the biota has the means to access the nutrients. Thus a key question is: When a pulsed food source enters the system, do all components of the food web benefit directly, or are resources exploited only through some pathways and not others?

Resource subsidies provided by nutrient-flow processes are especially important for oligotrophic systems, such as sandy beaches. Beach ecosystems are defined as the contiguous foredunes/back beach (supralittoral), intertidal (littoral) and surf zone (sublittoral) habitats (McLachlan 1980) that jointly function as a single, geomorphic unit, i.e. the littoral active zone (Tinley 1985; Fig. 1). Beaches generally have low primary productivity, and their food webs are almost entirely supported by marine allochthonous subsidies, e.g. macrophyte wrack and carrion (Colombini & Chelazzi 2003, Dugan et al. 2003, McLachlan & Brown 2006). Beach food webs comprise 3 discrete components: a macroscopic food web (centred around the macrofauna), an interstitial food web (centred around meiofauna) and the microbial loop (centred around bacteria). These 3 food webs, combined with the continual flushing of seawater through the unconsolidated sediment, make beaches exceptional at nutrient recycling (McLachlan et al. 1985). Although the flow of nutrients from allochthonous sources to sandy beach food webs has been well studied for wrack deposits (e.g. Stenton-Dozey &

Griffiths 1983, Lastra et al. 2008, Dugan et al. 2011), little is known about the effects of turtle-derived nutrients on beach ecosystems.

Biotic transport of nutrients between marine and terrestrial ecosystems is a key ecological role provided by sea turtles (Bouchard & Bjorndal 2000). Female turtles accumulate nutrients on the feeding grounds to prepare for reproduction, migrate to their breeding grounds and deposit these nutrients in the form of eggs in the supralittoral. This creates a seasonal resource pulse for tropical and subtropical beaches that are inherently oligotrophic systems. Although most of these nutrients return to the marine environment as hatchlings (Bouchard & Bjorndal 2000), unhatched and depredated eggs, dead and predated hatchlings, as well as chorioallantoic fluid and egg shells remain in the beach ecosystem. These nutrients can be incorporated by dune plants (Bouchard & Bjorndal 2000, Hannan et al. 2007, Vander Zanden et al. 2012), beach insects (Madden et al. 2008), terrestrial insects (Maros et al. 2006) and opportunistic vertebrate predators (Engeman et al. 2003, Barton & Roth 2008, Mendonca et al. 2010). Apart from predation by ghost crabs (e.g. Hitchins et al. 2004, Barton & Roth 2008, De Wet 2012; Marco et al. 2015), the potential effect of these nutrient subsidies on intertidal sandy beach food webs has been overlooked.
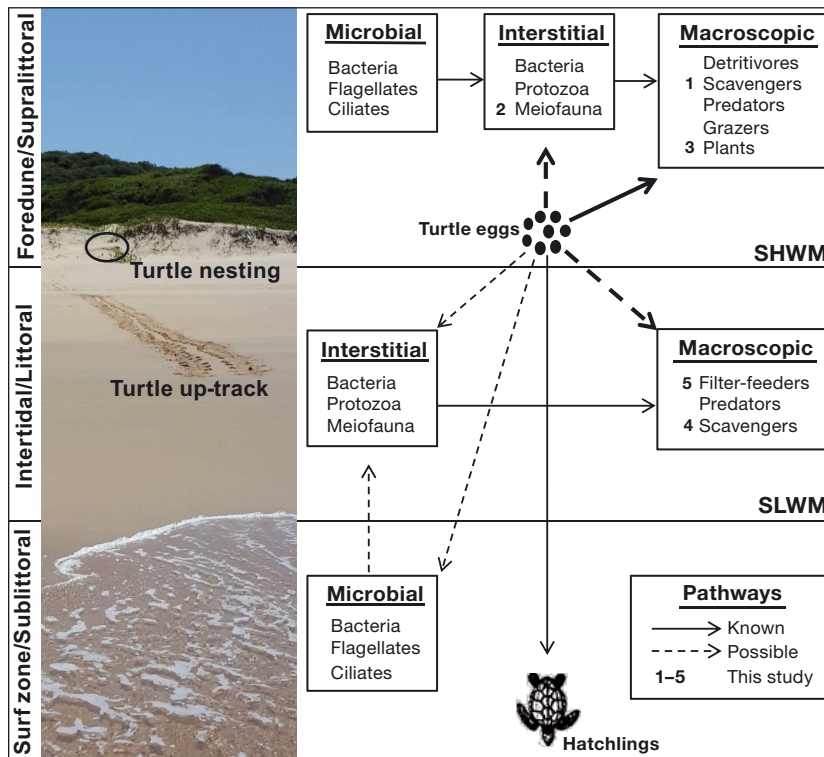

Fig. 1. Conceptual framework of the potential pathways that turtle-derived nutrients could follow through sandy shore food webs. Sandy shores comprise 3 connected coastal systems: the foredunes (supralittoral), intertidal (littoral), and surf zone (sublittoral), that jointly make up the littoral active zone. The zones are separated by the position of the spring high water mark (SHWM) and the spring low water mark (SLWM). Within the littoral active zone, there are 3 discrete food webs: macroscopic, interstitial, and the microbial loop. The boxes represent each food web per across-shore zone, with examples given of biota comprising each food web. Turtle eggs deposited at the dune–beach interface (within the supralittoral zone) thus have multiple potential pathways that the nutrients could follow, some of which are known (full arrows), and others not (dashed arrows). The predicted pathways tested in this study are numbered 1–5, and are indicated with bold-face arrows: 1 = high-shore scavengers; 2 = meiofauna; 3 = dune plants; 3 = low-shore scavengers; 5 = low-shore filter feeders

Energy flows through food webs and feeding relationships have increasingly been investigated using stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N; Peterson & Fry 1987, Vander Zanden & Rasmussen 1999, Bergamino et al. 2011). Marine systems are typically ^{15}N enriched relative to terrestrial food webs (Peterson 1999, Vander Zanden & Rasmussen 1999). This means that inputs of marine and terrestrial origin can be followed through trophic levels, which is especially useful in coastal ecosystems (Bergamino et al. 2011). For example, pathways of marine-derived nutrients to terrestrial ecosystems have been described for nutrient inputs via seabirds (Mizutani & Wada 1988, Erskine et al. 1998, Anderson & Polis 1999), sea lions (Farina et al. 2003) and sea turtles (Hannan et al. 2007, Vander Zanden et al. 2012). Given that turtle eggs have the highest δ^{15}N values of any known food source for consumers on sandy beaches (Hannan et al. 2007), and that stable isotope ratios of consumers have a fixed relationship with the isotope value of their diet (Vander Zanden & Rasmussen 1999), it should be possible to use this approach to trace turtle egg nutrient uptake through the beach food webs.

