

# **The effects of turtle-introduced nutrients on beach ecosystems**

By

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**Declaration**

In accordance with Rule G4.6.3, I hereby declare that the above-mentioned dissertation is my own work and that it has not previously been submitted for assessment to another university or for other qualifications.

**Signature:** .....

**Date:** .....

## Abstract

Resource subsidies are flows of nutrients from one ecosystem to another. Sandy beach ecosystems are at the interface between land and sea and thus receive nutrients from both land/seascapes. The seasonal nesting of sea turtles introduces large inputs of eggs, and so nutrients, onto sandy beach ecosystems, but little is known about the effects of these spatially and temporal variable nutrient input pulses on the dynamics of consumers in the recipient system. In this study, I examined the ecological role of sea turtles as vectors of nutrients that introduce large amounts of nutrients (in the form of eggs) from distant foraging grounds into nutrient-poor beach ecosystems. Although some of the nutrients return to the sea in the form of hatchlings, nutrients from unhatched and depredated eggs, dead and predated hatchlings, as well as chorioallantoic fluid and egg shells remain on the beach and presumably enter sandy beach food webs.

I hypothesized that turtle nutrients significantly increase the availability of nutrients to sandy beach ecosystems and that those nutrients are incorporated by both terrestrial and marine food webs. These hypotheses were tested by comparing isotopic signatures of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of consumers on beaches with high and low turtle nest densities. The response of meiofauna to the decomposition of turtle eggs was also investigated. I predicted that meiofaunal abundance is positively affected by turtle nutrients and that higher meiofaunal abundances will be obtained in decomposing, depredated nests. I tested this hypothesis by comparing meiofaunal abundance in naturally predated nests to densities away from turtle nests (as a control). An *in situ* experiment that mimics conditions of naturally predated sea turtle nest, was set up to test meiofaunal community responses to turtle nutrients over time.

The results indicate that of the five potential nutrient pathways tested, ghost crabs appear to consume egg nutrients in measurable quantities, altering their diet and feeding behaviour according to food availability. The study also showed that there was a strong, but short-lived positive response of meiofauna to the introduction of nutrients, with increased abundance of all taxa in predated nests and experimental treatments. This response was particularly strong for nematodes which peaked in abundance after seven days. I conclude that turtle-derived nutrients represent a pulsed resource subsidy that makes significant contribution to the energy budget of sandy beach/dune ecosystems.

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**Chapter 1: General Introduction: Nutrient inputs into sandy beach ecosystems - a review**

## **Introduction**

Flows of nutrients between spatially separated ecosystems are ubiquitous and can strongly influence biological communities and food web dynamics (Polis et al., 1997; Lastra et al., 2008). Nutrient subsidies, when occurring as discrete events can produce resource pulses (Yang et al., 2008). These, resource pulses are especially important in nutrient poor systems such as sandy shores where biotic communities rely almost entirely on nutrient subsidies that have originated from another habitat (McLachlan and Brown, 2006). Despite the frequent occurrence of resource pulses in many ecosystems, few studies have investigated how these pulses affect ecological processes of the recipient ecosystems (Yang et al., 2004).

## **Ecosystem functions of coastal habitats and sandy beaches**

Coastal ecosystems make an invaluable contribution to human livelihoods due to the processes and functions they perform, and the resources they contain (Schlacher et al., 2008). This resource provisioning is disproportionately greater on the coast with strong evidence that the narrow coastal strip produces goods and services that far exceed those from terrestrial or other marine systems (Costanza et al., 1997). Furthermore, the benefits derived from coastal systems extent into both the terrestrial and marine realms as they act as the interface between land and sea (Barbier et al., 2011). Ironically, of the coastal ecosystems, sandy beaches are frequently overlooked (Dugan et al., 2010), and yet are the most widely distributed intertidal habitat of the world's coastlines (Spilmont et al., 2005; Schoeman et al., 2009), and the most valuable per unit area (Costanza et al., 2006).

Situated at the interface between land and sea, sandy shores are highly sought after by human populations and are consequently considered to be among the most threatened ecosystems, globally (Schlacher et al., 2008). Pressures on sandy beach ecosystems are caused by the cumulative/combined effects of population growth and global climate change which create a range of threats (Schlacher et al., 2008; Defeo et al., 2009; Harris et al., 2014, 2015). Anthropogenic threats include: coastal development, recreational activities, resource exploitation, and pollution (Schlacher et al., 2008; Harris



et al., 2015). Climate change also poses a threat to beaches through coastal squeeze - that traps the beach between coastal development (infrastructures) on the landward side and sea level rise from the marine side – and increased extreme weather events (storm surges) that accelerates erosion (Schlacher et al., 2006, 2007, 2008; Dugan et al., 2010).

Short (1999) defined a beach as “the intertidal zone between lowest and highest water marks obtained during spring tides, the swept prism, undergoing periodical (tidal) inundation by marine water” (Figure 1.1). In the context of this study, beach ecosystems are defined as the coastal dunes, the intertidal area and the surf zone (McLachlan, 1980a). Sandy shores thus consist of three contiguous entities functioning as a single, connected unit, collectively referred to as the littoral active zone (Tinley, 1985).



**Figure 1.1:** Illustration of the different zones of a sandy beach, indicating the relative positions and names of each zone. Figure modified after Harris (2012).

Sandy beaches provide habitats for a wealth of organisms, some buried beneath the sand surface (Harris et al., 2014), but critical in providing ecosystem goods and services (McLachlan & Erasmus, 1983; Schlacher et al., 2008). These ecosystem goods and services include harvestable resources, production and processing of organic matter, flood protection, nursery area for juvenile fishes and human recreation (Defeo et al., 2009; Schlacher et al., 2008; Barbier et al., 2011; Harris et al., 2013). In particular,

sandy beach ecosystems filter and purify large volumes of water (McLachlan 1979; McLachlan et al., 1985; McLachlan, 1989) and thus are responsible for the breakdown of organic matter and pollutants, and nutrient mineralization and recycling (Rocha, 2008; Coupland et al., 2007; Dugan et al., 2011). These are considered to be the most important ecological functions of sandy beach ecosystems (McLachlan, 1981a). These processes are enabled by the porous sand filtering sea water, and the specialized biota that mineralize organic matter and recycle nutrients that in turn are available for primary production which is the base of marine food webs (Schlacher et al., 2008). Despite the critical role of these services, very little is known about the mechanisms driving some of these processes.

One general feature of sandy beach ecosystems though is that they are characterized by low primary productivity because the dynamic nature of the substrate prevents the establishment of macrophytes (Botton & Loveland, 2011; McLachlan & Brown, 2006). There are exceptionally productive beaches though with high density accumulation of surf diatoms which develop under high energy conditions with substantial nutrient inflows from aquifers (Campbell, 1996). Beach food webs are therefore almost entirely supported by and reliant on marine allochthonous subsidies (Colombini & Chelazzi, 2003; Dugan et al., 2003; McLachlan & Brown, 2006) including surf phytoplankton, wrack (stranded algae and seagrass), and carrion (McLachlan & Brown, 2006). A unique trait of beach ecosystems is thus the intense cross-system exchanges of nutrients and organic matter (Harris et al., 2015).

### **Nutrient subsidies**

Nutrient subsidies (material that has originated from another habitat) often link productive marine systems to a less productive terrestrial system (Huxel & McCann, 1998; Lastra et al., 2008; Vander Zanden et al., 2012). On beaches detritus materials from seagrass, macroalgae, and dead organisms are washed ashore and deposited on the sand and so provide resources for beach fauna (Lastra et al., 2008; Colombini et al., 2011; Bergamino et al., 2011; Barreiro et al., 2012; Bergamino et al., 2012). This transfer of nutrients represents the main conduit of marine subsidies to the terrestrial

environment and illustrates the connectivity between terrestrial and aquatic ecosystems (Colombini et al., 2011; Barreiro et al., 2012).

Polis et al. (1997) proposed that transport of allochthonous nutrients across boundaries can occur either via abiotic or biotic vectors. Abiotic mechanisms of nutrient transport pertain to nutrients (detritus, organisms) moved by wind and water, while biological transport occurs when mobile consumers carry nutrients from one ecosystem to another. Physical transports have been extensively studied in nutrient cycling research while the latter has been far less studied (Bouchard, 1998).

Most studies investigating biological transport of nutrient or energy from water to land have focused on (anadromous and catadromous) fish species or seabirds as vectors (Polis & Hurd, 1996; Polis et al., 1997). Fish like sardines, salmon and eels are effective transporters because they undertake seasonal migrations that result in the transfer of large amounts of nutrients between ecosystems. For example, Atlantic and Pacific salmon species deposit large amounts of marine-derived nutrients to nutrient-poor headwater streams via reproductive products (eggs and sperm), nutrient excretion, and to land ecosystems through predation (e.g. bears) and carcass decomposition after death (Ben-David et al., 1998a). These nutrient inputs can affect the recipient system by increasing primary and secondary productivity and produce numerical responses in their consumers which in turn can affect higher trophic levels (Polis et al., 1997). Another well-known example of a resource pulse is the Sardine Run along the eastern seaboard of South Africa. The Sardine Run is a phenomenon whereby large shoals of sardine (*Sardinops sagax*) migrate seasonally from temperate waters in the austral winter to warm subtropical waters (Hutchings et al., 2010). This event stimulates strong predator responses, with whales, dolphins, sharks and other predatory fish species following the sardines for hundreds of kilometers up the coast to capitalize on the high density prey items. The drivers of this phenomenon are poorly understood as are the consequences on marine food webs and on ecosystems (Fennessy et al., 2010). Hutchings et al. (2010) estimated that the sardine run annually contributes ca. 96 000 tons of nitrogen to the sub-tropical nearshore system. This is more than any other alternative source of nitrogen including upwelling, river and storm water runoff or groundwater discharge.

Similarly, seabirds feeding on fish and invertebrates concentrate and transport large quantities of nutrients from the sea to land as guano, food scraps, eggs, feathers, and carcasses of dead chicks and adults (Mizutani & Wada, 1988; Polis et al., 1997; Erskine et al., 1998; Anderson & Polis, 1999). On Marion Island for example, penguins, seabirds and seals supply up to 87% of the nitrogen requirements of the terrestrial ecosystems through guano and other materials. Almost 1 ton of carcasses.km<sup>-2</sup>.yr<sup>-1</sup> are deposited on the shore, and so have a significant impact on terrestrial food webs (Burger et al., 1978; Siegfried, 1981). Other animals have been found to act as vectors of nutrients from water to land, such as river otters (Ben-David et al., 1998b), sea lions (Farina et al., 2003), and horseshoe crabs (Botton & Loveland, 2011). These animals all contribute to nutrient transport through standard routes i.e. excretion, carcass decomposition or spawning/pupping events. Marine turtle eggs and hatchlings also represent important subsidies for food webs of many sub-tropical and tropical beaches (Bouchard & Bjorndal, 2000). In contrast to the other nutrient supplies, however, turtle-mediated subsidies are not continuously supplied, but rather are presented to beach food webs as resource pulses during the turtles' breeding season.

### **Resource pulses**

Resource pulses are rare, brief, and intense episodes of high resource availability in space and time that involve the spatial transport of resources across habitat and ecosystem boundaries (Yang, 2006; Yang et al., 2008). In this study, resource pulses are considered as a special component of the movement of nutrients across ecosystem boundaries. Resource pulses occur in a wide range of ecosystems including islands, forests, arid deserts, streams, and lakes, and include events such as El Nino rainfalls in arid systems (Polis et al., 1997; Yang et al., 2008), seed or fruit mast events (Curran and Leighton, 2000), insect outbreaks (cicadas) (Yang, 2004), marine upwelling events (Bode et al, 1997), and synchronous spawning events (salmon) (Botton and Loveland, 2011). Resource pulses are caused by both biotic and abiotic drivers and can vary widely in their magnitude, duration, and frequency (Yang et al., 2010). Resource pulses can strongly influence recipient systems and can affect consumer responses at the

individual level, population level through numerical responses, and community level through indirect effects (Yang et al., 2008).

A growing number of studies have recently focused on the effects of allochthonous subsidies from stranded wrack (Stenton-Dozey & Griffiths, 1983; Jeckzejczak, 2002; Dugan et al., 2003; Olabarria et al., 2007), macrophytes (Dugan et al., 2003; Lastra et al., 2008; Dugan et al., 2011), seaweeds (Spiller et al., 2010) to sandy beach communities (macro- and meiofauna). These studies showed that marine subsidies strongly influence beach food webs by enhancing the abundance, biomass and diversity of macro- and meiofauna and the production of secondary and of higher trophic levels (Dugan et al., 2003; Netto & Meneghel, 2014). Curiously, the role of reptiles, particularly marine turtles in nutrient transport across systems has been much less studied, despite the clear breaching of ecosystem boundaries (during migration) and the obvious deposition of large numbers of eggs onto beaches (during nesting).

### **Ecological roles of sea turtles in the marine environment**

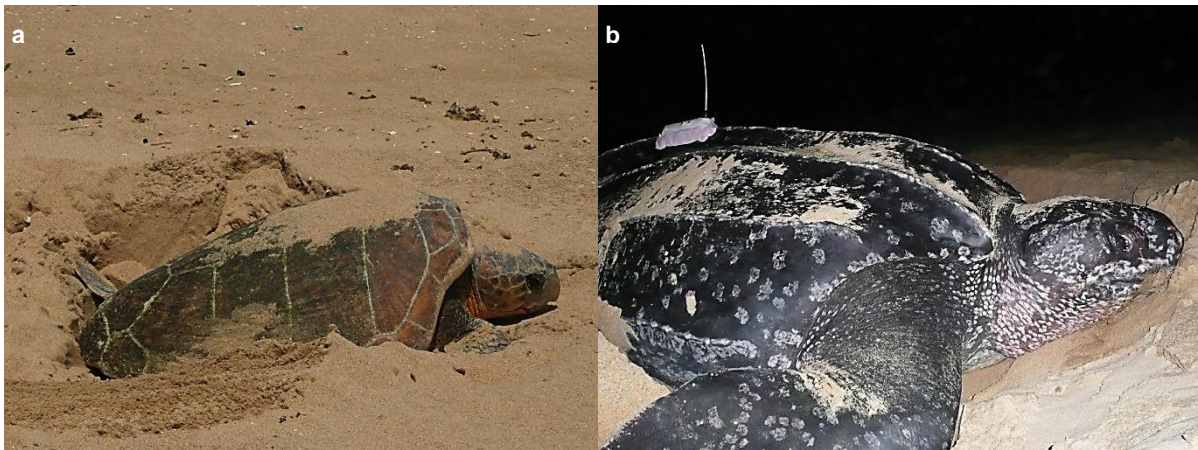
Sea turtles occupy reasonably unique niches and facilitate important ecological processes which until recently have been overlooked (Goatley et al., 2012). These unique ecological roles include maintaining of healthy seagrass beds and coral reefs, providing key habitats for other marine life (epibionts), maintaining a balanced food web, and serving as prey species, consumers, or competitors, and engineers of the physical environment (Bjorndal & Jackson, 2003). Despite the plethora of literature describing the conditions and requirements for successful nesting and incubation, there is very little information and few examples of the sea turtles' ecological roles and contributions to coastal (terrestrial or marine) environments, such as their effects on sandy shores.

### **Ecological contribution of sea turtles to terrestrial coastal ecosystems**

Marine turtles undertake long-distance migrations between feeding and nesting grounds and are capital breeders that fast during the nesting season and consume little or no food during the migration and nesting period (Plot et al., 2013; Perrault et al., 2014).

Consequently, all energy and nutrients that turtles deposit on the beach during reproduction originate from distant feeding grounds (Bouchard & Bjorndal, 2000). These nutrients are deposited in the form of eggs into the nutrient-poor beach environment. Sea turtle nesting aggregations on a single beach can reach extreme densities which results in the deposition of massive quantities of marine-nutrients. The east coast of Florida, for example, supports one of the largest loggerhead (*Caretta caretta*) nesting site in the world, with approximately 28 000 nests (or approximately 2 800 000 eggs) deposited along ~ 120 km of beach each year (Meylan et al., 1995). Olive ridley (*Lepidochelys olivacea*) sea turtles are famous for their synchronised mass-nesting behaviour called “arribadas”. Thousands of turtles nest over a few days on the beach. In Ostional, Costa Rica, between 3 564 - 476 550 nesting females deposit 1 050 000 – 142 800 000 eggs over a few nesting days in a single nesting season (Valverde et al., 2012). Similarly, arribadas in Orissa, India, can reach nesting densities of about 180 000 females nesting multiple times in a season (Shanker et al., 2003).