The aim of this study was to identify the potential (direct) pathways through which turtle-derived nutrients are assimilated in a beach (dune–intertidal–surf) ecosystem, using stable isotope analysis. We hypothesized that sea turtle eggs represent a pulsed resource subsidy influencing all 3 food webs, and are ultimately processed by both terrestrial (dunes) and marine (intertidal and surf zone) systems. We predicted 5 possible pathways by which turtle-derived nutrients (eggs) may be assimilated directly and tested these using the most dominant species per pathway for each across-shore zone. These include 3 pathways on the dune zone: (1) a scavenger path via ghost crabs *Ocypode ryderi*; (2) a grazer path via meiofauna (mainly nematodes); and (3) a terrestrial path via pioneer dune plant species (*Ipomoea pescaprae*; *Hydrophylax carnosa*). The other 2 pathways are through the intertidal zone: (4) a scavenger path via plough snails *Bullia natalensis* and (5) a filter-feeding path via mole crabs *Emerita austroafricana*, as mediated by surf zone particulate organic matter (Fig. 1). Because the study focussed on a pulsed nutrient source, we did not attempt to quantify the relative importance of turtle nutrients to each pathway, as this would be a transient solution that is highly dependent on time and space and could not be replicated. Instead, we aimed to determine the possible pathways through which turtle nutrients are utilized.

MATERIALS AND METHODS

Study site

The study took place on the north-eastern coast of South Africa in iSimangaliso Wetland Park, KwaZulu-Natal (Fig. 2a). iSimangaliso is a UNESCO World Heritage Site and a Ramsar Site, and comprises contiguous terrestrial and marine (Maputaland Marine Protected Area [MPA] and St Lucia MPA) reserves. The shoreline is predominantly made up of intermediate beaches, with some coarse-grained, steep reflective beaches, interspersed with mixed shores and rocky outcrops (Harris et al. 2011). The beaches form the southernmost nesting grounds of loggerhead *Caretta caretta* and leatherback *Dermochelys coriacea* sea turtles in the world (~27° S). The rookery is approximately 200 km long and supports nesting by 1000 loggerhead females and <100 leatherback females each year (Nel et al. 2013). The majority of nests are laid north of Sodwana, and particularly along 5 km of shore north of Bhanga Nek in the loggerhead nesting hotspot (Fig. 2b).

Sample collection

All sampling was undertaken with permission from the iSimangaliso Wetland Park Authority, Ezemvelo KwaZulu-Natal Wildlife and Department of Environmental Affairs: Oceans and Coasts (permit numbers: RES2013/10, RES2014/64, RES2015/69), and ethical clearance was granted by the Nelson Mandela Metropolitan University Animal Ethics Committee (REC-A13-SCI-ZOO-012). Samples were collected during the 2013/14 (hereafter referred to as 2013 in the text) and 2014/15 (referred to as 2014) sea turtle nesting seasons (which typically takes place from October to March, peaking in December).

Loggerhead eggs and hatchlings were collected to evaluate if there was variation in the isotopic values of turtle-derived nutrients. Sea turtle eggs were obtained from nesting adult females located during nightly patrols. Ten eggs were randomly selected at the time of oviposition (1 egg from 10 different nests, of the >5000 nests laid per annum). Seven dead hatchlings were collected as part of routine post-hatching nest excavations for loggerhead turtles. Eggs and hatchling samples were kept frozen until further processing. For comparison purposes, hatchlings and turtle egg shells were incorporated into the analyses but were not regarded as the main turtle-derived nutrients in this study. This is because hatch-
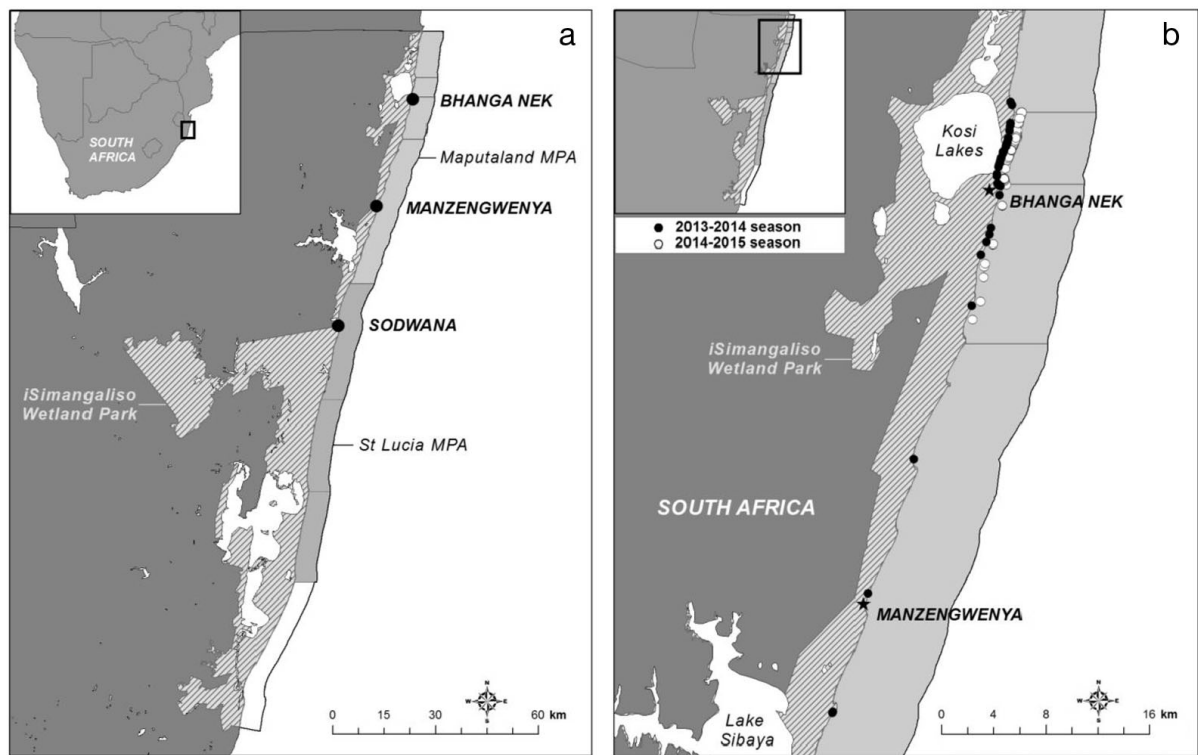
Fig. 2. Location of the study area indicating (a) the extent of iSimangaliso Wetland Park: contiguous terrestrial (hatched) and marine (light grey: Maputaland MPA; dark grey: St Lucia MPA; white: proposed expansion to the St Lucia MPA) reserves, which is largely the extent of the turtle rookery in South Africa. (b) A sample of loggerhead turtle *Caretta caretta* nests in the 2013/14 and 2014/15 seasons illustrates the nesting hotspot north of Bhanga Nek, which effectively gives beaches of high and low turtle nest density, north and south of Bhanga Nek, respectively. Sampling locations are marked with stars

lings hatch only at the end of the nesting season (and would not have been incorporated into the food webs at the time of macrofauna sampling). Further, egg shell was not expected to be the main component utilized by beach fauna given our observations of shell remains from predated nests and in post-hatching nest excavations.

Samples of each species/taxon were collected from 2 sites of different turtle nest densities: Bhanga Nek, with a high nest density of 105 nests km^{-1}, and Manzengwenya, with a low nest density of only 7 nests km^{-1} (Fig. 2b). Samples of all taxa were collected at both sites in the 2013 and 2014 turtle nesting season, with additional, opportunistic sampling of ghost crabs (n = 9) in winter (July) 2014. Sampling was done towards the end of the season, to maximize time for the turtle-derived nutrients to be incorporated into the consumers' body tissue. Ghost crabs *Ocypode ryderi* were caught with pitfall traps baited with sardine and were released after 2 legs were removed from each individual. Samples of mole crabs *Emerita austro-africana* and plough snails *Bullia natalensis* were collected using a 1 mm mesh sieve bag in the intertidal using standard beach sampling techniques (Schlacher

et al. 2008), or by hand from the saturation zone (low-shore). Nematodes were chosen for the meiofaunal grazer pathway because this was the most abundant taxon present and dominated all samples throughout the study. Nematodes were collected (within the experimental turtle nests at 30 cm depth) from the sediment samples obtained from a previous *in situ* experiment (Le Gouvello et al. 2017).

Dominant dune vegetation was sampled by removing 2 leaves from 10 individual plants from the front of the foredune (where turtles are likely to nest) of each of the following species: goat's foot *Ipomoea pes-caprae* and dune creeper *Hydrophylax carnosa*. Particulate organic matter (POM) was sampled during the 2014 season from both sampling sites to provide support for the filter feeding path via mole crabs. Approximately 5 l of water were collected from the surf zone (0.5 m depth) and poured through a 1 mm and a 45 µm sieve to eliminate larger fauna and flora from the particulate matter. Samples were then filtered through Whatman GF/C fibreglass filter paper (pre-combusted at 550°C for 12 h) of 1.2 µm pore size. All samples were preserved in 70% alcohol, except POM that was kept frozen, until further analysis.

Stable isotope analyses

Muscle tissue was used for the macrofauna samples, as it is considered an indicator of diet due to its slow turnover rate (Lorrain et al. 2002, Rubenstein & Hobson 2004). The muscular foot was used for the plough snails, and leg-muscle tissue was used for the ghost crabs and mole crabs. Meiofauna was analysed whole due to the impracticality of extracting muscle tissue in very small species. Nematodes were handpicked with a fine needle, rinsed in distilled water and placed in 1.5 ml sample vessels. To attain sufficient biomass for stable isotope analysis (0.4–0.6 mg dry mass), 50 to 200 individuals (per replicate of each major taxon) were pooled per sample (Moens et al. 2002, Nascimento et al. 2012). A sterile 6 mm disposable biopsy punch was used to take sea turtle hatchling skin samples in the region between the neck and the front flipper. Turtle eggs were thawed, and the yolk, albumen and shell were separated.

Lipid extraction is commonly used to correct the $\delta^{13}C$ values because synthesized lipids have lower $\delta^{13}C$ values and can mask the $\delta^{13}C$ value of a consumer's diet (Ingram et al. 2007). However, there are some concerns that lipid extraction can cause shifts in $\delta^{15}N$ values (Logan et al. 2008, Carpentier et al. 2015). Therefore, a subset of the faunal samples was treated (lipid-extracted), while the remaining samples were left untreated (original) to test the effect of chemical lipid correction on nitrogen isotope values.

Lipid extraction followed a modified method of Bligh & Dyer (1959). Samples that were subject to lipid extractions (all except plants and egg shells) were oven-dried at 60°C for 48 h, homogenized and immersed in 2:1 chloroform:ethanol solution for 50 min to remove free lipids. Samples were then oven-dried at 60°C for 2 h. A subset of plant and egg shell samples was acid-washed with 0.1% hydrochloric acid for 50 min to remove carbonates and dried for 2 h at 60°C.

All original and treated samples were rinsed with distilled water, oven-dried at 60°C for 24 h and ground to a fine powder using mortar and pestle. Protein aliquots of 0.3–0.5 mg and plant samples of 1 mg were weighed into pre-cleaned tin cups. Analyses of C and N isotope ratios followed the method described by Vander Zanden et al. (2012) and were undertaken at the Stable Isotope Analysis Laboratory of the Mammal Research Institute (Pretoria, South Africa). Samples were analysed by continuous-flow isotope ratio mass spectrometry using a Flash EA 1112 Series elemental analyser connected via an interface (Conflo III) to a Thermo Fisher Scientific Delta V Plus isotope ratio mass spectrometer. A calibrated laboratory standard (Merck Gel, $\delta^{13}C$ = −20.6‰ and $\delta^{15}N$ = 6.8‰) and blank samples were run after every 12 unknowns. Stable isotope ratios are expressed in delta (δ) notation, defined as parts per thousand (‰) deviation from a standard material:

$$\delta R ‰ = ([R_{sample} / R_{standard}] − 1) \times 1000 \qquad (1)$$

where R is the heavy-to-light isotope ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). The standard material is Vienna Pee Dee Belemnite (PDB) limestone for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$. The precision of the standard analyses was 0.13‰ for $\delta^{13}C$ and 0.14‰ for $\delta^{15}N$.

Statistical analyses

Differences in the $\delta^{13}C$ and $\delta^{15}N$ values from treated (lipid extracted and acid washed) and original samples were evaluated using paired t-tests. These tests could not be performed for sample sizes smaller than 3, in which case the original isotopic values were used (*O. ryderi* and *E. austroafricana* at the low nest density site). The incorporation of turtle-derived nutrients into sandy beach food webs was then tested in 2 ways. First the isotopic overlap between consumers and source signatures of turtle nutrients was quantified, taking into account the enrichment occurring during assimilation. Comparisons were made by testing within the range of commonly accepted discrimination factors: 3.4‰ for nitrogen and 1‰ for carbon (De Niro & Epstein 1978, Minagawa & Wada 1984). Second, the isotopic composition of consumers sampled on beaches of high and low turtle nest density were compared using t-tests.