Two sea turtle species nest on the east coast of South Africa (Fig. 1.2), which is the southernmost nesting site for sea turtles. These are modest populations of loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) turtles. It is estimated that ~ 581 000 eggs are introduced into the beach system annually (Nel et al., 2013).



**Figure 1.2:** Photographic examples of the two species of sea turtle nesting in South Africa, (a) loggerhead (*Caretta caretta*) and (b) leatherback (*Dermochelys coriacea*) sea turtles.

Mobile consumers that connect habitats through nutrient transfers during migrations are termed “mobile links” (Lundberg & Moberg, 2003; Jeltsch et al., 2013; Bauer and Hoye, 2014). Such organisms can provide important indirect ecosystem services that are crucial for ecosystem functioning. When transporting nutrients from areas of higher productivity (e.g., reefs and seagrass beds) into areas of low productivity (e.g., sandy beaches), sea turtles act as mobile links and can influence the recipient systems (Huxel & McCann, 1998; Vander Zanden et al., 2012).

Evidence of sea turtles acting as vectors of nutrients is given by the following six studies: (1) Bouchard and Bjorndal (2000) showed that 59-66% of the energy, organic matter, lipids, and nutrients from unhatched eggs, eggs shells, and dead hatchlings or embryos that remain in the beach ecosystem, is available to plants, predators, detritivores and decomposers. (2) High  $\delta^{15}\text{N}$  and total N values in dune sand and plants were shown to be positively correlated with loggerhead and green turtle (*Chelonia mydas*) nest densities (Hannan et al., 2007). These results are similar to an independent study in Costa Rica, (3) where high  $\delta^{15}\text{N}$  values in plants were recorded in areas of high nest densities of green turtles, with the nesting phenomenon estimated to have introduced approximately  $507 \text{ kg.km}^{-1}$  of N and  $45 \text{ kg.km}^{-1}$  of P in a single year to these beaches (Vander Zanden et al., 2012). (4) Plog et al. (2003) found similar results, and suggested that a mutually beneficial relationship whereby sea turtles provide nutrients to dune vegetation and the vegetation in turn provides a stable nesting environment. (5) Turtle nesting can also influence the supralittoral community structure of sandy beaches by increasing the abundance of beach insects (fly larvae, fungi, mites, beetles, crickets and ants) (Madden et al., 2008). Finally, (6) nutrients from turtle eggs can be exploited by terrestrial insects that burrow into the nests (Maros et al., 2006). Thus, although sea turtles lay their eggs in discrete nests in the sand, the potential pathways for the nutrients extend to both the marine and terrestrial realms.

The nitrogen in sea turtle eggs and hatchlings is a higher quality than the N in algal wrack for example (McLachlan & McGwynne, 1986), and the highest  $\delta^{15}\text{N}$  values of any known food source for consumers on Florida beaches (Davenport, 1997; Plog, 2004). The liquid resource of broken eggs is potentially available for uptake and recycling by a

wider range of organisms than plant-based nutrients. The nutrients contained in sea turtle eggs may follow several pathways. About two thirds of the nutrients from nests return to the marine environment as hatchlings (Bouchard & Bjorndal, 2000). This process is very well understood from the perspective of sea turtle reproductive biology, with metrics such as hatchling success, emergence success, and egg and hatchling predation usually quantified as standard practice in turtle monitoring programs (Zbinden et al., 2011; Nel et al., 2013). However, nutrients from unhatched and depredated eggs, dead and predated hatchlings, as well as chorioallantoic fluid and egg shells certainly remain in the beach and enter sandy beach ecosystem, but their full contribution to the beach food webs remains largely unquantified.

### **Sandy beach food webs**

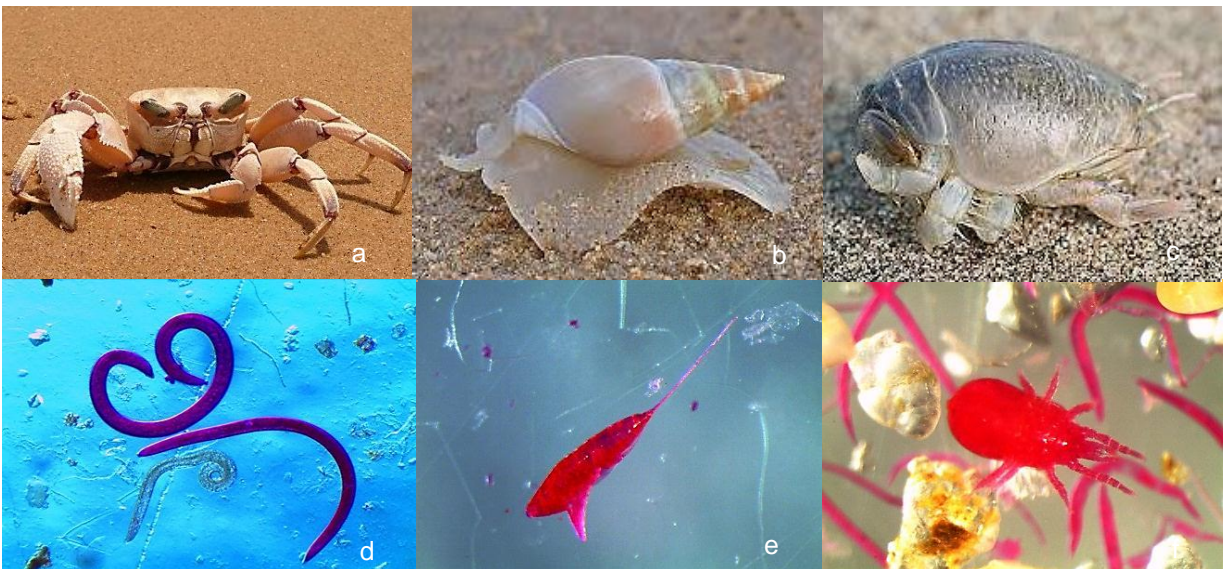
Ecological processes on beaches are dominated by physical factors particularly the interaction between wave energy, tidal exchange and sand particle size (Heymans & McLachlan, 1996). These factors combine to create different morphodynamic states ranging in the extreme from dissipative to reflective beach states. Dissipative beaches are characterized by a wide surf zone, fine sand and flat beach profile (Short, 1999; Lastra et al., 2005). Reflective beaches on the other hand, are dominated by a short surf zone, coarse sand and steep slope (Lastra et al., 2005). As the beach type changes from dissipative, through intermediate towards reflective conditions, the environment becomes more stressful to biotic communities. This is reflected in a decline of species richness and abundance from dissipative towards reflective beaches respectively (McLachlan, 1990; McLachlan et al., 1993).

Sandy beach food webs are generally characterized by three broad trophic assemblages discriminated by size and hence their ecological functioning (McLachlan et al., 1981b). These are - the macroscopic food web comprising animals retained by a 1 mm mesh sieve (Defeo et al., 2009) (Fig. 2 a-c); the interstitial food web ranging between 1 mm and 63  $\mu$ m sieve (Giere, 2009) (Fig. 1.3 a-f); and microbial loop of which the organisms are only a few micro-meters in size. As a result of the size limits, meiofauna include temporary and permanent members. Temporary members are



juvenile stages of the macrofauna (as newly settled larvae that later grow to become macrofauna), while permanent members are species with small adults sizes (McIntyre, 1969; Giere, 2009).

The macroscopic food web is characterized by benthic invertebrate taxa such as crustaceans, molluscs, polychaetes, zooplankton, as well as vertebrates like fish and birds. These organisms are generally either predators/scavengers or filter/deposit feeders (Bally, 1987). Interstitial organisms, such as meiofauna comprise the interstitial food web. These species live in the sand and feed on dissolved and particulate organic matter that is generally flushed into the beach by wave and tidal action (McLachlan et al., 1981). Meiofauna are small benthic invertebrates that occur in all aquatic systems and climatic zones (Giere, 2009). Meiofauna occur in high densities in beach sediments, and are often orders of magnitude more abundant and more diverse than macrofauna (Koop & Griffiths, 1982; Nascimento et al., 2012). Meiofauna contribute to the ecological functioning of beaches as they recycle particulate organic matter and facilitate sediment bioturbation (Lindgren et al., 2013). The microbial loop is responsible for degrading organic matter and recycling inorganic nutrients (Lindgren et al., 2012).



**Figure 1.3:** Examples of major macrofauna species commonly found on South African subtropical sandy beaches: (a) ghost crab (*Ocypode ryderi*), (b) plough snail (*Bullia* species), (c) mole crab (*Emerita austroafricana*) and major meiofauna taxa, (d) nematodes, (e) copepod, (f) halacarid mite.

Meiobenthic organisms differ from macrofauna in size but also in having direct benthic development, continuous reproductive activity, and short generation times with about one month life cycle and two to four generations produced annually (McIntyre, 1969; Gerlach, 1971). Nematodes are generally the most abundant group followed by harpacticoid copepods, turbellarians and oligochaetes (Koop & Griffiths, 1982; Ansari et al., 1990; Li et al., 1997; Coull, 1999; Rodriguez et al., 2001; Netto & Gallucci, 2003; Nozais et al., 2005; Albuquerque et al., 2007; Sajan et al., 2010; Harguinteguy et al., 2012). Distribution and abundance of intertidal meiofauna are mainly controlled by sediment characteristics and food availability. For example sediment grain size, temperature, and salinity affect the interstitial space, including water content and availability of food and oxygen (McIntyre, 1969; Coull, 1999; Vincx et al., 1990). It is thus suggested that highest meiofaunal densities occur when the balance between organic input and oxygen availability approach an optimum (McGwynne et al., 1988).

High shore faunal communities above the driftline differ from the intertidal ones. On the high shore, three food chains may be found: a grazing food chain including herbivorous insects, mammals and birds; a detrital food chain occupied mainly by detritivore insects; and an interstitial food chain in the sand comprised of bacteria, fungi and meiofauna (McLachlan, 1991). In this habitat, wind is a major physical factor controlling sand movement, microclimate, seed and detritus dispersal, and salt spray (McLachlan, 1991). Although, high shore sands are well supplied with moisture, they are generally poor in nutrients and the food chain is fueled by autochthonous inputs from the dune flora and organic materials from the sea and land. High shore meiofaunal communities are less influenced by tidal actions and more by desiccation which explains why nematodes are the dominant taxon of meiofauna in this type of environment (McLachlan, 1980). Indeed, nematodes are more adapted to these dry sand conditions found in the high shore zone than other meiofauna taxa, due to their hard cuticle, enabling them to withstand higher temperatures (Moens and Vincx, 1997; Gheskiere et al., 2004; Tahseen, 2012). Although sandy beach food webs are well understood independently, little is known about trophic interactions between communities or their effects on the structure and dynamics of sandy beach macro-and meiofaunal communities (McLachlan, 1983).

There is currently still a gap in knowledge regarding the trophic interaction between meiofauna and macrofauna (Menn, 2002). It was generally accepted that no trophic links exist between the macroscopic and interstitial food webs, and that they comprise two separate food webs (McLachlan, 1977; Bezuidenhout, 2010). Indeed, McLachlan and Erasmus (1983) described the macrofauna and the meiofauna of sandy beaches as comprising two entirely separate faunal components with no overlap or exchange of energy. However, studies have shown that meiofauna may serve as food for macrofauna such as juvenile crabs, shrimps and worms (Reise, 1979; Li et al., 1997). Nematodes may also be ingested passively by non-selective deposit-feeders and surface grazers or actively ingested by small predators (Coull, 1990, 1999). Some fish species for example, do not eat meiofauna throughout their entire life cycle but only as juveniles and then switch to bigger prey when they grow (Coull, 1990). This suggests that ontogenetic shifts in diet of predators may affect their prey choice. Much uncertainty remains regarding the manner in which meiofauna prey are utilized by macrofauna and how much meiofauna contribute to the diet of higher trophic levels (McCall & Fleeger, 1995; Leduc & Probert, 2009). One possible way to trace nutrient paths through food webs is to use stable isotopes.

### **Stable isotope analyses (SIA)**

SIA works on the principle that “you are what you eat” (DeNiro & Epstein, 1978). This suggests that the isotopic signatures of consumers reflect isotopic signatures of their food sources. Nitrogen isotope ratios are used to determine the trophic position of food web components, while carbon isotopes are used to trace the flow of organic matter to organisms within food webs (Fry, 1991). Dual stable isotope analysis thus provides a tool to map trophic interactions in aquatic food webs (Peterson, 1999; Moens et al., 2005). SIA has become a standard tool to reconstruct diets, map trophic relationships, elucidate patterns of resource allocation, and construct food webs (Peterson & Fry, 1987; Boecklen et al., 2011).

Trophic enrichment or fractionation is defined as the difference in the isotopic signature between the consumer and its diet (Rubenstein & Hobson, 2004; Tiunov, 2007).

Isotopic carbon values of consumers are expected to increase by  $\sim 1\text{‰}$  relative to their food source (Peterson & Fry, 1987). In contrast, a trophic enrichment factor of  $3.4\text{‰}$  (De Niro & Epstein, 1981; Minagawa & Wada, 1984; Post, 2002) for nitrogen is widely accepted and allows the determination of an organism's trophic level (Perkins et al., 2014).

Despite the fact that these enrichment values for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  have been widely accepted, much variation still remains in the isotopic shift between diet and consumer (McCutchan et al., 2003; Boecklen et al., 2011). Vander Zanden and Rasmussen (1999) showed considerable variation in  $\delta^{15}\text{N}$  of invertebrate lake consumers with values ranging from  $-2$  to  $+9\text{‰}$ . Similarly, Post (2002), found values of  $\delta^{15}\text{N}$  that varied between  $4.5\text{‰}$  and  $13.6\text{‰}$  and of  $\delta^{13}\text{C}$  between  $-14\text{‰}$  and  $-28\text{‰}$  for snails and mussels among different lakes. McCutchan et al. (2003) revealed trophic shifts ranging from  $-0.2\text{‰}$  to  $+1.3\text{‰}$  for  $\delta^{13}\text{C}$  and from  $1.4\text{‰}$  to  $3.3\text{‰}$  for  $\delta^{15}\text{N}$  and demonstrated that parameters such as sample treatment, tissue type, diet type and modes of excretion to influence isotope signature. Additionally, variation between seasons, sites, species, and individuals are other factors that can influence isotope ratios (Jardine et al., 2003). Much uncertainty remains regarding the predictability of enrichment in consumer tissues and the accuracy with which we can interpret stable isotope data since inaccurate enrichment values can introduce errors in estimates of trophic shifts and trophic position (McCutchan et al., 2003).

Within an environment of limited food sources, turtle eggs are believed to represent an important food item for sandy beach consumers. As far as I am aware, to date, no studies have evaluated the use of resource pulse subsidies mediated by turtle nesting to intertidal ecosystems, particularly the meiofauna. The most abundant and diverse metazoans of sandy beach fauna are the nematodes (Gheskiere et al., 2004; Giere, 2009), yet the effect of turtle-derived nutrients to these organisms has been ignored. Additionally, sea turtles, through nesting have the potential to subsidize consumer populations and modify the dynamics of food webs, but it is still unclear how and at what scale this energy input impacts the recipient ecosystem (Giroux et al., 2012).

In this study, I quantify the turtle-derived nutrients introduced into nesting beaches and determine the potential for these nutrients to subsidize and be incorporated into the sandy beach food webs. I further investigate the response of the meiofauna to the decomposition of turtle eggs over time. I hypothesize that turtle-derived nutrients represent a resource pulse that affect the sandy beach ecosystem and are incorporated into beach food webs. I test this hypothesis by comparing isotopic signatures (carbon and nitrogen) of beach fauna in two areas of sandy beaches known to differ in sea turtles nesting activity (Nel et al., 2013); one with high turtle nesting density and one with low turtle nesting density (where egg numbers are several orders of magnitude lower). I also hypothesize that meiofaunal abundance is positively affected by turtle-derived nutrients. This hypothesis is tested with an *in situ* experiment and by comparing meiofaunal abundance in depredated nests.