We worked on the premise that if turtle-derived nutrients were being taken up through the predicted pathway, then the isotopic values of the representative taxon should deviate towards those of the turtle eggs on the high nest-density beaches compared to that measured at low nest-density beaches, taking trophic enrichment into account (+1‰ for $\delta^{13}C$ and +3.4‰ for $\delta^{15}N$; De Niro & Epstein 1978, Minagawa & Wada 1984). Since we focus on a pulsed resource, it is not entirely necessary to know the exact trophic discrimination factor, as the organisms in the study almost certainly would not equilibrate their tissues with the transient turtle-egg diet. The extent of this deviation will be dependent on the tissue turnover time relative to the pulsed nutrient input, and the relative contribution of non-turtle-derived nutrients in the diet. A pathway is confirmed if the stable isotope

ratios of tested biota from the high nest-density beach overlap with (if eggs are a large part or sole source of the diet) or are closer to (if eggs are only part of the diet) that of the turtle eggs, compared to the stable isotope ratios of the same species on the low nest-density beaches.

RESULTS

Treatment effect

Correcting for lipids was an important step, as the results showed that it changed the isotopic values of some organisms. For samples with no significant difference in either $\delta^{15}N$ or $\delta^{13}C$ values between original (non-lipid-extracted and acid-washed) or treated samples, values from original (non-treated) samples

were used for further analyses. However, for samples with a significant difference, the $\delta^{15}N$ values from original samples and $\delta^{13}C$ values from treated samples were used.

Isotope values of turtle nutrients

High variability was found in both carbon and nitrogen isotope ratios for each turtle-derived component (egg yolk, egg shell and hatchling). From samples collected in 2014, $\delta^{15}N$ and $\delta^{13}C$ values respectively ranged from 6.6 to 11.7‰ and from −20.7 to −16.2‰ for egg yolks, 6.0 to 9.2‰ and −15.8 to −10.8‰ for egg shells and 7.0 to 9.2‰ and −16.2 to −14.6‰ for hatchlings. Sample size of egg yolk (n = 1) in 2013 was much smaller compared to that in 2014 (see Table 1); however, the value measured in 2013 (8.4 ‰ for $\delta^{15}N$

Table 1. Carbon and nitrogen isotope ratios (mean ± SD) for loggerhead sea turtle *Caretta caretta* tissues and beach biota (numbered 1–5 by predicted pathway; see Fig. 1), as used in the analyses. Values presented are for the untreated samples (plain text), unless there are significant difference in in $\delta^{15}N$ and $\delta^{13}C$ values in the paired *t*-tests comparing original and treated (lipid-extracted or acid-washed) samples. In cases where there were significance differences (p < 0.05) between original and treated sample values, the mean value for the treated sample is given (**bold** text) and used in subsequent analyses. n: number of replicates; W: winter sampling; Bhanga Nek: high nest-density beach; Manzengwenya: low nest-density beach; POM: particulate organic matter

| Sample	Beach	n Original	Treated	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
2013 season					
1 *Ocypode ryderi*	Bhanga Nek	5	5	9.8 ± 0.47	−17.9 ± 0.21
	Manzengwenya	4	2	**8.7 ± 0.64**	−17.9 ± 1.06
2 Nematoda	Bhanga Nek	4	3	17.3 ± 1.87	−19.7 ± 0.56
4 *Bullia natalensis*	Bhanga Nek	5	5	**10.6 ± 0.15**	**−17.3 ± 0.10**
	Manzengwenya	5	5	**10.3 ± 0.23**	**−17.8 ± 0.23**
5 *Emerita austroafricana*	Bhanga Nek	2	0	7.7 ± 0.38	−17.1 ± 0.14
	Manzengwenya	5	3	7.5 ± 0.16	**−18.3 ± 0.07**
Shell	Bhanga Nek	5	5	8.2 ± 1.17	−16.8 ± 1.37
Yolk	Bhanga Nek	–	–	8.4	−18.17
2014 season					
1 *Ocypode ryderi*	Bhanga Nek	9	10	8.0 ± 0.99	−19.3 ± 1.23
	Manzengwenya	8	9	7.8 ± 1.38	−19.9 ± 1.26
	Bhanga Nek W	9	10	**8.6 ± 0.37**	**−18.5 ± 0.58**
	Manzengwenya W	10	9	8.8 ± 0.53	−18.3 ± 0.36
2 Nematoda	Bhanga Nek	6	6	15.3 ± 0.96	−23.8 ± 0.53
3 *Hydrophylax carnosa*	Bhanga Nek	10	10	**3.1 ± 0.73**	**−26.1 ± 0.42**
	Manzengwenya	10	10	**3.1 ± 1.03**	**−25.6 ± 0.80**
3 *Ipomoea pes-caprae*	Bhanga Nek	10	10	1.4 ± 2.71	−25.2 ± 0.54
	Manzengwenya	9	8	0.8 ± 1.76	−24.6 ± 0.65
4 *Bullia natalensis*	Bhanga Nek	10	10	10.2 ± 0.17	−17.6 ± 0.30
	Manzengwenya	9	10	10.1 ± 0.43	**−16.9 ± 0.25**
5 *Emerita austroafricana*	Bhanga Nek	10	10	8.0 ± 0.24	**−17.3 ± 0.25**
	Manzengwenya	10	10	7.7 ± 0.22	−18.1 ± 0.19
POM	Bhanga Nek	10	9	**−1.2 ± 0.67**	**−21.9 ± 0.56**
	Manzengwenya	10	8	**−2.2 ± 0.53**	**−24.4 ± 1.40**
Shell	Bhanga Nek	10	10	6.9 ± 1.28	−13.8 ± 1.41
Yolk	Bhanga Nek	10	9	8.6 ± 1.47	**−16.5 ± 1.10**
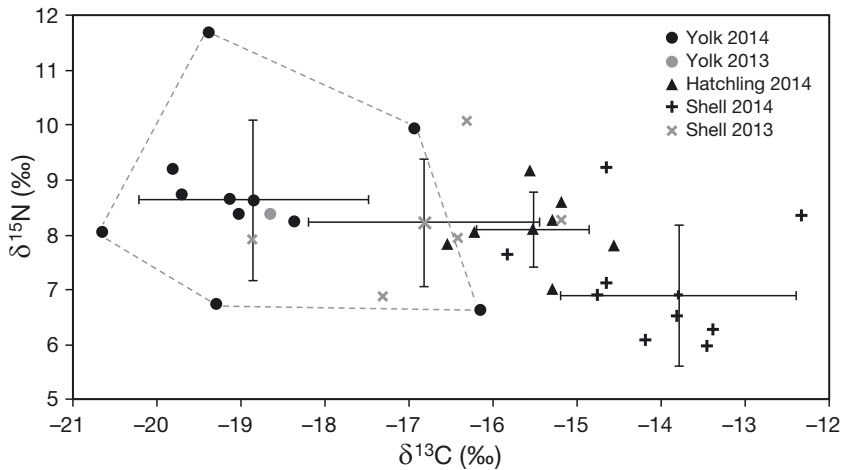
Fig. 3. Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios (‰) of the different loggerhead turtle *Caretta caretta* tissues (hatchling, egg yolk and egg shell) collected at Bhanga Nek during the 2013 and 2014 nesting seasons. Symbols with error bars represent means ± SD. Grey dashed line represents the boundary (range) of isotope values of turtle egg yolk