## **Dissertation outline**

The dissertation starts with a brief literature review to outline the state of knowledge on turtle-derived nutrients in beach ecosystems and potential ecological roles of sea turtles (**Chapter 1**). The rest of the Dissertation is written as a series of discrete chapters that stand alone, but collectively address the broad aims described above. Note that although every effort is made to minimize repetition in content among chapters, this was unavoidable in some places.

**Chapter 2** provides context of the size of South African sea turtle rookery and trends in the conservation and monitoring programme along the KwaZulu-Natal (KZN) coastline. The nutrient input is quantified per individual loggerhead (*Caretta caretta*) female into the beach over the nesting season, which is then scaled to a population level. This chapter also illustrates the role of sea turtles as nutrient vectors from sea to land and quantifies the amount of energy imported onto Maputaland sandy beach ecosystems (in the 2013/14 and 2014/15 season) from loggerhead and leatherback sea turtle nesting.

The aim of **Chapter 3** is to identify the potential pathways of turtle nutrients through the Maputaland beach ecosystem using stable isotope analysis. This chapter assesses the

different nutrient pathways, thereby quantifying the fate of turtle-introduced nutrients on the high- and the low density nesting areas using stable isotope analyses.

**Chapter 4** assesses the response of meiofauna to the decomposition of turtle eggs over time. This chapter compares the meiofauna densities in depredated nests relative to densities outside of nests. It also quantifies the response of meiofauna to nutrient inputs over time through an *in situ* “basket” experiment. This experiment mimics conditions of naturally predated sea turtle nests and monitors changes in faunal communities as the eggs mature and decompose.

**Chapter 5** provides a synthesis and conclusion from all the chapters. This chapter summarizes the main findings in each of the content chapters and explains the critical ecological role of sea turtles as biological transporters of nutrients across ecosystems.

**Chapter 2: Quantifying turtle-introduced nutrient inputs to  
the Maputaland sandy shores, South Africa**

## **Abstract**

Sandy shores are dynamic systems where beach food webs are almost entirely supported by erratic allochthonous subsidies. Sea turtles nest on sandy beaches and deposit large amounts of eggs seasonally in those nutrient-poor ecosystems, but no studies have quantified the amount of energy introduced by sea turtles. This study quantified the turtle-derived nutrient inputs by determining the energy value of eggs and hatchlings of two species of sea turtles nesting on South African sandy beaches. These results were then scaled to a population level for both species. The study demonstrated that loggerhead turtle along shore distribution is not uniform, having a high nest density to the north ( $105 \text{ nests.km}^{-1}$ ) and low nest density to the south ( $7 \text{ nests.km}^{-1}$ ). However, a total number of *ca.* 554,025 loggerhead and leatherback sea turtle eggs are deposited on this sandy shore annually. Subtracting the nutrients that leave the beach in the form of successfully incubated hatchlings it is estimated that a total of 37,521,567 kJ of energy remains in the beach ecosystem and potentially available to beach food webs. This equates to *ca.*  $670 \text{ kJ.m}^{-1}$  in a single nesting season or  $7.4 \text{ kJ.m}^{-1}.\text{day}^{-1}$ . These results confirm that the seasonal input of eggs from sea turtles is a pulsed resource subsidy of small temporal scale that makes substantial contributions to the energy budget of sandy beach ecosystems.

**Keywords:** Sandy beach, sea turtle eggs, energetics, resource pulse, South Africa



## Introduction

Resource supply and availability is rarely constant in natural environments as it fluctuates with seasonal and annual cycles. Instead the frequency and magnitude of resources are highly variable (Ostfeld and Keesing, 2000). This is especially true in sandy beach ecosystems where resource availability is erratic changing with tides, seasons or storms, and are not well understood. Most nutrients on sandy beach ecosystems come in the form of allochthonous subsidies.

Sandy beaches are poorly recognised as ecosystems mainly because of the apparent absence of attached plants and thus, obvious primary productivity. For the most part, beach food webs rely on allochthonous inputs, such as wave-cast wrack and carrion (McLachlan and Brown, 2006). Sandy beaches and their associated fauna are proficient in remineralising nutrients. In fact, they are so efficient at processing/recycling nutrients, that it is one of the key ecosystem services beaches provide (McLachlan, 1981b; McLachlan and brown, 2006). However, resources are not distributed equally on sandy shores.

Beaches in cool temperate systems are generally well supplied in macroalgal and macrophyte wrack inputs, such that it strongly subsidizes those habitats. Indeed, studies have shown that marine-derived wrack represents a significant subsidy to intertidal and supratidal herbivore and decomposer communities, often permitting macrofauna densities that would otherwise not be sustained (Stenton Dozey and Griffiths, 1983; McGwynne et al., 1988; Van der Merwe and McLachlan, 1987; Jedrzejczak, 2002; Dugan et al., 2003; Ince et al., 2007; Orr et al., 2005; Lastra et al., 2008; Coupland and McDonald, 2008; Beeler, 2009). In contrast, (sub)tropical beaches are oligotrophic with little phytoplankton production and no kelp-derived matter feeding beaches. Further, wave action, is generally, so that diatom accumulations do not form (Campbell, 1996). These beaches are thus nutrient-limited (and dependent on sporadic supply of seagrass and algae depositions from distant coral or rocky reefs). Fortunately, (sub)tropical sandy beaches are however the nesting grounds of sea turtles.

Marine turtles are widely distributed and nest off all tropical and subtropical oceans (Bolten, 2003). Sea turtles are also highly mobile and sexually mature females

undertake long-distance migrations, between feeding areas (frequently on temperate coasts) to tropical breeding grounds, to nest (Davenport, 1997). Sea turtle nesting aggregations can reach extremely high densities even on a single beach (e.g., Valverde et al., 2012). Resultantly, massive quantities of eggs bring nutrients onto beach ecosystems. However, about two thirds of the nutrients return to the sea as hatchlings, but the other third remain in the beach in the form of unhatched and depredated eggs, dead and predated hatchlings, as well as chorioallantoic fluid and egg shells (Bouchard and Bjorndal, 2000).

Several studies have shown that turtle-derived nutrients can be incorporated into sandy beach food webs. Species consuming these nutrients include: dune plants (Plog et al., 2003; Hannan et al., 2007; Vander Zanden et al., 2012); terrestrial vertebrates (e.g., raccoons and birds; Bouchard & Bjorndal, 2000); coastal insects (e.g., fly larvae, mites, beetles, crickets and ants; Madden et al., 2008; Maros et al., 2006); and intertidal/beach invertebrates (e.g., ghost crabs; Bouchard & Bjorndal, 2000); Thus, although sea turtles are marine organisms they can also influence the functioning of terrestrial ecosystems (on coastal sandy shores). However, the extent of the potential benefit to the receiving system depends critically on the magnitude of the resource pulse. Despite the large amount of eggs deposited into South African sandy beaches, no studies have quantified the amount of energy introduced by sea turtles annually and how much is made available to the ecosystem and subsequently leave the beach.

The aim of this Chapter is to quantify the turtle-derived nutrient inputs to oligotrophic sandy beach ecosystems in South Africa. To achieve this, I first calculated the seasonal reproductive output per female turtle, and scale this up to a population level per species (loggerhead and leatherback); secondly, I determined the nutrient value of eggs and hatchlings of each species; and finally, quantified the nutrient input introduced into beaches, the amount that leaves the beach in the form of hatchlings, and the amount that remains in the beach ecosystem. I suggest that turtle-derived nutrients represent a resource subsidy that makes significant nutrient contribution to sandy beach ecosystems and is potentially available to beach food webs.

## Materials and Methods

### Study area

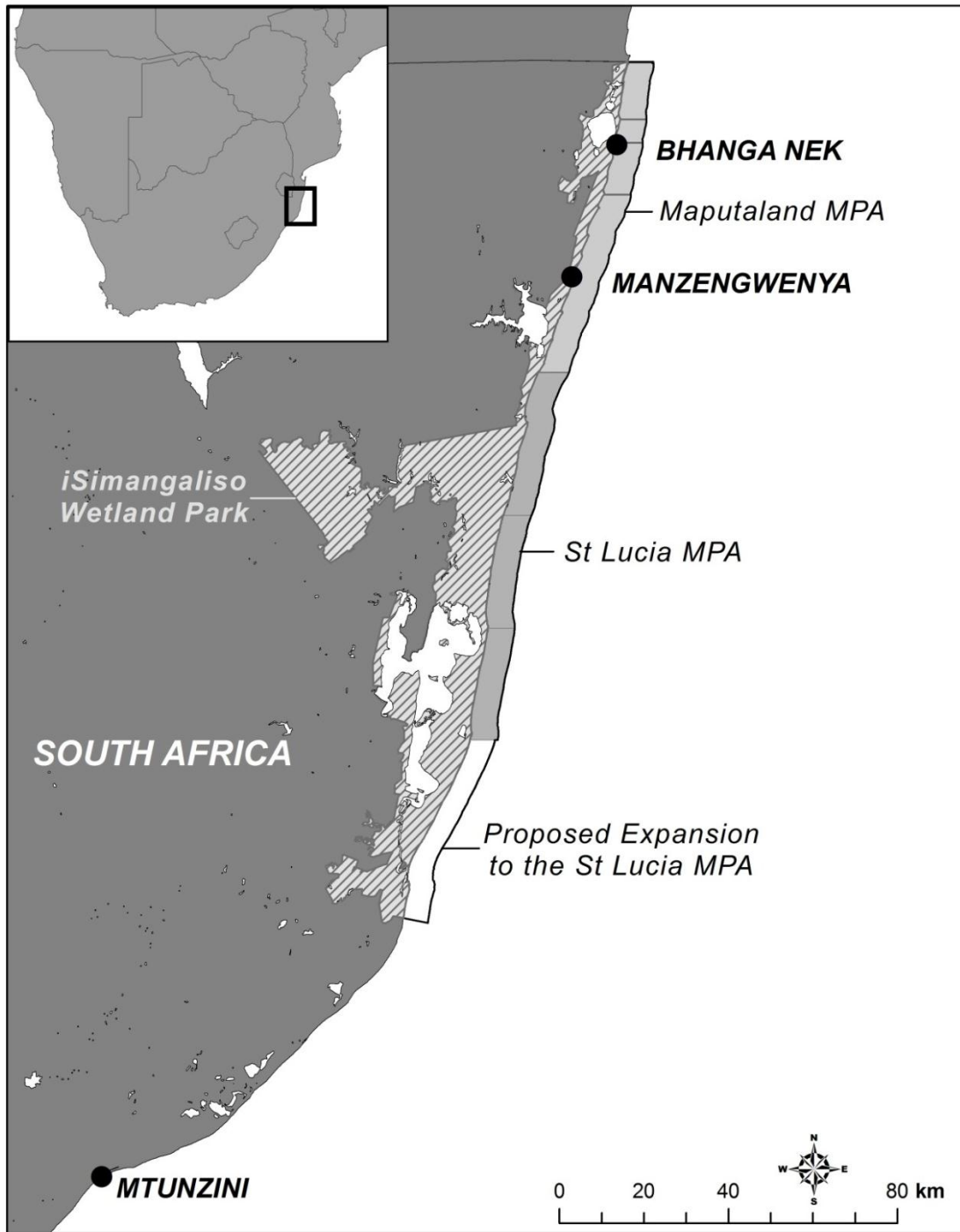
The study area is located on the north-eastern coast of South Africa on the Maputaland beaches in iSimangaliso Wetland Park, Kwa-Zulu-Natal (Figure 2.1). iSimangaliso was proclaimed a UNESCO World Heritage Site in 1999 and Ramsar site (Cowan & Van Riet, 1998) and includes contiguous terrestrial and marine reserves. The marine reserves comprise two adjacent marine protected areas (MPAs): the St Lucia and Maputaland Marine Reserves, which extend three nautical miles seaward.

The study area is located within the bioregional transitional zone between the tropics to the north and subtropical coastal conditions to the south (Branch et al., 2010). The climate can be classified as humid, subtropical and characterized as warm to hot in summer (28°C) and mild to warm in the winter (22°C) (Lubbe, 1997). The mean annual rainfall is 1228 mm of which 76% falls in the summer months from September to April. The Maputaland beaches are influenced by the warm Agulhas Current which flows southward towards the tip of Africa (Lutjeharms & Ansorge, 2001). The sea surface temperature of the Agulhas Current is approximately 28°C summer and 21°C in winter and reaches a maximum speed off Maputaland of 1.5 m.s<sup>-1</sup> (Schumann & Orren, 1980).

There are three major waterbodies within iSimangaliso; Lake St Lucia to the south of the Park, and Lake Sibaye, and the Kosi Bay Lake System (KBLS) in the north. The KBLS consists of four interconnected lakes oriented parallel to the coastline and separated from the sea by a strip of forested sand dunes (Hughes, 1989; Kyle, 1991). Freshwater enters the KBLS through rivers and smaller streams at several locations around the lakes, while salt water enters through the Kosi Mouth. The dune vegetation is dominated by *Ipomoea* spp. and *Scaevola plumieri*. The dominant beach morphodynamic state in the iSimangaliso Wetland Park is intermediate beaches with some coarse grained, steep reflective beaches as well as the occurrence of some mixed shores and rocky outcrops (Harris et al., 2011). The beaches of the iSimangaliso Wetland Park extend for approximately 200 km from the Mozambican border to the north to Mapelane, just south of the St Lucia Estuary mouth.

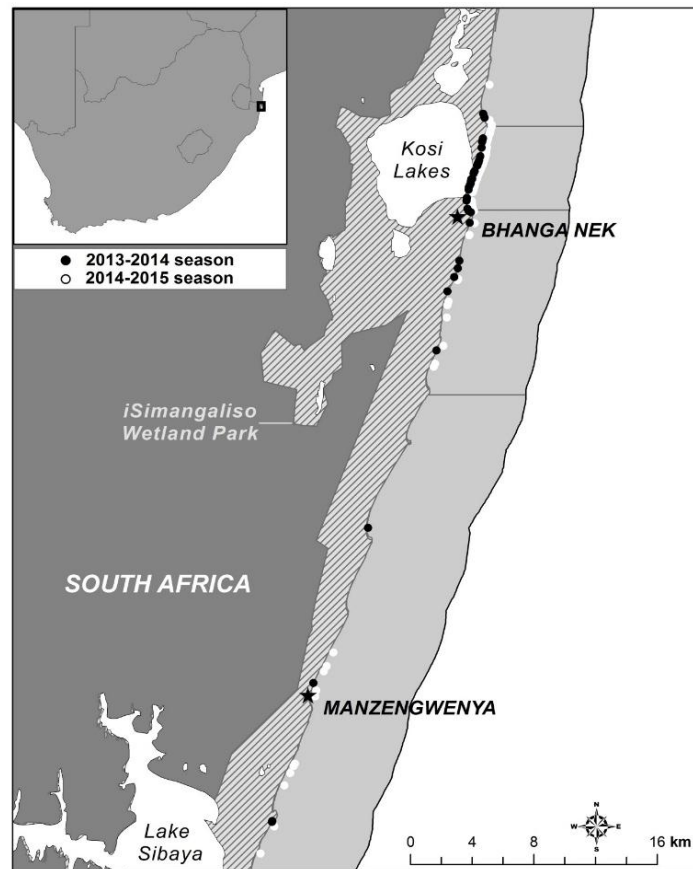
The Maputaland beaches form the southernmost nesting grounds of loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles in the world (~27°S). Turtles were first protected in South Africa in 1916 by the Natal Ordinance, but efficient protection was only achieved when the conservation and monitoring program was established in 1963 (McAllister et al., 1965). The program has run every year since then, making it one of the longest running sea turtle conservation programs in the world (Nel et al., 2013). The monitored area has expanded over time, and currently spans 77 km from the Mozambique border to Sodwana Bay. Turtle tracks and nests are counted relative to a set of reference with marker poles (beacons) spaced 400 m apart, with each beacon numbered according to the distance and direction (north: N, or south: S) from the Bhanga Nek research station (0N) at Botellier Point. Monitoring takes place during the entire nesting season (October to March), with peak nesting occurring in December-January.

The two turtle rookeries overlap and utilize the same nesting beach, and initial low numbers of nesting females in both species, contrasting population recovery trends are found. Despite both species been equally protected and 51 years of monitoring, the vulnerable loggerhead population is increasing exponentially (<1000 nesting females per annum), but the critically endangered leatherback population has remained low with <100 nesting females per annum (Nel et al., 2013; Harris et al., 2015). A loggerhead nesting hotspot is found between beacon 0N and 12S. The Kosi lakes are adjacent to Bhanga Nek beach which has the highest interannual nesting density distribution, concentrated on an 8 km portion of the beach (Fig. 2.2), and constituting the loggerhead “hotspot”. The reason for this selection by loggerhead is unknown although it has been speculated that nest site selection appears to be near a body of water and driven by fresh-water cue from the Kosi Lake system situated behind the beach (Hughes, 1974).



**Figure 2.1:** Study area indicating the marine reserves and the turtle beaches. Black dots indicate the location of the high (Bhangane Nek) and low (Manzengwenya) nest density beaches, as well as the non-nesting beach (Mtunzini).

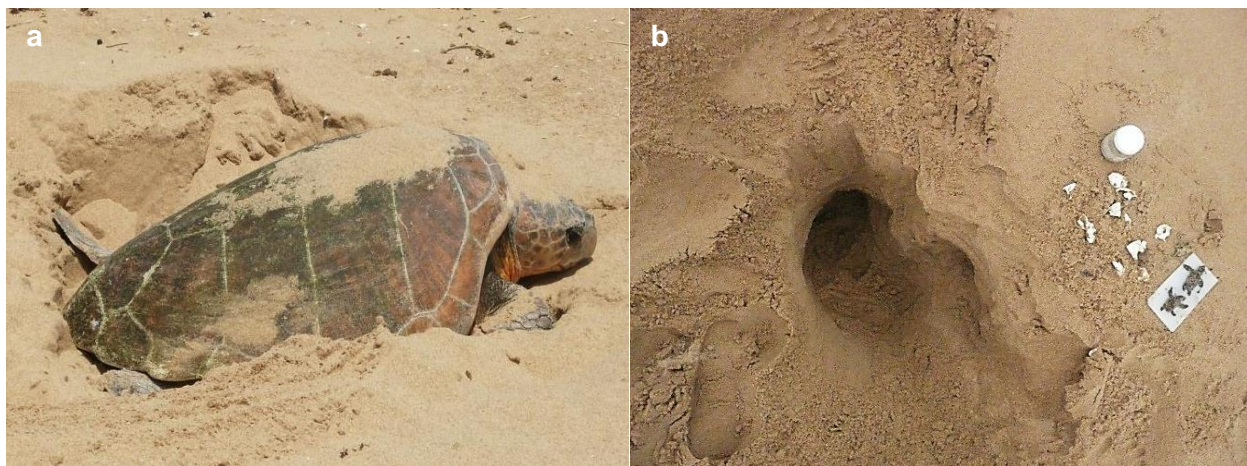
Sampling specifically for this study was conducted in the high nest density area at Bhanga Nek ( $26^{\circ}53'40.17''\text{S}$ ;  $32^{\circ}52'50.31''\text{E}$ , beacon 0N), and in the low nest density area at Manzengwenya ( $27^{\circ}26'72.6''\text{S}$ ;  $32^{\circ}77'28.0''\text{E}$ , beacon 72S). Sampling took place over two seasons, from December 2013 to February 2014, and again from December 2014 to March 2015. All research was undertaken in agreement with local authorities (iSimangaliso Wetland Park and Ezemvelo KwaZulu-Natal Wildlife), with ethics clearance (Nelson Mandela Metropolitan University: A13-SCI-ZOO-012), and relevant collection permits (Department of Environmental Affairs: RES2013/10, RES2014/64 & RES2015/69).



**Figure 2.2:** Study area indicating a sub-sample of loggerhead nesting distributions in the 2013/14 (black circles) and 2014/15 (white circles) seasons at the high and low nest density beaches (black stars).

## Sample collection

Quantifying turtle-derived nutrient inputs (in kilo joules) required samples of eggs and hatchlings. Fresh loggerhead eggs ( $n = 20$ ) were obtained from nesting females (two eggs from 10 females) during nightly patrols (Fig. 2.3a), and dead *in situ* hatchlings ( $n = 8$ ) were collected as part of the routine post-hatching nest excavations (Fig. 2.3b). All samples were collected at Bhanga Nek and were kept frozen until laboratory analysis could be concluded.



**Figure 2.3:** (a) Fresh eggs were collected from loggerhead (*Caretta caretta*) sea turtles while they were laying; and (b) egg shells and dead hatchlings were collected during post-hatching nest excavations.

## Nutrient determination

In the laboratory, frozen eggs were thawed and weighed using a digital scale to the nearest 0.1 g. For each defrosted egg the albumen, yolk and shell were separated and weighed. To separate water mass from component mass, samples were oven dried at 60°C for 48 h, re-weighed and ground to a powder using mortar and pestle (Venkatesan et al., 2005; Zbinden et al., 2011). All hatchlings were blended to attain a mix of all materials, and were similarly dried and ground into a homogeneous powder.

All dried homogenized samples were analyzed for energy content by bomb calorimetry following standard methods and techniques (Bouchar & Bjorndal, 2000; Venkatesan et al., 2005). Bomb calorimetry determines the energy content of organic substances by incinerating dried material at high pressure oxygen. The heat produced by the reaction is absorbed by water around the bomb, and the resulting change in water temperature is used to determine the caloric or energy content (J) in the sample (Kunz & Orrell, 2004; Patel, 2013).

### **Data analysis**

Data of loggerhead and leatherback reproductive outputs for the last eight years (2005-2013) were compiled from the Ezemvelo monitoring database providing the total number of nests per species per season (Nel et al., 2013; Tucek, 2014) (Table. 2.1). Calculations of the number of eggs per seasons were scaled on a 'per nest' basis obtained from Tucek (2014) that counted eggs per nests, for three seasons (2010-2013). The total number of eggs laid (per nest) per species per season, was thus calculated for both, loggerhead and leatherback turtles. Hatching success was defined as the percentage of successfully developed individuals that emerged out of the eggs, and emergence success as the fraction of these hatchlings that reached the sand surface (Miller 1999). The total number of eggs that were laid, hatched and emerged as hatchlings were therefore calculated for each species.

Energy content for freshly laid eggs was used for all calculations involving eggs. These values<sup>1</sup> (loggerhead: fresh egg =  $171.21 \pm 4.64$  kJ; hatchling =  $113.53 \pm 1.50$  kJ), together with the results from the bomb calorimetry, were used to determine the total amount of energy (kJ) turtles introduced into the beach. This was accomplished by multiplying the total number of eggs and hatchlings remaining in the beach by the egg and hatchling energy values. Lastly, the total nutrient contribution per area of beach was

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<sup>1</sup> Due to technical problems with the bomb calorimeter that was sent for repairs but could not be fixed in time, my supervisor advised me to use values from the literature (for the same species) for the sake of deadline. These will be corrected for publication.



calculated by dividing the total amount of energy introduced by turtles by the (monitored) beach length of 56 km.

Leatherback calculations were made by using the same loggerhead (Cc) egg and hatchling energy values and changing them to the egg and hatchling size values of leatherback (Dc). This was obtained by the following calculations:

$$(Dc \text{ egg size} \times Cc \text{ egg kJ value}) / Cc \text{ egg size} = Dc \text{ egg value kJ}$$

$$(Dc \text{ hatchling size} \times Cc \text{ hatchling kJ value}) / Cc \text{ hatchling size} = Dc \text{ hatchling value kJ}$$

A sub-sample (2012-2015) of loggerhead and leatherback along shore distributions was used to illustrate both species nesting densities per beacon (mean  $\pm$  SD).

**Table 2.1:** Data summary on reproductive output and success of the South African loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtle populations (Derived from Tucek, 2014). Data are presented as mean  $\pm$  SD per season from 2005-2013.

Parameter	Loggerhead	Leatherback
Clutch size (mean $\pm$ SD)	112 $\pm$ 20	100 $\pm$ 23
Egg size (mm $\pm$ SD)	40.2 $\pm$ 1.3	51.0 $\pm$ 2.0
Hatchling size (mm $\pm$ SD)	44.0 $\pm$ 1.2	58.6 $\pm$ 2.2
Number of nests per season per female (mean $\pm$ SD)	3.7 $\pm$ 0.8	6.7 $\pm$ 1.5
Nesting numbers of females per season (mean $\pm$ SD)	1147.1 $\pm$ 222.17	122.9 $\pm$ 75.04
Hatching success (mean $\pm$ SD %)	74.9 $\pm$ 27.5	76.3 $\pm$ 22.4
Emergence success (mean $\pm$ SD %)	73.6 $\pm$ 27.7	73.8 $\pm$ 22.7

## Results

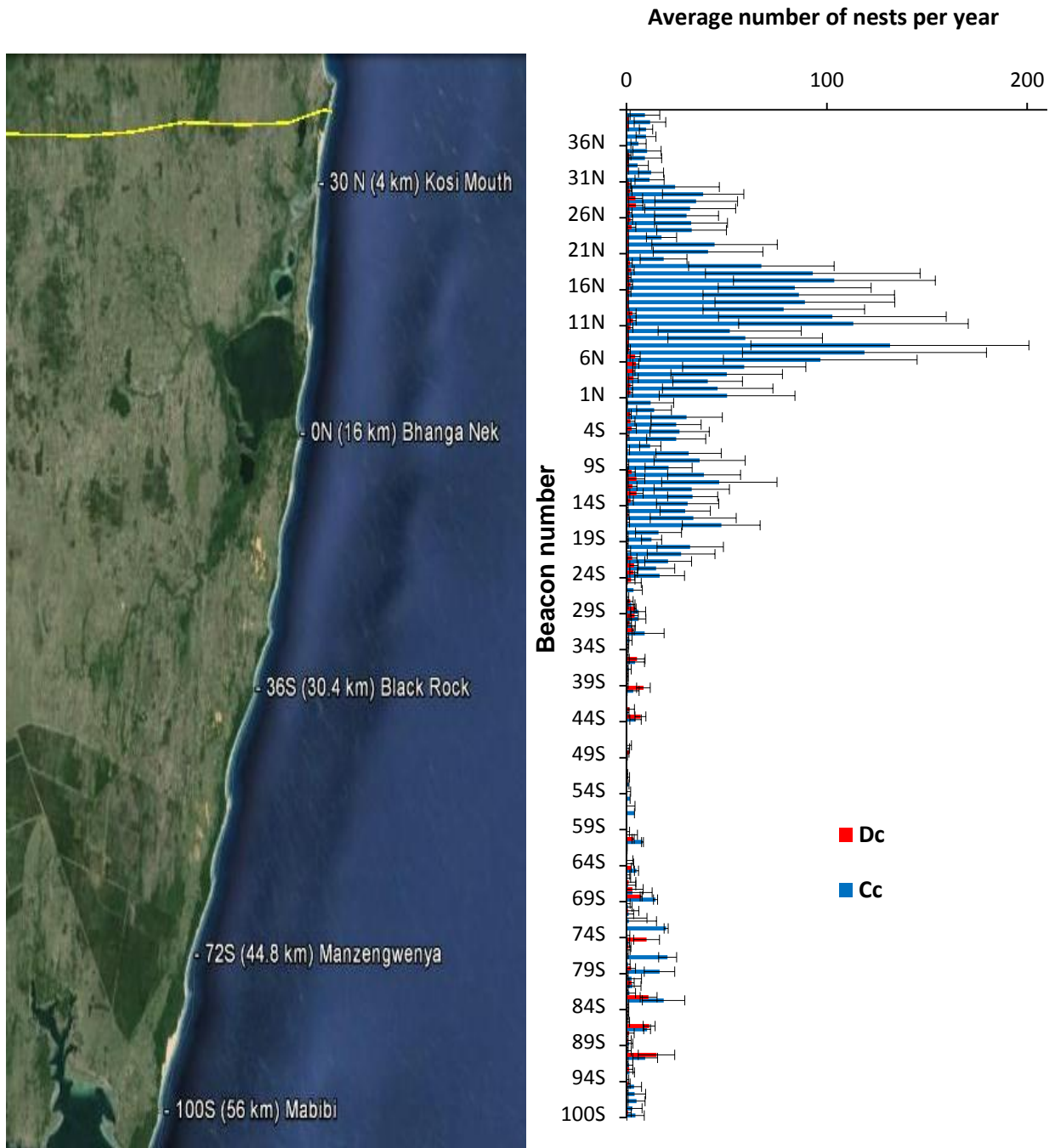
The energy content (kJ) of fresh loggerhead sea turtle eggs (mean = 171.21  $\pm$  4.64 kJ, n = 20) and hatchlings (mean = 113.53  $\pm$  1.50 kJ, n = 23) were obtained from Bouchard (1998).

It was estimated that a total number of ca. 554,025 loggerhead and leatherback sea turtle eggs were deposited on South African sandy shores per season (Table. 2.2). There were more eggs produced by loggerhead turtles (475,369), contributing to more energy (81,387,858 kJ) than leatherback (78,656 eggs and 17,084,870 kJ of energy) turtles. However, leatherback turtles contributed more energy (20,748 kJ) per nest than loggerhead (19,175 kJ) turtles due to the larger size of individual eggs even with fewer eggs per nest. After hatchlings leave the beach, a total of 37,521,567 kJ of energy remain in the beach ecosystem. In a 56 km stretch of beach, a total of 670 kJ.m<sup>-1</sup>.y<sup>-1</sup> (loggerheads = 555 kJ.m<sup>-1</sup>.y<sup>-1</sup>; leatherbacks = 115 kJ.m<sup>-1</sup>.y<sup>-1</sup>) was introduced into the system (Table. 2.2).

Table 2.2: Estimated energy (kJ) contribution to coastal ecosystems by loggerhead and leatherback sea turtles per nesting season (between 2005-2013).

Species	Total # of eggs introduced into beach (kJ)	Total egg energy introduced into beach (kJ)	Total egg energy introduced per nest (kJ)	Total egg energy remaining in beach (kJ)	Total hatchling energy remaining in beach (kJ)	Total energy remaining in beach (kJ)
<b>Loggerhead</b>	475,369	81,387,858	19,175	20,428,353	10,672,535	31,099,888
<b>Leatherback</b>	78,656	17,084,870	20,748	4,049,114	2,372,566	6,421,679
<b>Total</b>	554,025	98,472,728	39,923	24,477,467	13,045,101	37,521,567

The distribution along the shore for both loggerheads and leatherbacks showed a clear trend of high and low turtle nest densities (Fig. 2.4). Loggerhead turtle nest density was highest in the north, from beacon 40N to beacon 24S (25 km), with 104.9 nests.km<sup>-1</sup>, as oppose to the lower nest density area to the south (beacon 25S to 100S, 30 km) with only 7.4 nests.km<sup>-1</sup>. The trend was reversed and less pronounced for leatherbacks with higher nest density in the south (4.1 nests. km<sup>-1</sup>) than in the north (0.1 nests. km<sup>-1</sup>) (Fig. 2.4).



**Figure 2.4:** Study area indicating a sub-sample of loggerhead (black bars) and leatherback (grey bars) mean ( $\pm$  SD) nest numbers per beacon in the 2012 to 2015 seasons at the high and low nest density beaches. (DC = *Dermochelys coriacea*, leatherback turtle; Cc = *Caretta caretta*, loggerhead turtle).

## Discussion

In natural environments, energy and nutrients generally flow from more to less productive habitats, providing significant subsidies to recipient systems (Huxel and McCann, 1998; Nakano and Murakami, 2001). The present study revealed that the energy contribution of leatherback turtles per nest was higher than loggerheads, due to the larger size of their eggs. However, the total energy contribution of loggerheads was higher than that of leatherbacks. This is not surprising since nesting loggerhead turtles are more numerous than leatherbacks. However, both species contribute to the energy budget of sandy beach ecosystems by introducing a total of 37,521,567 kJ of energy annually. Within an environment of limited food source such as sandy beaches, such amounts of nutrients and energy are believed to represent an important food item that is then potentially available to high shore beach food webs.