and −18.7‰ for δ^{13}C) was close to the mean of egg yolk values from the 2014 season (8.6‰ for δ^{15}N and −18.9‰ for δ^{13}C; lipid-corrected value = −16.5‰). In contrast, δ^{15}N and δ^{13}C values of egg shells ranged from 6.9 to 10.1‰ and from −18.9 to −15.2‰, respectively, representing a very different range compared to that measured in 2014. Overall, δ^{15}N values for the different turtle nutrient inputs were ranked: shell < hatchling < yolk (Fig. 3).

Isotope values of dune biota

Among the dune biota, *Ocypode ryderi* had highly variable carbon and nitrogen isotope values in both years and at both sites (Table 2, Fig. 4a,b). There was an overlap between the adjusted egg isotope ratios and *O. ryderi* values in the 2013 season. Additionally, stable isotope variability was lower in the high nest-density beach for *O. ryderi* (Tables 1 & 3). The δ^{13}C

Table 2. Mean range of carbon and nitrogen isotope ratios of dune, intertidal and surf zone biota across years and beaches. POM: particulate organic matter

Species/taxa	δ^{15}N (‰)	δ^{13}C (‰)
Ocypode ryderi	5.2 to 10.2	−22.0 to −16.5
Bullia natalensis	9.3 to 10.9	−18.0 to −16.4
Emerita austroafricana	7.3 to 8.2	−18.4 to −17.0
Nematoda	14.6 to 19.0	−20.5 to −19.2
Hydrophylax carnosa	1.9 to 6.0	−27.2 to −24.7
Ipomoea pes-caprae	−2.4 to 7.6	−25.8 to −23.7
POM	−2.9 to 0.2	−23.1 to −18.7

values of the dune plants are of little consequence in this analysis because the C is assimilated directly from the atmosphere, and the results simply indicate that they follow a C3 photosynthetic pathway. The δ^{15}N of the dune plants is suggestive of the N source of the plants. The comparison between high and low nest-density sites for each of the plant species yields δ^{15}N values that are indistinguishable within the analytical errors (δ^{15}N *Hydrophylax carnosa* = 3.1 ± 0.7‰ and 3.1 ± 1.0‰, *Ipomoea pes-caprae* = 1.4 ± 2.7‰ and 0.8 ± 1.8‰ for the high and low nest-density sites, respectively). One of the *I. pes-caprae* specimens from the high nest-density site has a δ^{15}N value that is substantially more positive than all the other plant samples (7.6‰) and needs closer scrutiny. Among the animals, nematodes showed the lowest δ^{13}C and the highest δ^{15}N values in both the 2013 and 2014 seasons. They had high variability in nitrogen values across years, while carbon isotope values had a clear separation between seasons with little variation (1.3‰; Table 2, Fig. 4e).

Isotope values of intertidal biota

The carbon and nitrogen isotope values of *Bullia natalensis* and *Emerita austroafricana* were clustered and overlapped between seasons, with minimal variability (Table 2, Fig. 5a–d). For *O. ryderi*, there was an overlap between the adjusted egg isotope ratios and *B. natalensis* values in both seasons, and stable isotope variability was lower in the high nest-density beach for *B. natalensis* (Tables 1 & 2). Nitrogen isotope ratios of *E. austroafricana* across beaches (both high and low nest-density) were much lower overall than that of the boundary of isotopic ratios of turtle egg yolks.

Nitrogen isotope ratios of POM across beaches (both high and low turtle nest density) were overall much lower than that of the boundary of isotope ratios of turtle egg yolks. In the 2014 season, both carbon and nitrogen values of POM were significantly different between Bhanga Nek (high nest density; higher carbon isotope values) and Manzengwenya (low nest density beach; Table 3). The carbon isotope ratios of POM overlapped with the isotope ratios of turtle egg yolks in the high nest-density beach (Fig. 5e).
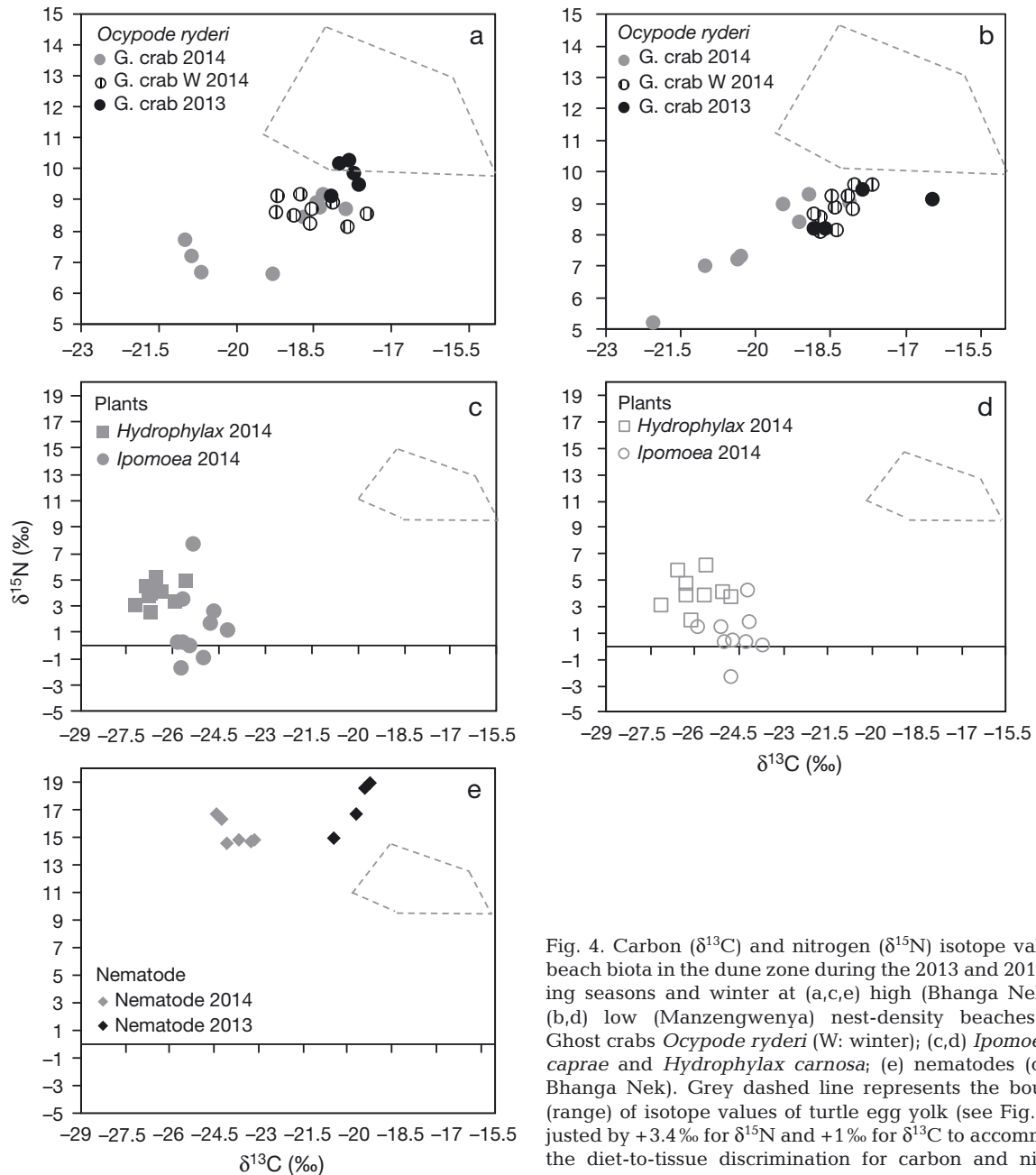
Fig. 4. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of beach biota in the dune zone during the 2013 and 2014 nesting seasons and winter at (a,c,e) high (Bhanga Nek) and (b,d) low (Manzengwenya) nest-density beaches. (a,b) Ghost crabs *Ocypode ryderi* (W: winter); (c,d) *Ipomoea pescaprae* and *Hydrophylax carnosa*; (e) nematodes (only at Bhanga Nek). Grey dashed line represents the boundary (range) of isotope values of turtle egg yolk (see Fig. 3) adjusted by +3.4‰ for $\delta^{15}N$ and +1‰ for $\delta^{13}C$ to accommodate the diet-to-tissue discrimination for carbon and nitrogen

DISCUSSION

Despite large amounts of nutrients being deposited into sandy beaches annually by sea turtles, very few studies have investigated if turtle nutrients are utilized by beach biota. We sought to identify pathways by which turtle-derived nutrients may be directly processed through sandy beach food webs, via both supralittoral and intertidal biota, by comparing carbon and nitrogen isotope values of consumers at beaches of high and low turtle nest densities. The

study showed that turtle-derived nutrients are taken up by plants and animals that have direct access to nests, and thus that it is primarily the supratidal food webs that benefit from this resource pulse, initially at a very localized scale.

Supralittoral pathways

Of the 3 direct pathways we predicted that the nutrients could follow through supralittoral food

Table 3. Results of t-tests comparing $\delta^{15}N$ and $\delta^{13}C$ values of species sampled at the high (Bhanga Nek) and low (Manzengwenya) nest-density beaches. **Bold** values are significant (p < 0.05). Numbers 1–5 with the species names refer to the pathway they represent (see Fig. 1). Meiofauna (pathway 2) are not included here because of the different sampling protocol (see 'Materials and methods' for details). POM: particulate organic matter

Sample	——— $\delta^{15}N$ ———			——— $\delta^{13}C$ ———		
	df	t	p	df	t	p
2013 season						
1 *Ocypode ryderi*	5.55	2.74	**0.035**	3.26	0.12	0.910
4 *Bullia natalensis*	6.83	2.29	0.057	7.97	−0.36	0.727
5 *Emerita austroafricana*	1.14	0.5	0.695	5.00	7.61	**0.001**
2014 season						
1 *Ocypode ryderi*	12.64	0.40	0.692	14.72	0.98	0.340
3 *Hydrophylax carnosa*	17.0	0.13	0.89	17	−1.36	0.192
3 *Ipomoea pes-caprae*	16.0	0.21	0.83	16.0	−2.15	**0.047**
4 *Bullia natalensis*	9.93	0.81	0.439	13.33	−1.67	0.117
5 *Emerita austroafricana*	17.96	2.92	**0.009**	17.86	1.92	0.071
POM	17.04	3.76	**0.002**	15.33	4.35	**0.001**

webs, only 2 seem likely based on their isotope values: via high-shore scavengers, such as *Ocypode ryderi*, and (potentially) via dune plants. These results were partly unexpected for 3 reasons. First, we anticipated a much stronger overlap between *O. ryderi* and turtle nutrient isotope ratios based on numerous observations of direct predation of turtle eggs and hatchlings by the crabs. Second, we similarly expected a stronger response from the dune plants because of past studies that have confirmed this pathway (Bouchard & Bjorndal 2000, Hannan et al. 2007, Vander Zanden et al. 2012). Third, greater isotopic overlap was expected between the meiofauna and turtle eggs because *in situ* experiments demonstrated a strong response to turtle-egg nutrients by nematodes: their abundance increased by orders of magnitude in the presence of eggs (Le Gouvello et al. 2017).

O. ryderi isotope ratios range broadly at both sampling sites, and outside of the turtle nesting season (winter). *O. ryderi* display a remarkable trophic plasticity, occupying several trophic levels as omnivores. They are sediment sorters (feeding on psammophyllic microalgae and meiofauna), scavengers (of any beach-cast carrion) and predators of both invertebrate (multiple macrofauna species) and vertebrate prey (turtle eggs and hatchlings; Vinagre et al. 2007, Barton & Roth 2008, Morrow et al. 2014; for a review, see Lucrezi & Schlacher 2014). Thus, although *O. ryderi* reportedly switch to a turtle-derived diet during turtle nesting seasons (Barton & Roth 2008), they likely do not feed exclusively on turtle nutrients

(eggs and/or hatchlings) during this time. Additionally, nitrogen enrichment is not constant but is rather species-specific and narrows with increasing dietary $\delta^{15}N$ (Hussey et al. 2014). For example, $\delta^{15}N$ enrichment has been shown to be lower (<2‰) for omnivorous consumers than the theoretical enrichment factor of 3–4‰ (e.g. Cabana & Rasmussen 1994, Marguillier et al. 1997, McCutchan et al. 2003, Caut et al. 2008, 2009). Consequently, the enrichment factor we used for nitrogen might be an overestimate, which in turn will underestimate the overlap between source and consumer. Therefore, the omnivorous diet of *O. ryderi*, together with the likely inflated isotope trophic discrimination for this species, could account for the limited direct isotopic overlap between *O. ryderi* and turtle eggs.