Previous studies have determined energy budgets for beach ecosystems, however, most were conducted in temperate or cold systems (with higher primary productivity), whereas sea turtles nest on oligotrophic sub/tropical beaches, which makes comparison difficult. A study by McLachlan et al (1981b) investigating beach energy budget showed that a total of  $5,120 \text{ kJ.m}^{-1}.\text{y}^{-1}$  ( $2,155 \text{ kJ.m}^{-1}.\text{y}^{-1}$  from carrion washing ashore;  $497 \text{ kJ.m}^{-1}.\text{y}^{-1}$  from insects blown onto the beach; and  $2,468 \text{ kJ.m}^{-1}.\text{y}^{-1}$  from unspecified sources) of energy was introduced into beach and dune ecosystems. In this study, although sea turtles may introduce less total nutrients ( $670 \text{ kJ.m}^{-1}.\text{y}^{-1}$ ) than other sources over a year, many other turtle rookeries in the world are bigger than the South African ones. Bouchard (1998) found that the energy introduced by loggerhead turtles exceeded ( $7,854 \text{ kJ.m}^{-1}.\text{y}^{-1}$ ) those found by McLachlan et al (1981b), and this should be even more so in systems experiencing arribadas. It must also be noted that the nutrient contribution of sea turtles might be underestimated since emergence success does account for mortalities occurring while hatchlings crawl to the ocean (e.g., ghost crabs and other vertebrates) and after they reach the water (fishes and storm events).

Additionally, most subsidies on sandy beaches are deposited in the surf and intertidal zones, while sea turtles nests are laid primarily in the high shore (supratidal and fore dune) (Colombini and Chelazzi, 2003; McLachlan and Brown, 2006). Although, sea

turtles may introduce less nutrients than other allochthonous subsidies (macrophyte wrack and carrion), turtle nutrients are expected to have greater effects because they are deposited into nutrient-deprived habitats as opposed to nutrients introduced into a nutrient-rich environment (Polis and Hurd, 1996; Bouchard, 1998). Furthermore, the turtle nesting season takes place over a very small temporal scale (90 days) which means that all the nutrients are introduced in 90 days then disappear, as oppose to other subsidies than are introduced throughout the year. Thus, if the McLachlan (1981b) values are divided by 365,  $14.0 \text{ kJ.m}^{-1}.\text{day}^{-1}$ , the difference with nutrients introduced by sea turtles ( $7.4 \text{ kJ.m}^{-1}.\text{day}^{-1}$ ) annually is much smaller. This strongly highlights that turtle nutrients are introduced as a pulsed resource (which are characterized by a short duration).

The along shore distributions for both loggerheads and leatherbacks are in accordance with previous research done in these population that shows a clear nesting hot spot for loggerheads to the north adjacent to the Kosi Lakes (Hughes, 1974; Nel et al., 2013). Leatherbacks on the other hand, appear to have higher nest densities to the south, probably even outside the monitoring area (Harris et al., 2015). It is therefore expected that the turtle nutrient inputs are not consistent along the shore and will affect the beach ecosystems differently, depending on high or low nutrient availability.

Nevertheless, this research suggests that sea turtles may play important ecological role by introducing large amounts of nutrients to sandy beach ecosystems. Nutrient subsidies are however only valuable if the recipient system incorporate/utilize the nutrients, which is expected to be the case for turtle-introduced nutrients as these are easily available and very high in protein, lipids, and carbohydrates (as sea turtles produce eggs with “extra” yolk that nourishes the hatchling for weeks after emergence from the egg; Kunz and Orrell, 2004). The results of this study are consistent with the growing body of evidence highlighting the ecological importance of nutrient transfers generated by biotic vectors that cross boundaries between two ecosystems (Polis and Hurd, 1996; Caut et al., 2012). Studies have demonstrated that, in coastal and marine island systems, allochthonous inputs (transported by seabirds, pinnipeds etc.) can greatly subsidize terrestrial food webs worldwide (Polis and Hurd, 1996; Bosman and

Hockey, 1988; Erskine et al., 1998; Anderson and Polis, 1999; Caut et al., 2012). Several studies have shown that sea turtle nutrients affect several levels of beach food webs (plants, insects, vertebrates), which in turn illustrate that sea turtles may play a major role in the structure and dynamics of beach communities (Bouchard and Bjorndal, 2000; Maros et al., 2006; Hannan et al., 2007; Madden et al., 2008; Vander Zanden et al., 2012; Chapter 3-4 this dissertation).

Sandy beach ecosystems lie at the interface between land and sea and thus receive allochthonous subsidies from both habitats. This study showed that the movement and transport of nutrients across habitat boundaries can substantially increase the energy budget of a system as a pulse resource of small temporal scale. While ecological roles of sea turtles in the marine environment have been well documented (Bjorndal and Jackson, 2003), there are fewer examples of sea turtles fulfilling ecological role in terrestrial ecosystems. I suggest that sea turtle-derived nutrients represent a pulsed resource that has the potential to affect sandy beach biotic communities. Furthermore, such effects should be even more significant in systems experiencing mass nesting events such as arribadas. Thus, any fluctuation in sea turtle populations, or even in their marine prey or diet item, can lead to important cascading effects in the overall ecosystem function sea turtle provide (Bauer and Hoye, 2014; McConkey and O’Farrill, 2015, Doughty et al., 2015). Further research should investigate if consumers of the recipient system incorporate turtle-derived nutrients.

**Chapter 3: Identifying potential pathways for turtle-derived  
nutrients cycling through beach ecosystems: a multi-trophic  
approach**

## **Abstract**

Resource fluxes between spatially separated ecosystems are ubiquitous and can strongly influence biotic communities and food web dynamics. When nutrient transfer occurs as a rare, short, and intense episode of increased resource availability it is called a resource pulse. In this study, I examined the role of sea turtles as vectors of nutrients that introduce substantial amounts of nutrients into nutrient-poor beach ecosystems by depositing great numbers of eggs on the high shore. This study identified potential pathways through which turtle-derived nutrients can be incorporated into beach food webs. This was done by comparing isotopic signatures of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of potential egg consumers on beaches with high (105 nests.  $\text{km}^{-1}$ ) and low (7 nests.  $\text{km}^{-1}$ ) turtle nest densities. Of the five levels tested, only ghost crabs appear to consume egg nutrients. This confirms that turtle derived nutrients subsidize high shore/dune beach fauna but no evidence of such a strong link was obtained for the intertidal. The results also highlighted great variability in ghost crab isotope signatures (which varied in space and time) suggesting an alteration in diet and feeding behaviour according to food availability.

Keywords: sea turtle eggs, resource pulse, sandy beach food webs, nutrient pathways, stable isotope analysis



## Introduction

Resource pulses affect populations and community structures in many ecosystems (Polis & Hurd, 1996; Polis et al., 1997; Cross et al., 2006). Resource pulses are known as rare, short, and intense episodes of increased resource availability (Yang et al., 2008). These pulses have been described in a wide range of ecosystems including islands, forests, arid deserts, streams, and lakes, and include events such as El Nino rainfalls in arid systems (Polis et al., 1997; Yang et al., 2008), seed or fruits mast events (Curran and Leighton, 2000), insect outbreaks (cicadas) (Yang, 2004), marine upwelling events (Bode et al, 1997), and synchronous spawning events (salmon) (Botton and Loveland, 2011). Resource pulses can also be caused by both biotic and abiotic drivers and can vary widely in their magnitude, duration, and frequency (Yang et al., 2010).

When resource subsidies occur in pulses, they have different effects across the ecosystem: they can affect consumer responses at the individual level (switch in diet); can generate aggregative responses at the population level (numerical recruitment); and create indirect effects at the community level (like bottom-up effects, delayed effects such as increase in the density of one consumer which in turns becomes a secondary prey for consumers at higher trophic levels) (Polis et al., 1997; Lundberg & Moberg, 2003; Yang et al., 2008), and ecosystem level (e.g. when the loss of large marine fauna that are vectors of nutrients have important consequences for broad-scale nutrient cycling) (Lundberg and Moberg, 2003; Jeltsch et al., 2013; Bauer and Hoye, 2014; Doughty et al., 2015).

The flow of nutrients across two ecosystems is especially important for nutrient poor systems, such as sandy beaches. Sandy beaches generally have low primary productivity and beach food webs are almost entirely supported by marine allochthonous subsidies (Colombini & Chelazzi, 2003; Dugan et al., 2003) such as macrophyte wrack (stranded algae and seagrass), and carrion (McLachlan & Brown, 2006). The flow of nutrients from allochthonous sources to sandy beach food webs has been well studied for macrophytes and stranded wrack deposits (Stenton-Dozey & Griffiths, 1983; Jeckzejczak, 2002; Dugan et al., 2003; Olabarria et al., 2007; Lastra et al., 2008; Dugan et al., 2011) but little is known about the effects of turtle-derived

nutrients on recipient food webs. Marine turtles also contribute to beach subsidies by importing nutrients which are potentially available to beach food webs.

A key ecological role of sea turtles is that they are biotic transporters of nutrients between marine and terrestrial ecosystems (Bouchard & Bjorndal). Female sea turtles create a resource pulse into nutrient poor systems by accumulating large amounts of nutrients on the feeding grounds and then migrating to nesting areas. The females move periodically onto the beach to nest, depositing much of the accumulated nutrients in the form of eggs, into the sands of tropical (and subtropical) beaches which are characteristically nutrient poor (Polis and Hurd, 1996; McLachlan and Brown, 2006).

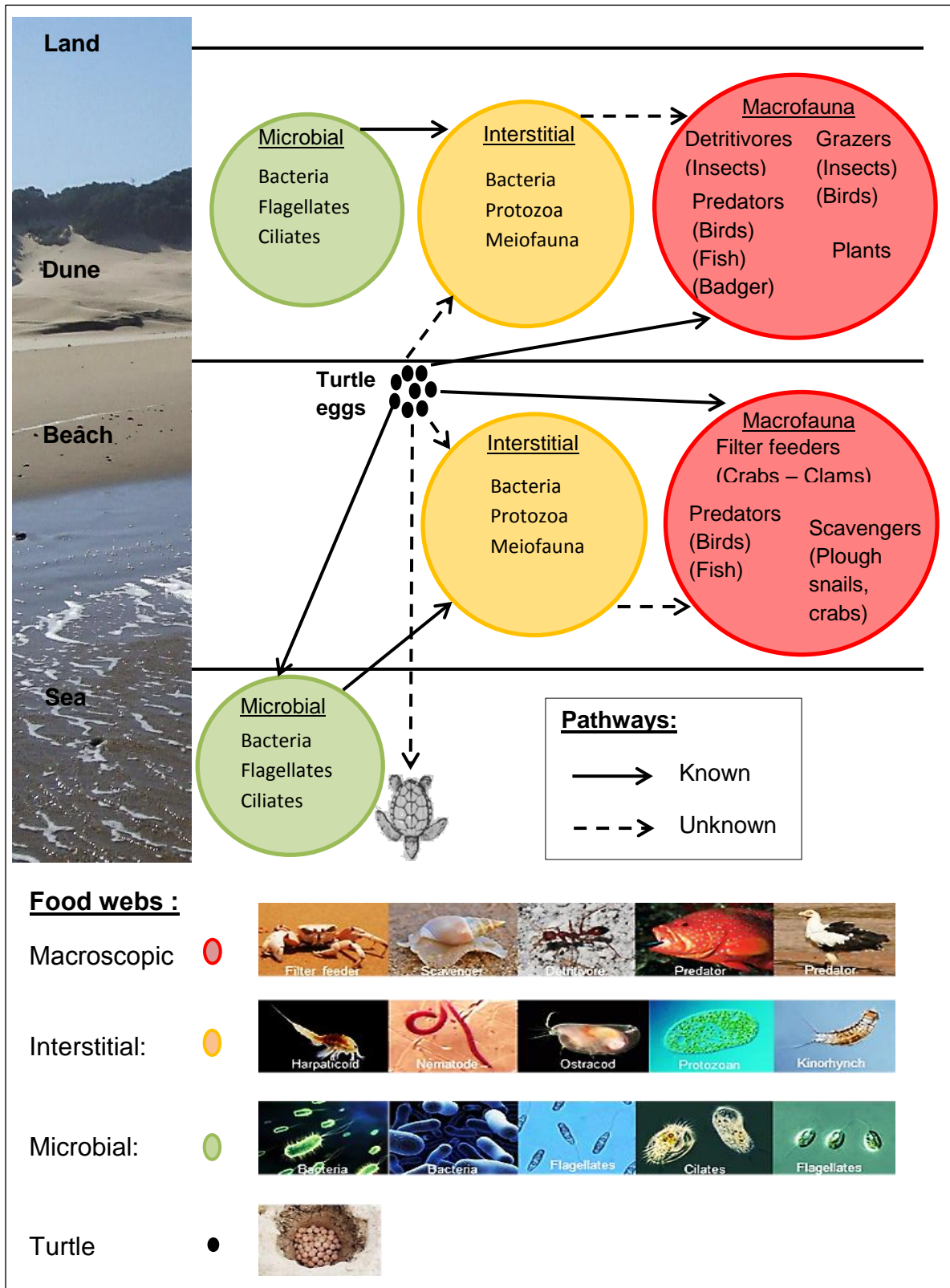
Nutrients contained in sea turtle eggs may follow several pathways. Most of the nutrients from nests return to the marine environment as hatchlings (Bouchard & Bjorndal, 2000). However, nutrients from unhatched and depredated eggs, dead and predated hatchlings, as well as chorioallantoic fluid and egg shells certainly remain in the beach and enter sandy beach ecosystem. The full contribution of these subsidies to beach food webs remains largely unquantified to date. Turtle-derived nutrients may be consumed by predators, such as ants, crabs, and raccoons that prey upon incubating nests. Most natural predators of sea turtles are site- or region-specific; for example raccoons and armadillos are among the most significant sources of egg mortality for sea turtles species that nest on the Atlantic Coast of the United States (Engeman et al., 2003; Barton & Roth, 2008), whereas foxes and wolves destroy sea turtles eggs and consume hatchlings in Oman (Mendonca et al., 2010). In South Africa predation by ants, honey badgers, monitor lizards, mongooses, domestic dogs, and ghost crabs is the greatest source of loggerhead and leatherback turtle nest mortality (18.4%) (De Wet, 2012). However, when predation occurs, most of the eggs are damaged but not consumed entirely, leaving nutrients behind and making these available to other organisms.

Sea turtle-derived nutrients have been shown to be incorporated by dune plants (Bouchard and Bjorndal, 2000; Plog et al., 2003, Hannan et al., 2007, Vander Zanden et al., 2012), beach insects (Madden et al., 2008), and terrestrial insects (Maros et al., 2006). Although the effects of sea turtle resource subsidies have been studied at the

population level, it still remains largely unknown how such resources affect the recipient communities or ecosystems such as sandy beaches (Huxel & Mc Cann, 2008; Giroux et al., 2012). One possible way to trace nutrient paths through food webs is to use stable isotopes.

Stable isotope ratios of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) have increasingly been used to provide information about feeding relationships and energy flows through food webs (Peterson & Fry, 1987; Vander Zanden & Rasmussen, 1999; Bergamino et al., 2011). Marine systems are typically  $^{15}\text{N}$  enriched relative to terrestrial food webs (Peterson, 1999; Vander Zanden & Rasmussen, 1999) so inputs of marine and terrestrial origin can be followed through trophic levels, which are especially useful in coastal ecosystems (Bergamino et al., 2011). Several studies have described pathways of marine derived nutrients on terrestrial ecosystems, e.g., 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). Turtle eggs have the highest  $\delta^{15}\text{N}$  of any known food source for consumers on sandy beaches (Plog, 2004) and since the basic principle of SIA is that stable isotope markers of consumers have a fixed relationship with the isotope signature of their diet (Vander Zanden & Rasmussen, 1999), it should be possible to follow turtle egg nutrient isotopic signatures through the beach food webs.

The aim of this study was to identify the potential pathways of turtle-derived nutrients through the Maputaland beach ecosystem using stable isotope analysis. I hypothesized that sea turtle eggs represent a pulsed resource subsidy that is consumed by both terrestrial and marine consumers (Figure. 3.1). I predicted five pathways of turtle eggs from the most dominant species: 1) a filter feeding path with the mole crab (*Emerita austroafricana*); two scavenger pathways with the 2) plough snail (*Bullia natalensis*) on the low shore and 3) the ghost crab (*Ocypode ryderi*) on the high shore; 4) a terrestrial path with pioneer dune plant species; and 5) a grazer path through meiofauna (mainly nematodes). I tested these hypotheses by comparing isotopic signatures of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of these consumers on two beaches with high (105 nests.  $\text{km}^{-1}$ ) and low (7 nests.  $\text{km}^{-1}$ ) turtle nest densities, over two sea turtle nesting seasons.



**Figure 3.1:** Conceptual framework of the potential pathways of turtle-derived nutrients through the different beach food webs.

## Materials and Methods

### Study site

The study area was located in the iSimangaliso Wetland Park, on the eastern seaboard of South Africa (Fig. 2.1 and 2.2; see Chapter 2). Samples were collected over two seasons, from December 2013 to February 2014 and from December 2014 to February 2015 at Bhanga Nek, Manzengwenya, and Mtunzini beaches.

### Sample collection

To identify the potential pathways of turtle-derived nutrients I analyzed isotopic signatures of carbon and nitrogen of beach fauna. Samples were collected during the 2013/14 and 2014/15 sea turtle nesting seasons (which typically take place from December to February). Samples of macrofauna were taken from the beach in high (Bhanga Nek, 105 nests. km<sup>-1</sup>) and low (Manzengwenya, 7 nests. km<sup>-1</sup>) nest density beaches (See *study area* in Chapter 2 with map). The sampling targeted the dominant and most abundant species present in this area that also represent specific trophic groups, namely ghost crabs (*Ocyropode ryderi*), mole crabs (*Emerita austroafricana*), and plough snails (*Bullia natalensis*) (McGwynne, 1988; Harris et al., 2014). Samples were collected using a 1mm sieve bag in the intertidal (for details of the methods see Schlacher et al., 2008) or by hand from the swash zone. Ghost crabs were caught with pitfall traps baited with sardine, and were released after two legs were removed from each individual. Additionally, dominant dune vegetation – including salt bush (*Scaevola plumieri*), goat's foot (*Ipomea pes-caprae*), and dune creeper (*Hydrophylax carnosa*) were collected from the supratidal of both high and low nest density beaches. This was done by selecting two leaves from 10 individual plants of each species. In addition, opportunistic sampling of ghost crabs (n = 9) was done in winter (July) 2014 in the high and low nest density beaches as well as in a non-nesting beach (Mtunzini, ~250 km South off Bhanga Nek). Particulate organic matter (POM) was sampled during the 2014/15 season from the high and low nest density areas. 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 from the particulate matter. Samples were then

filtered through Whatman GF/F fiberglass filter paper (precombusted at 550°C for 12 h) of  $\mu\text{m}$  pore size. All samples were preserved in 70% alcohol, except POM that were kept frozen, until further analyses.

Loggerhead (*Caretta caretta*) sea turtle eggs were obtained from nesting adult females located during nightly patrols. Ten eggs were haphazardly selected at the time of oviposition. 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 the grazer pathway of meiofauna, only nematodes were chosen as it was the most abundant taxon present and dominated all samples throughout the study. Nematodes were collected from the sediment samples obtained in the *in situ* basket experiment, and were preserved in 4 % formaldehyde solution and stained with Rose Bengal to facilitate identification and counts.

### **Stable isotope analyses**

In order to carry out the isotope analysis, small animals (meiofauna) were analyzed whole due to the impracticality to separate muscle tissue in very small species. Stable isotopic composition of organisms differs according to tissue type, and consequently, differential isotope fractionation occurs among different tissues (Lorrain et al., 2002). Muscle tissue was used for the macrofauna samples as it is considered as a useful indicator of diet due to its slower turnover rate (Lorrain et al., 2002; Rubenstein & Hobson, 2004). The muscular foot was used for the plough snails (*Bullia natalensis*), and leg-muscle tissue was used for the ghost crabs (*Ocypode ryderi*) and mole crabs (*Emerita austroafricana*) (Bezuidenhout, 2010). Muscle tissue was extracted from one set of limbs, dried at 60° C for 48 h and ground into a powder with mortar and pestle. Nematodes were handpicked with a fine needle, rinsed in distilled water and placed in eppendorf tubes. In order to achieve sufficient biomass for reliable SIA to produce a single sample (0.4-0.6 mg dry mass), 50 to 200 individuals (per replicate of each major taxon) were pooled (Moens et al., 2002; Nascimento et al., 2012). Turtle eggs were

thawed and the yolk and shell were separated. A sterile 6-mm disposable biopsy punch was used to take skin samples of the hatchlings (in the region between the neck and the front flipper).

Lipid extraction is commonly used in SIA to correct for the  $\delta^{13}\text{C}$  of consumers to better reflect  $\delta^{13}\text{C}$  of their diet because synthesized lipids have lower  $\delta^{13}\text{C}$  and can mask the  $\delta^{13}\text{C}$  of a consumer's diet (Ingram et al., 2007). However, there are some concerns that lipid extraction can cause shifts in  $\delta^{15}\text{N}$  and significantly affect the isotopic values in some tissues (Logan et al., 2008; Carpentier et al., 2015). It was therefore decided to analyze both treated (lipid-extracted) and untreated samples.

Lipid extraction was carried out using a modified Bligh and Dyer method (Bligh & Dyer, 1959). Samples that were extracted for lipids (all except plant and shell) were oven-dried at 60 ° C for 48 h and homogenized. Subsequently, samples were immersed in 2:1 chloroform: ethanol solution for 50 minutes to remove free lipids, and then oven-dried at 60 ° C for 2 h. Plant and egg shell samples were acid washed with 0.1% hydrochloric acid for 50 min to remove carbonates because structures containing carbonates are enriched in  $\delta^{13}\text{C}$  compared to organic tissues (DeNiro & Epstein, 1978). Samples were then dried for 2 h at 60 ° C. Carbon and nitrogen isotopic composition was measured in both treated (lipid-extracted and acid washed) and non-treated samples to examine the effect of pre-treatments on stable isotope values.

All (untreated and treated) samples were rinsed with distilled water, placed in tin capsules and oven-dried at 60°C for 24 h and ground to a fine powder (using mortar and pestle), in preparation for SIA. For isotopic determination, 0.3-0.5 mg was used for animal samples and 1 mg for plant samples. Analyses of elemental content of C and N isotope ratios in all samples followed those described in Bezuidenhout (2010) and Vander Zanden et al. (2012), and were undertaken at the Stable Isotope Analysis Laboratory of iThemba Labs (Johannesburg, South Africa). Stable isotope ratios are expressed in delta ( $\delta$ ) notation, defined as parts per thousand (‰) deviation from a standard material:

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

where R is the heavy-to-light isotope ratio ( $= {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$ ). The standard material is Pee Dee belemnite (PDB) limestone for  $\delta^{13}\text{C}$  and atmospheric nitrogen for  $\delta^{15}\text{N}$ . The total number of samples (n) collected from both seasons is shown in Appendix 1.

For comparison purposes, hatchlings and turtle egg shells were incorporated in the analyses but were not regarded as the main turtle-derived nutrients in this study, since hatchlings only hatch at the end of the nesting season (and would have not been incorporated yet) and because egg shell was not expected to be the main nutrient to be incorporated by beach fauna.

### **Statistical Analyses**

Differences in the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from lipid-extracted samples and non-lipid-extracted samples (original samples) were evaluated using *t* tests. The assumptions of normality and homogeneity of variances were tested before performing the *t* tests (Kolmogorov-Smirnov and Levene's test).

The incorporation of turtle-derived nutrients into sandy beach food webs was assessed by first determining the isotopic overlap between consumers and source signatures of turtle nutrients. Taking into account the enrichment occurring during assimilation of food, the values were then tested within the range of commonly accepted enrichment factors, which is between 3 and 4‰ for nitrogen and close to 1‰ for carbon (DeNiro and Epstein, 1978, 1981). Secondly, a comparison of isotope signatures of consumers sampled on high and low turtle nest density beaches was conducted using *t* tests.



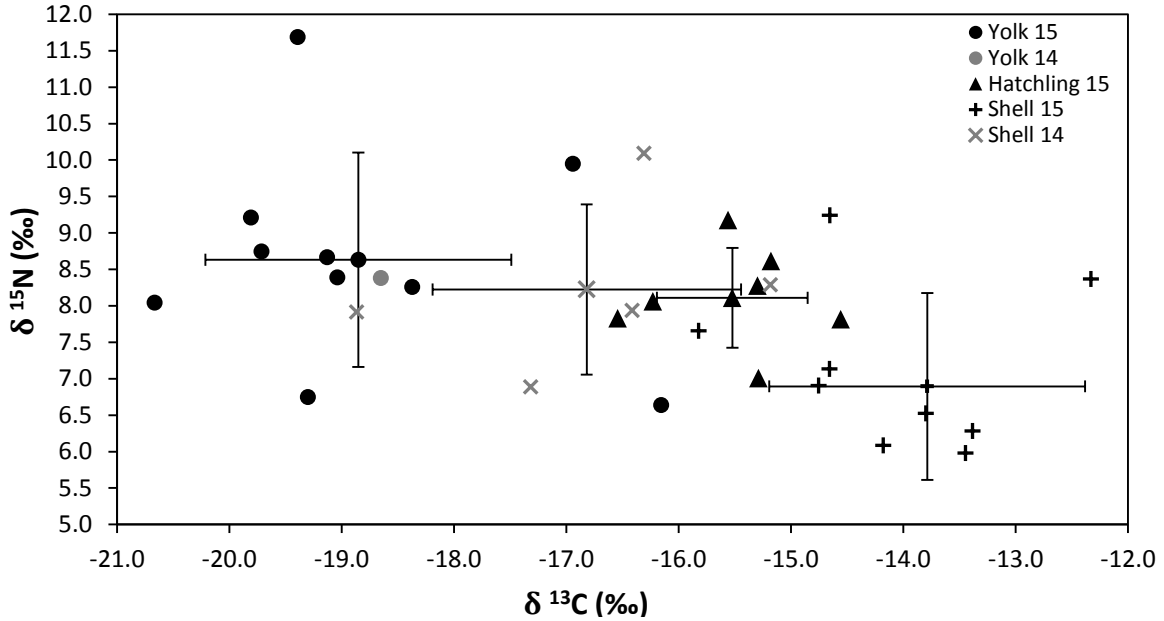
## Results

### Treatment effect

Carbon and nitrogen ratios (C:N) varied between turtle tissue and beach fauna from 3.8 to 36.9, indicating differences in lipid content of turtle tissue and macrofaunal samples (Appendix 1). For samples with no significant difference (*t* test) in either  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  values between original (non-lipid-extracted and acid-washed) or treated samples, values from original (non-treated) samples were used in the study (Appendix 1). However, for samples with significant difference the  $\delta^{15}\text{N}$  values from original samples and  $\delta^{13}\text{C}$  values from treated samples were used for further analysis. This is justified by the fact that lipid extraction as well as decalcification (hydrochloric acid) usually affects the carbon fractionation of isotopic values but not that of nitrogen (Fantle et al., 1999; Carabel et al., 2006; Bodin et al., 2007; Post et al., 2007; Kaufman et al., 2014).

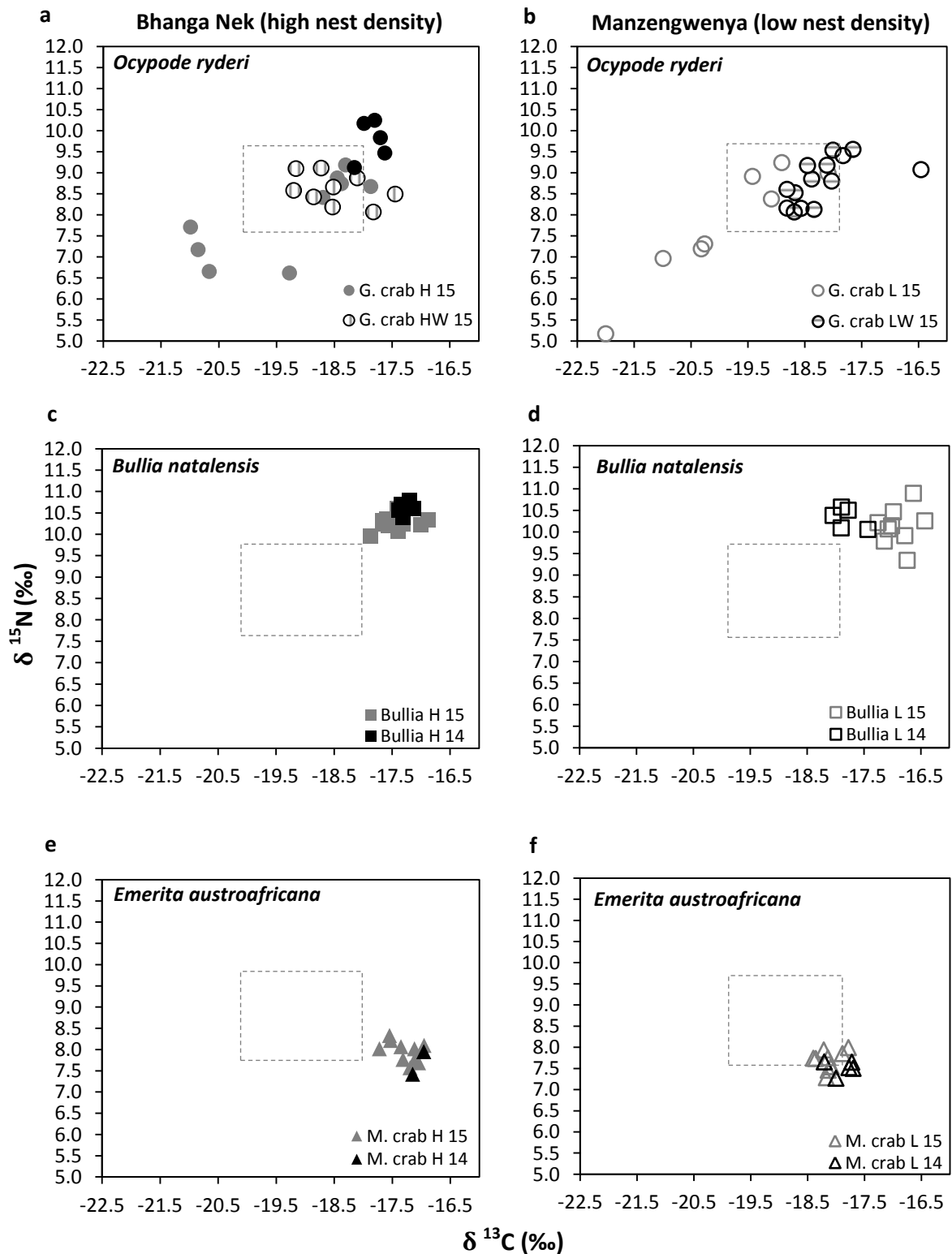
### General Patterns

Isotopic signatures of the three turtle tissues examined (egg yolk, egg shell and hatchling) are summarized in Fig. 3.2. High variability was found in both carbon and nitrogen isotopic ratios for each turtle-derived component. The 2014/15 egg yolk values ranged from 6.6‰ to 11.7‰ for  $\delta^{15}\text{N}$  and from -16.2‰ to -20.7‰ for  $\delta^{13}\text{C}$ , while values of hatchlings ranged from 7.0‰ to 9.2‰ and from -14.6‰ to -16.2‰, and values of egg shells from 6.0‰ to 9.2 and from -10.8‰ to -15.8‰ respectively. The 2013/14 egg yolk value ( $n = 1$ ), was within the range of values determined for eggs from the 2014/15 season (8.4‰ for  $\delta^{15}\text{N}$  and -18.7‰ for  $\delta^{13}\text{C}$ ), and values of egg shells ranged from 6.9‰ to 10.1‰ and from -15.2‰ to -18.9‰ respectively. Overall,  $\delta^{15}\text{N}$  signatures of the different turtle nutrient inputs for both nesting seasons followed the same decreasing trend and were ranked as shell < hatchling < yolk (Fig. 3.2).