The nitrogen isotope values of the 2 plant species generally accord with those reported for other nitrogen-fixing plants (Virginia & Delwiche 1982, Heaton 1987). These plants acquire their nitrogen from the soil atmosphere, as a result of symbiotic associations with nitrogen-fixing bacteria (such as in legumes) and free-living cyanobacteria (blue-green algae) (Peterson & Fry 1987, Yamamuro 1999). This is not surprising, as typical dune pioneer species inhabit dynamic, nutrient-poor sand dunes. We hypothesize that uptake of egg nutrients is highly localized, where if a turtle nests in vegetation, then only the surrounding plant will access the nutrients. Certainly we have excavated hatched nests to find small new roots growing into the egg chamber and surrounding unhatched, depredated eggs. Given this likely localized effect, and that loggerheads generally nest at the dune base rather than in the vegetation, we may have sampled plants with limited or even no access to the egg-derived nutrients. The $\delta^{15}N$ value of one of the *Ipomoea pes-caprae* specimens from the high-density site was 7.6‰, which is exceptionally positive relative to the other plant samples, and could suggest potential uptake of turtle-derived nutrients. Such a high $\delta^{15}N$ value would normally reflect the $\delta^{15}N$ value of the soil organic matter, and would be associated with higher soil organic content than is found in dunes (Craine et al. 2015). A soil organic content with a high $\delta^{15}N$ value is atypical of dune sand, and the nitrogen source may be presumed to be derived from the turtle eggs.

The nematodes used in this study were sampled from an independent experiment that demonstrated
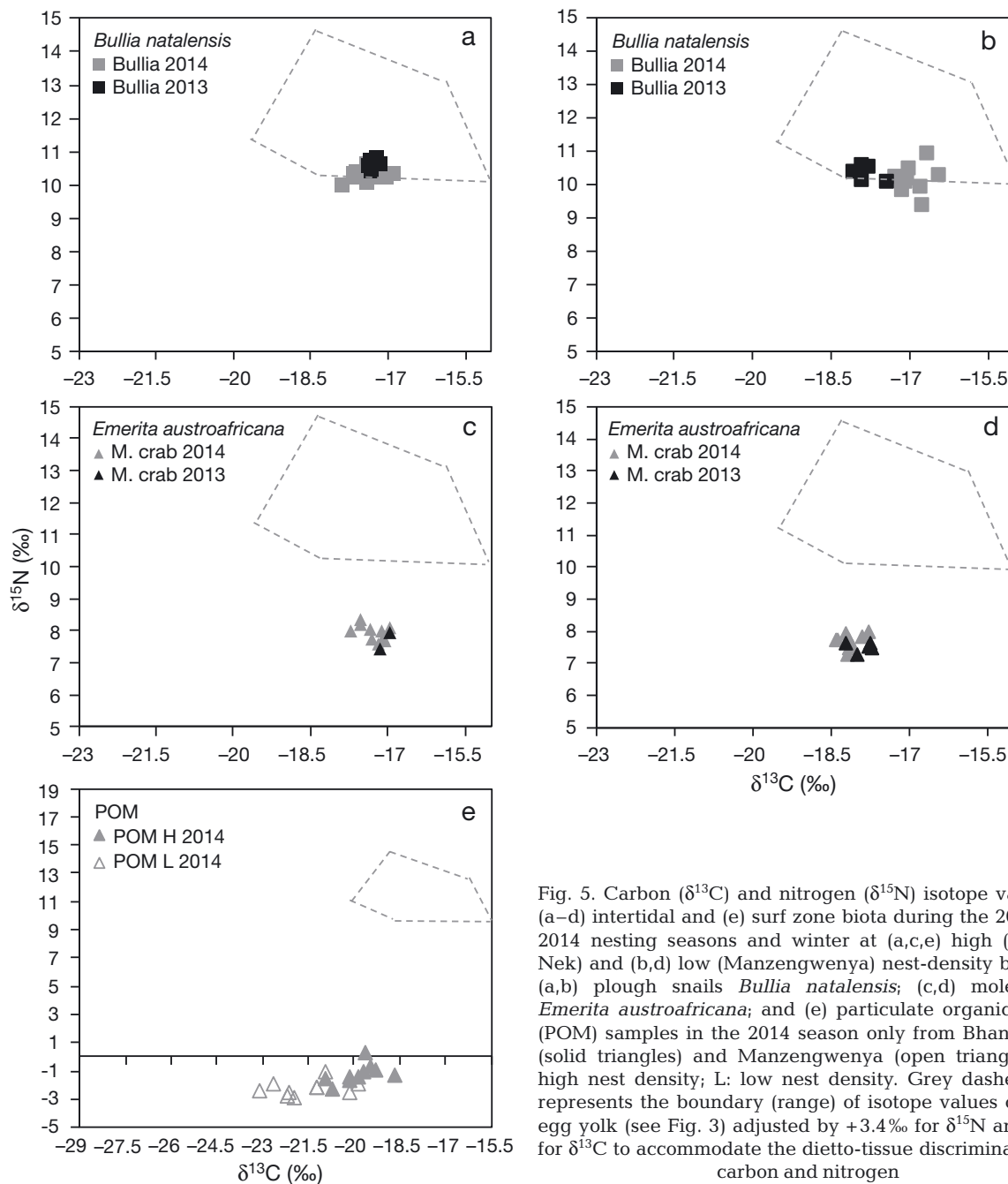
Fig. 5. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of (a–d) intertidal and (e) surf zone biota during the 2013 and 2014 nesting seasons and winter at (a,c,e) high (Bhanga Nek) and (b,d) low (Manzengwenya) nest-density beaches. (a,b) plough snails *Bullia natalensis*; (c,d) mole crabs *Emerita austroafricana*; and (e) particulate organic matter (POM) samples in the 2014 season only from Bhanga Nek (solid triangles) and Manzengwenya (open triangles); H: high nest density; L: low nest density. Grey dashed lines represents the boundary (range) of isotope values of turtle egg yolk (see Fig. 3) adjusted by +3.4‰ for $\delta^{15}N$ and +1‰ for $\delta^{13}C$ to accommodate the dietto-tissue discrimination for carbon and nitrogen

an increased in nematode abundance by orders of magnitude in the presence of turtle eggs (Le Gou-vello et al. 2017). This suggests that these meiofauna assimilated turtle-derived nutrients either directly or indirectly. The carbon isotope values of nematodes that we found suggest that this taxon does not respond to turtle-egg nutrients directly, but rather to an intermediate trophic level, such as bacteria and other microfauna that themselves utilize the egg nutrients directly. Further, their nitrogen isotope

values were particularly high, which may similarly indicate the presence of an intermediate trophic link(s) between nematodes and turtle eggs. However, the high $\delta^{15}N$ values recorded here are more likely an artefact of our methodology. Rose Bengal dye, which was added to nematode samples to assist in identification and counting of the animals, might have altered nematode isotope values, as demonstrated by De Lecea et al. (2011) for zoo-plankton. We also note that the nitrogen isotope val-

ues of nematodes had high variability, which may suggest that several feeding guilds occurred in one sample (since samples were pooled to get enough material for stable isotope analysis). Taking into account evidence from our results and those of another study (Le Gouvello et al. 2017), it seems that egg nutrients may be utilized indirectly by meiofauna (nematodes), via microbes that utilize the nutrients directly.