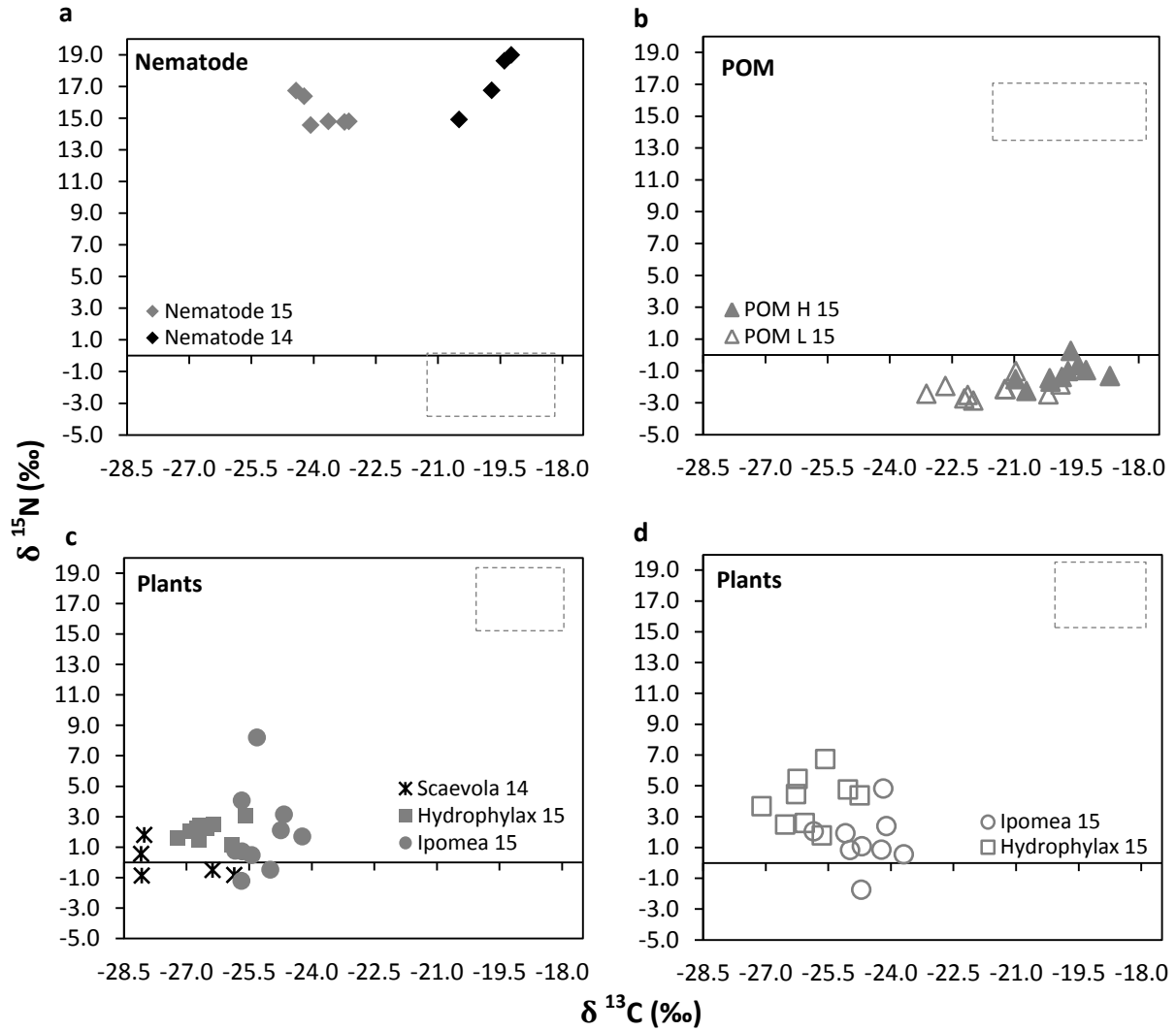
**Figure 3.2:** Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) ratios (‰) of the different loggerhead (*Caretta caretta*) sea turtle egg materials collected at Bhanga Nek during the 2013/14 and 2014/15 seasons. Symbols with error bars represent means ( $\pm$ SD). (14 = 2013/14 turtle season, 15 = 2014/15 turtle season, yolk = egg yolk, shell = egg shell).

Isotope signatures of the dominant beach macrofauna across years on the high and low nest density beaches as well as winter are presented in Fig. 3.3. Overall, ghost crabs had highly variable carbon and nitrogen signatures between years and between nest densities compared to plough snails and mole crabs, which were highly clustered and overlapped between seasons, with minimal variability. The average difference in ghost crab ratios across years and beaches was 5‰ for  $\delta^{15}\text{N}$  (range 5.2‰ to 10.2‰) and 5.5‰ for  $\delta^{13}\text{C}$  (range -16.5‰ to -22.0‰). In contrast, plough snails had a small difference in  $\delta^{15}\text{N}$  of 1.6‰ (range 9.3‰ to 10.9‰) and 1.6‰ difference between beaches in  $\delta^{13}\text{C}$  (range -16.4‰ to -18.0‰), and mole crabs an even smaller difference in  $\delta^{15}\text{N}$  of 0.9‰ (range 7.3‰ to 8.2‰) and a 1.4‰ difference in  $\delta^{13}\text{C}$  (range -17.0‰ to -18.4‰). Additionally, in the 2013/14 season the  $\delta^{15}\text{N}$  ratio of ghost crabs was higher and significantly different (Appendix 2) at Bhanga Nek (mean  $9.8 \pm 0.47$ ‰) than at Manzengwenya (mean  $8.7 \pm 0.59$ ‰). Mole crabs  $\delta^{13}\text{C}$  ratio in 2013/14 and  $\delta^{15}\text{N}$  ratio in 2014/15 were significantly different between the two beaches (Appendix 2).



**Figure 3.3:** Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) ratios (‰) of beach macrofauna samples during the 2013/14 and 2014/15 nesting seasons and winter at high (Bhanga Nek, filled symbols) and low (Manzengwenya, empty symbols) nest density beaches for *Ocypode ryderi* (a-b), *Bullia natalensis* (c-d), *Emerita austroafricana* (e-f). (H = high nest density beach; w = winter samples; L = low nest density beach; 14 = 2013/14 nesting season; 15 = 2014/15 nesting season). Grey dashed line represents the boundary of isotopic signatures of turtle egg yolk (2014/15).

In contrast to our expectations, dune plants were not identified as nutrient pathways. The carbon and nitrogen signatures of the three dominant dune plant species across years and beaches were overall much lower than the mean values of loggerhead eggs (Fig. 3.4). The nitrogen ratio of *Scaevola plumieri* in 2013/14 was much lower than the turtle egg ratio (mean 8.4‰) (Fig. 3.4). Similarly in 2014/15  $\delta^{15}\text{N}$  ratios were also lower at both beaches for *Hydrophylax carnosus* (high mean  $2.1 \pm 0.57\text{‰}$ , low mean  $4.0 \pm 1.57\text{‰}$ ) and *Ipomea pes-caprae* (high mean  $1.9 \pm 2.71\text{‰}$ , low mean  $1.4 \pm 1.76\text{‰}$ ) than the egg values (yolk mean  $8.6 \pm 1.47\text{‰}$ , shell mean  $6.9 \pm 1.28\text{‰}$ ) (Fig.3.5b). Except for dune plants, nematodes in the 2013/14 season showed the most depleted  $\delta^{13}\text{C}$  signature (mean  $-19.7 \pm 0.56\text{‰}$ ), and the highest  $\delta^{15}\text{N}$  enrichment (mean  $17.3 \pm 1.87\text{‰}$ ) as well as in the 2014/15 season (mean  $15.3 \pm 0.96\text{‰}$ ) than any other organism (Fig. 3.4). Overall, nematodes had a high variability in nitrogen signatures across years with a differences of  $4.4\text{‰}$  (range  $14.6\text{‰}$  to  $19\text{‰}$ ), while carbon ratios had a clear separation between seasons with little variation ( $1.3\text{‰}$ ) (Fig. 3.4). Carbon and nitrogen ratios of particulate organic matter across beaches (both high and low turtle nesting densities) were overall much lower than the boundary of isotopic signatures of turtle egg yolks (Fig. 3.4). In the 2014/15 season, both carbon and nitrogen values of POM were significantly different between Bhanga nek (high nest density) and Manzengwenya (low nest density beach) (Appendix 2).



**Figure 3.4:** Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) ratios (‰) of nematode (a), POM (b), and plant samples (c-d) collected during the 2013/14 and 2014/15 nesting seasons at the high (Bhanga Nek) and low (Manzengwenya) nest density beaches. The different samples are identified by the following symbols: diamonds for nematodes; triangles for POM, circles for *Ipomea*; squares for *Hydrophylax*; stars for *Scaevola*. (*Scaevola* was only sampled in the 2013/14 season; POM only in the 2014/15 season and nematodes only in the high nest density beach). Grey dashed line represents the boundary of isotopic signatures of turtle egg yolk (2014-15).

## Discussion

### Turtle-derived nutrients pathways

The present study provides the first detailed information on turtle-derived nutrient utilization by sandy beach fauna, using a dual carbon and nitrogen stable isotope approach. The results of this study for sea turtle egg tissues were similar to those found in other studies where yolk was the most carbon-depleted and nitrogen-enriched of all turtle tissues (Ceriani et al., 2014). Isotopic signatures of turtle egg yolk were similar for carbon and slightly less for nitrogen to those found in other studies (Maros et al., 2006; Zbinden et al., 2011; Ceriani et al., 2014). In contrast to previous studies (Carpentier et al., 2015), egg yolks had higher nitrogen isotope signatures than hatchlings. This is based on the fact that the metabolic process that forms a hatchling body parts (skin, bone, etc.), have different chemical pathways, and the difference noticed between hatchling and yolk signatures is the result of the tissues' formation chemistry. The high variability in  $\delta^{15}\text{N}$  of turtle egg in this study might be due to the fact that the turtle tissues sampled in this study originate from female turtles foraging in isotopically distinct areas that affect the isotopic signature of consumers (Hatase et al., 2002; Ceriani et al., 2014; Vander Zanden et al., 2014). Although, I recognize the shortcomings linked to our small sample size (egg  $n = 1$ ) in 2013/14, I am confident that the signatures were comparable to those in other studies since it has been demonstrated that there is no significant intra- or inter-clutch variations in  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  egg yolks from the same female during a nesting season, and the isotope signature of a single egg can be used for isotopic analyses (Hatase et al., 2002; Ceriani et al., 2014).

The stable isotope analyses revealed important aspects of the foraging ecology of beach consumers as well as the role of turtle nutrients for beach communities. Our hypothesis that turtle nutrients would be incorporated by pioneer dune plants did not hold true for this study. The nitrogen signature of the three plant species was very low and in accordance with those reported for other  $\text{N}_2$  fixing plants (Virginia and Delwiche, 1982; Heaton, 1987). These plants get all their nitrogen from the air, as a result of symbiotic associations with nitrogen-fixing bacteria (such as 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.

The isotopic signatures of certain, but not all, consumers varied among beaches with different nesting densities. Our hypothesis that turtle nutrients would follow scavenger pathways holds true for ghost crabs only in the 2013/14 season, and not for plough snails. The difference that appeared in the nitrogen signatures of the two scavenger species between beaches of high and low nesting densities was only clearly demonstrated by the results of the ghost crabs. Ghost crabs had higher  $\delta^{15}\text{N}$  values on the high nesting density beach (Bhanga) than at the low nesting density beach (Manzengwenya) in 2013/14 (Appendix 2). From the mean egg yolk nitrogen value of 8.4‰ (in 2013/14) and according to the assumed nitrogen enrichment factor (3-4‰), ghost crab consuming exclusively eggs should have a ratio close to 11.4‰, which is not what was found since the highest ghost crab signature was 10.2‰. Taking the mean egg yolk value (8.4‰) and the mean ghost crab value (9.8‰), it appears that the enrichment factor for ghost crabs in this study is closer to 1.4‰. It is likely that this enrichment factor is due to the fact that ghost crabs eat some egg yolk and other items, which is why the fractionation is low. This implies that the commonly used enrichment factor of 3-4‰ for nitrogen might be overestimated. Our enrichment factor of 1.4‰ falls within the range of mean  $\delta^{15}\text{N}$  enrichment found for the blue crab (*Callinectes sapidus*) (0.1 to 3.1‰; Vanderklift and Ponsard, 2003). Additionally, Hussey et al (2014) recently showed that nitrogen enrichment is not constant and narrows with increasing dietary  $\delta^{15}\text{N}$  and is species-specific (and should be lower for omnivorous consumers).

The higher nitrogen signature of ghost crabs in 2013/14 suggests that on high nesting density beaches, ghost crabs' diet is more homogeneous (consisting predominantly of turtle eggs). This is not surprising as the high nest density site receives a substantially larger nutrient subsidy from sea turtle nests than the low nest density site over time. Ghost crab predation on turtle eggs and hatchlings has been frequently observed in numerous studies (e.g. Barton & Roth, 2008, De Wet, 2010). This is most likely due to the fact that these crabs are highly mobile and the fastest crustaceans on land, reaching speeds of  $4 \text{ m s}^{-1}$ , hence capable of covering long distances during foraging trips

(Lucrezi & Schlacher, 2014). This ability allows ghost crabs to have a broad across-shore distribution, occupying a wide band across the dune-beach-surf gradient, extending from the lower intertidal up to 400 m inland (Lucrezi & Schlacher, 2014). What this study clearly highlighted is the high variability of ghost crab isotopic signatures illustrating that they feed on a large variety of food sources. Ghost crabs display a remarkable trophic plasticity, occupying several trophic levels as omnivores. Ghost crabs can be deposit feeders (microalgae, meiofauna), scavengers (stranded carcasses of fish, whales, insects, birds, jellyfish etc.), and predator of both invertebrates (clams, amphipods, mole crabs, isopods etc.) and vertebrate prey (turtle eggs and hatchlings) (Barton & Roth, 2008; Robertson & William, 1981; Vinagre et al., 2007; Correa et al., 2014; Morrow et al., 2014; for a review see Lucrezi & Schlacher, 2014). Thus, although ghost crabs are well equipped to predate on turtle eggs and are known to switch to a turtle-derived diet during turtle nesting seasons (Barton & Roth, 2008), their diets are determined by food availability in beach habitats. Sandy beaches are harsh and dynamic systems with erratic food supply and beach fauna must survive nutritional deprivation constantly. Hence, ghost crabs are exposed to great variation in the items of their diet and therefore alter their feeding behaviour according to the food availability of the habitat (Vinagre et al., 2007). Additionally, less turtles were found to nest in the 2014/15 (Ezemvelo, Unpublished data) season (compared to the 2013/14 season) which might explain why I did not find the same trend of higher nitrogen signatures on the high nest density beach in the 2014/15 season, if ghost crabs competition for eggs was higher and fewer eggs were available per crab.

In contrast, our hypothesis did not hold true for the plough snail or mole crab path of turtle nutrients on the intertidal. Both species appear unaffected by turtle nutrients on beaches with different nesting densities. This finding might indicate that they did not have direct access to nutrients as they remain in the intertidal zone and cannot move on the high shore where the nests are located and thus must feed on other sources of nutrients. Furthermore, plough snails are carnivorous scavengers adapted to feed on carrion (rachiglossan radula, Brown, 1982) and would not utilize particulate organic matter if it reached the intertidal and rather predate on other invertebrate beach residents if food is scarce (Brown, 1982). I also expected the nutrients from turtle eggs



to leach back into the surf zone and to be utilized by mole crabs, via phytoplankton or other particulate matter that incorporated turtle-derived nutrients. However, this study could not demonstrate such a trophic link. It is possible that most nutrients from the eggs remained deep in the sand layers and were decomposed by microbial activity and were not available to organisms further down in the surf zone. Alternatively, the results of *t* tests showed that there was significant difference of mole crab carbon signature in 2013/14 and in nitrogen in 2014/15 between beaches of high and low nest densities. Interestingly, both carbon and nitrogen values of POM were also significantly different between beaches. This could indicate that I could not find a strong egg signature in mole crabs because turtle nutrients could have been diluted and thus not be a direct path, but rather incorporated in nearshore phytoplankton. The present study might show some indication of a turtle nutrient effect, however, we do not know the specific mechanisms taking place and caution should be exercised when interpreting the data. Potential food sources for mole crabs have been reported to be particulate organic matter, macroalgae and carrion (Bezuidenhout, 2010). It is also possible that there is a delayed effect and that it takes a long time for turtle nutrients to be made available in the surf zone. In this case, a lagged response by mole crabs could occur. However, the isotopic signature in the consumer could be much smaller and might not be noticeable.