Intertidal pathways

Even though turtle eggs are deposited in the supra-littoral, there are 2 plausible mechanisms by which turtle-egg nutrients could be made available to intertidal macrofauna. First, eggs are occasionally eroded out of the dunes by wind or waves and roll down the shore during large storms (pers. obs.), or second, the nutrients could leach through the intertidal via the groundwater as POM. Although these mechanisms are possible, we expected the intertidal pathways to be secondary to the supratidal pathways on the basis of spatial proximity and likelihood of interaction. It was thus unexpected to find that the isotope values of *Bullia natalensis* overlapped most with that of the turtle eggs. Although it is indeed possible that *B. natalensis* are assimilating turtle-derived nutrients as POM or even eroded eggs (Brown 1971, 1982, Stenton-Dozey & Brown 1988), it seems more likely that they are feeding on organisms that have an isotopic range similar to that of turtle eggs (e.g. fish carrion, jellyfish). This is because isotopic overlap is approximately equal at beaches of both high and low nest density; if it was truly a response to turtle eggs, the effect should be stronger on the high nest density beaches.

Emerita austroafricana are fossorial feeders that assimilate phytoplankton and POM in the swash. There was no isotopic overlap between either *E. austroafricana* or POM and turtle eggs. However, there was significant difference in *E. austroafricana* $\delta^{13}C$ values in 2013, and in $\delta^{15}N$ in 2014 between the 2 sampling sites. Interestingly, both $\delta^{13}C$ and $\delta^{15}N$ isotope values of POM were also significantly different between beaches, with overlap in $\delta^{13}C$ between POM and turtle eggs at the high nest density beaches only. This might potentially suggest a turtle-nutrient effect, with POM isotope values being diluted and thus less easily identifiable in the consumer isotope values. Given the inconsistency between years, it is difficult to confirm whether this pathway is indeed valid or not.

Recommendations for future work

We have 2 key recommendations for future studies looking to track turtle-egg nutrients through beach food webs. First, it would be beneficial to have an independent, parallel experiment to quantify species-specific trophic enrichment factors to better estimate the isotopic overlap between species and turtle eggs. Second, it was difficult in some cases to determine whether the shift in isotope values between beaches was due to turtle-derived nutrients or to other potentially available food sources. Consequently, we recommend applying isotope mixing models by sampling all potential food sources, not only turtle eggs, to obtain the relative contribution of the different food sources in the diet of each consumer.

We also recommend study sites with high turtle abundances (and nest densities) for future comparative work. The loggerhead and leatherback populations in South Africa are marginal, located at the edge of both species' distributions, and are considered small relative to other populations (Wallace et al. 2011). At more than 200 km long, the rookery is also very large. Here, predation rates are low, and hatching and emergence success rates are among the highest in the world (Nel et al. 2013). Consequently, the quantity of turtle-derived nutrients remaining in this beach system is likely among the lowest globally, and yet we were still able to detect a response through some of the predicted pathways. The extreme comparison to our study site would be tropical beaches that support arribadas of olive ridley turtles, where more than 180 000 nests are deposited annually (Shanker et al. 2004). We predict that in these systems, such large amounts of nutrients would have a much more pronounced effect on local sandy beach biota, possibly to a much greater extent for intertidal biota than we were able to demonstrate, and that the pathways generally may be much easier to detect. Additional sampling of plant roots, chorio-allantoic fluid (during oviposition) and sediment organic matter will be helpful in identifying pathways for future work. Stable isotope analyses of nematodes should also investigate the effects of Rose Bengal dye on isotope values of different species.

Conclusions

Combining our results with those of other studies, we can draw the following conclusions about how turtle-derived nutrients are processed through sandy beach ecosystems. The majority of nutrients depo-

sited by turtles are eggs that hatch to produce viable hatchlings that disperse via ocean currents, and thus net nutrient transport is back to the marine environment (e.g. Bouchard & Bjorndal 2000). However, the remaining deposited nutrients are either consumed by mobile terrestrial or high-shore predators (vertebrates and invertebrates, opportunists and residents; e.g. Engeman et al. 2003, Barton & Roth 2008, Mendonca et al. 2010), taken up by foredune plants (Hannan et al. 2007, Vander Zanden et al. 2012) or are decomposed *in situ* by microbes and meiofauna, particularly nematodes (Le Gouvello et al. 2017). Pathways through the intertidal seem secondary to those in the supralittoral, likely due to their spatial separation from the nests, and because beaches are inherently highly efficient at nutrient cycling (McLachlan et al. 1985, McLachlan & Brown 2006, Dugan et al. 2011). However, intertidal pathways may be more important on beaches with higher turtle abundances and/or lower hatching and emergence success rates, which may result in more nutrients being released into the beach system. This in turn may make dissolved organic matter and POM more likely to leach through the groundwater and to be more readily available to intertidal fauna. In short, as is the case for seabird guano (Caut et al. 2012), the turtle-egg resource pulse appears to have highly localized effects on beach food webs, with the majority of nutrients that are not incorporated into viable hatchlings being exported to the supralittoral/terrestrial environment.

This study provides the first detailed information on turtle-derived nutrient utilization through sandy beach food webs (particularly the intertidal), using a carbon and nitrogen stable isotope approach. It is also the only study to our knowledge that considers this resource pulse in the context of sandy beaches as ecosystems. The ecological process that links sea turtles as biotic transporters of nutrients to their oligotrophic nesting beaches that are so efficient at nutrient recycling highlights both the value of migratory species and the value of beaches in providing key ecosystem services at the land–sea interface. This in turn has implications for the dynamics of sandy beach food webs because turtle nutrients will also benefit higher consumers (i.e. birds, mongooses) that would feed on consumers of turtle-derived nutrients, such as ghost crabs. In nutrient-poor tropical/subtropical sandy beaches that rely solely on allochthonous inputs, sea turtles and sea turtle nutrients thus have important ecological roles and boost ecosystem functioning. Yet there is still much to learn and to test, and we encourage other turtle ecologists to include the intertidal as well as the supralittoral when undertaking similar studies.

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