The carbon isotopic signatures of nematodes found in this study showed clear differences between the 2013/14 and 2014/15 seasons which can be explained by the fact that the turtle eggs used in the two seasons were from sea turtles that came from isotopically distinct foraging areas (Hatase et al., 2002; Ceriani et al., 2014; Vander Zanden et al., 2014). The nitrogen ratios 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). Nematode nitrogen isotopic ratios found in this study were abnormally high which can be explained by the fact that a dye (Rose Bengal) was added to nematodes samples (to assist in identification and count) and might have altered their isotopic signature. A study by De Lecea et al. (2011) showed that adding Rose Bengal to formalin caused a large enrichment in nitrogen ratios of zooplankton. However, the reasons for this change in fractionation are species-dependent and not yet fully understood.

### **Spatio- temporal variation of turtle-derived nutrients**

The spatial distribution of sea turtle nests on a beach is patchy and might have more localized effects than previously expected. A study by Caut et al. (2012) that compared the effect of seabird guano on different terrestrial compartments (plants, arthropods, rodents, reptiles) on islands with large seabird colonies and island with no seabirds revealed that nitrogen enrichment by birds was highly localized. Differences in isotopic values were recorded in areas only 50-200 m apart. Thus, in the present study, the samples collected might have been just outside the range of the potential nitrogen enrichment by sea turtle nutrients. Furthermore, our results suggest that turtle nutrients only had an effect on the high shore/dune part of the beach and not the intertidal or surf zone. This demonstrates the importance of spatial scale, especially regarding sampling selection, when defining the impacts of nutrient transport by biotic vectors.

Resource pulses can have direct short term effects as well as indirect long term effects. A direct marked numerical/aggregative response from consumers is usually observed rapidly after the occurrence of a pulse event (Holt, 2008; Yang et al., 2008, 2010; Spiller et al., 2010). Although resource pulses are generally short, their ecological effects can persist long after the pulse itself has diminished. Delayed reproductive responses may have more persistent effects on local communities (Yang et al., 2008, 2010; Spiller et al., 2010). Thus, when using stable isotopes it is suggested that the temporal implications of the sampling protocol must be considered.

### **Ecological implications**

In this study, turtle-derived nutrients were mainly exploited by ghost crabs, and showed that marine turtle nutrients entered the beach food web only on the high shore/dune part of the beach. However, other studies have shown several pathways of turtle nutrients through beach ecosystems: terrestrial plants (Plog et al., 2003; Hannan et al., 2007; Vander Zanden et al., 2012); terrestrial vertebrates (e.g., raccoons and birds; Bouchard & Bjorndal, 2000), terrestrial invertebrates (e.g., fly larvae, fungi, mites, beetles, crickets and ants; Madden et al., 2008; Maros et al., 2006), and intertidal/beach invertebrates (e.g., ghost crabs; Bouchard & Bjorndal, 2000). Although, nutrient subsidies on sandy

beaches can come from a variety of sources (macrophytes, stranded wrack) it is likely that sea turtle nesting (thousands or millions of eggs per season) contributes even greater quantities of nutrients and energy than other subsidies. Moreover, such nutrient contributions to beach food webs by sea turtles should be amplified in systems that experience arribadas, i.e., mass synchronized nesting of olive ridley turtles, where nest density exceeds 180 000 nests (Shanker et al., 2004).

Much uncertainty remains regarding the predictability of enrichment in consumer tissues and the accuracy with which we can interpret stable isotope data since inaccurate enrichment values can introduce errors in identification of diets and estimates of trophic position (McCutchan et al., 2003). However, those shortcomings can be revised with more data collection in the field and laboratory experiments. It appears that integrating stable isotope analysis into the study of pulsed resources holds great promise and knowledge on isotopic variations due to sea turtle nutrient input will contribute to the interpretation of the potential role of sea turtles in ecosystem functioning.

In conclusion, tracking the ecological effects of turtle nutrient subsidies through the beach ecosystem has proven challenging, especially given the complexities of beach food webs. The present study demonstrated that there was a clear response in ghost crabs to turtle-derived nutrients. However, turtle resources did not affect all beach food webs and it appears that the effects are species dependent - influenced by trophic guild, zonation on the beach, and mobility of the species (since *Bullia*, which occupy the same trophic guild as ghost crabs but not the same zone, did not respond to turtle nutrients). The study illustrated that ghost crabs are an opportunist species that alter their diet in response to pulses of turtle-nutrients and according to the food availability of the habitat. Further studies are needed to understand how turtle nutrients affect terrestrial and marine food webs. Studies should also consider sampling over a longer time scale after the pulse to detect delayed effects or assess patterns over several years.

**Appendix 1:** Carbon and nitrogen ratios (C:N) for loggerhead sea turtle tissues and beach fauna analyzed and results of *t* tests comparing  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values before and after treatment (lipid removal for all samples except plant and shell samples that were acid washed). *n* = sample number; W = winter sampling; Mtu = Mtunzini (non-nesting beach); Bhanga Nek = high nest density beach; Manzengwenya = low nest density beach. Bold numbers indicate significance ( $p < 0.05$ ); na = not applicable).

Sample	<i>n</i>		Beach	C:N	Significance ( <i>p</i> value)	
	Untreated	Treated			$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
<b>2013/14 turtle season</b>						
<i>Ocypode ryderi</i>	5	5	Bhanga Nek	4.1	0.950	0.300
<i>Ocypode ryderi</i>	2	4	Manzengwenya	4.1	<b>0.013</b>	0.967
<i>Bullia natalensis</i>	5	5	Bhanga Nek	4.1	<b>0.010</b>	<b>0.031</b>
<i>Bullia natalensis</i>	5	5	Manzengwenya	4.0	<b>0.000</b>	<b>0.000</b>
<i>Emerita austroafricana</i>	2	0	Bhanga Nek	3.8	na	na
<i>Emerita austroafricana</i>	5	2	Manzengwenya	4.3	0.129	<b>0.030</b>
Nematode	4	3	Bhanga Nek	11.5	0.978	0.332
<i>Scaevola plumieri</i>	5	5	Bhanga Nek	22.7	0.758	0.427
Shell	5	5	Bhanga Nek	5.7	0.630	0.552
Yolk	1	2	Bhanga Nek	7.4	0.667	0.386
<b>2014/15 turtle season</b>						
<i>Ocypode ryderi</i>	9	10	Bhanga Nek	4.4	0.238	0.445
<i>Ocypode ryderi</i>	8	9	Manzengwenya	4.3	0.921	0.535
<i>Ocypode ryderi</i> W	9	10	Bhanga Nek	4.2	<b>0.004</b>	<b>0.048</b>
<i>Ocypode ryderi</i> W	10	9	Manzengwenya	4.2	0.360	0.639
<i>Ocypode ryderi</i>	8	9	Mtunzini	3.9	0.759	0.946
<i>Bullia natalensis</i>	10	10	Bhanga Nek	4.4	0.067	0.574
<i>Bullia natalensis</i>	9	10	Manzengwenya	4.4	0.199	<b>0.001</b>
<i>Emerita austroafricana</i>	10	10	Bhanga Nek	4.6	0.826	<b>0.000</b>
<i>Emerita austroafricana</i>	10	10	Manzengwenya	4.5	0.917	0.287
Nematode	6	6	Bhanga Nek	7.4	0.975	0.276
<i>Hydrophylax carnosus</i>	10	10	Bhanga Nek	36.9	<b>0.008</b>	<b>0.040</b>
<i>Hydrophylax carnosus</i>	9	10	Manzengwenya	32.2	0.136	0.424
<i>Ipomea pes-caprae</i>	10	10	Bhanga Nek	21.1	0.693	0.520
<i>Ipomea pes-caprae</i>	9	8	Manzengwenya	19.2	0.507	0.354
POM	10	9	Bhanga Nek	9.4	<b>0.003</b>	<b>0.000</b>
POM	10	8	Manzengwenya	6.8	<b>0.001</b>	<b>0.000</b>
Shell	10	10	Bhanga Nek	7.4	0.213	0.130
Yolk	10	9	Bhanga Nek	8.5	0.667	<b>0.001</b>

**Appendix 2:** Results of paired *t* tests comparing  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in the high (Bhanga Nek) and low (Manzengwenya) nest density beaches. Bold numbers indicate significance ( $p < 0.05$ )

Sample	Beach	N			C		
		<i>df</i>	<i>T</i> Stat	<i>p</i>	<i>df</i>	<i>T</i> Stat	<i>p</i>
<b>2013/14 season</b>							
<i>Ocypode ryderi</i>	high vs low	5.55	2.74	<b>0.035</b>	3.26	0.12	0.910
<i>Bullia natalensis</i>	high vs low	6.83	2.29	0.057	7.97	-0.36	0.727
<i>Emerita austroafricana</i>	high vs low	1.14	0.5	0.695	5.00	7.61	<b>0.001</b>
<b>2014/15 season</b>							
<i>Ocypode ryderi</i>	high vs low	12.64	0.40	0.692	14.72	0.98	0.340
<i>Bullia natalensis</i>	high vs low	9.93	0.81	0.439	13.33	-1.67	0.117
<i>Emerita austroafricana</i>	high vs low	17.96	2.92	<b>0.009</b>	17.86	1.92	0.071
<i>Hydrophylax carnosa</i>	high vs low	9.98	-3.51	<b>0.006</b>	13.15	-2.10	0.055
<i>Ipomea pes-caprae</i>	high vs low	15.60	0.54	0.597	15.91	-2.22	<b>0.041</b>
POM	High vs low	17.04	3.76	<b>0.002</b>	15.33	4.35	<b>0.001</b>

**Chapter 4: Quantifying meiofaunal responses to sea turtle  
egg decomposition over time**

## Abstract

Nutrient flows across ecosystem boundaries strongly influence consumer populations and food web dynamics. Consequently, it is hypothesized that sandy beaches, which are nutrient-poor ecosystems and almost exclusively subsidized by allochthonous inputs, should respond to nutrient inputs deposited by sea turtles. Large quantities of nutrients in the form of eggs are deposited on the high shore during the turtle nesting season. This study quantifies the response of meiofauna to the decomposition of turtle eggs over time. I first determined meiofaunal densities in predated nests. Secondly, I experimentally quantified their response to nutrient inputs over time, *in situ*, by comparing meiofauna communities from five artificially predated pseudo-nests with those from five control pseudo-nests, sampled daily at three depths for three weeks. There was a strong temporal response of the meiofauna in the experimental treatment compared to that in the controls. After five days, the meiofaunal communities in the experimental treatment were significantly different to those in the control treatment, with abundance of all taxa higher in the experimental treatment, particularly nematodes. The peak of the response (maximum nematode abundance:  $10 \times 10^5$  ind. $40$  ml $^{-1}$ ) was observed after eight days. Thereafter, their density declined until the control treatment density ( $<1000$  ind. $40$  ml $^{-1}$ ) was reached again after 20 days. Given the large quantity of turtle eggs deposited above the high tide mark, these seasonal inputs represent a pulsed resource with a significant contribution to the energy budget of sandy beach/dune ecosystems. Turtle nesting may thus play a key ecological role in structuring faunal communities of sandy beach ecosystems.

Keywords: Sea turtle, sandy beach, nematode, resource pulse, South Africa

## Introduction

Nutrient fluxes across habitats can strongly influence populations and community dynamics in many ecosystems (Polis & Hurd, 1996; Polis et al., 1997; Cross et al., 2006). The most dramatic effects are produced in response to resource pulses, which are ephemeral events of increased resource availability that combine low frequency, large magnitude and short duration (Yang, 2004; Yang et al., 2008; Holt, 2008). In such events, resources are gradually accumulated over time and then released to consumers in a pulse, e.g., the salmon migration (Fennessy et al., 2010), sardine run (Hutchings et al., 2010), and insect outbreaks (Yang, 2004). The associated population responses include increased primary (plant) and secondary (animal) productivity, followed by an increased abundance of consumers (Polis et al., 1997; Cross et al., 2006). When resource pulses are spatially localized, consumers should generally aggregate, build up in numbers, and then disperse to adjacent patches when those resources are depleted (Holt, 2008). In this way, resource pulses play important ecological roles, influencing nutrient flows which in turn affect the productivity, food webs, and community structure and dynamics of ecosystems (Polis et al., 1997; Loreau and Holt, 2004). However, the question remains how communities respond in nutrient-poor systems where resources are inherently scarce, such as in sub-/tropical sandy beach ecosystems?

Sandy beaches are at the interface between marine and terrestrial ecosystems and are generally characterized by low primary productivity due to the absence of macrophytes/plants in the surf and intertidal zones (McLachlan & Brown, 2006; Botton & Loveland, 2011). Food availability is highly erratic and beach food webs are almost entirely supported by allochthonous subsidies, e.g. macrophyte wrack particularly abundant adjacent to cold, kelp-dominated systems, stranded algae and seagrass, and carrion (McLachlan & Brown, 2006). Under particular conditions (off long, high energy beaches with dissolved nutrient inflows) phytoplankton stocks can be extremely high due to surf diatom accumulations (Campbell, 1996; Netto & Meneghel, 2014). Studies on sandy beach subsidies thus have largely concentrated on the effect of macrophyte wrack inputs on macrofauna frequently in temperate systems (Stenton-dozey & Griffiths, 1983; Colombini et al., 2000; Jedrzejczak, 2002; Dugan et al., 2003, 2011; Olabarria et al., 2007; Lastra et al., 2008). In contrast, the effects on meiofauna have received



substantially less attention, despite the high diversity and density of these animals in the sediment (which can be orders of magnitude more abundant than macrofauna, reaching  $1 \times 10^6$  individuals per square meter; Gheskiere et al., 2004; Mclachlan & Brown, 2006; Giere, 2009). Similarly, the effects of sea turtle eggs as a pulsed nutrient source has also been largely overlooked, even though it likely represents an important resource subsidy given the quantity of eggs deposited and high quality of the nutrients. Further, turtle nesting is restricted to tropical and subtropical shores which are adjacent to oligotrophic oceans (Raymont, 1980; Schlosser et al., 2014), thereby enhancing the relative importance of this resource to beach/dune ecosystems.

Several studies have shown that turtle-derived nutrients can be incorporated into dune food webs in a variety of ways. These include - terrestrial vertebrates, like raccoons and birds (Bouchard & Bjorndal, 2000); coastal insects, including fly larvae, mites, beetles, crickets and ants (Maros et al., 2006; Madden et al., 2008); dune plants (Plog et al., 2003; Hannan et al., 2007; Vander Zanden et al., 2012). To date, however, the potential effect on meiofaunal communities has not been measured. Because meiofauna have such a rapid generation time, it is possible that these organisms may respond dramatically to a pulsed resource, such as the turtle nesting phenomenon, if they can access these nutrients.

Meiofauna feed on bacteria, diatoms and protists, with the main food sources for beach meiofauna including microphytobenthos and phytoplankton (Moens et al., 2002; Nozais et al., 2005). However, knowledge of the trophic position of meiofauna in marine sediment is still contradictory (Rzeznik-Orignac & Fichet, 2012). In sandy beaches, free-living aquatic nematodes are usually the most abundant group of meiofauna (McIntyre, 1969, Giere, 2009). These nematodes are generally considered to be herbivores, grazing on microalgae and bacteria, but also feeding on dissolved organic matter. However, comparison of buccal cavity morphology among nematode taxa suggests that other feeding guilds are possible, including omnivores, deposit feeders, epistrate feeders, scavengers and predators (Heip et al., 1985; Jensen, 1987; de Goede et al., 1993; Moens & Vincx, 1997; Moens et al., 2002). Given that Wall et al. (2002) found increasing numbers of omnivorous nematodes in relation to increasing organic matter

accumulations, it is plausible that beach meiofauna – and particularly nematodes – will show the classic biological responses to a resource pulse.

The aim of this study is thus to assess the response of the meiofauna to the decomposition of turtle eggs over time. I hypothesize that turtle-derived nutrients represent a resource pulse that affects sandy beach meiofaunal communities. Consequently, I predict that meiofaunal abundance is positively affected by turtle nutrients and that higher meiofaunal abundance will be found in response to egg decomposition over time. Specifically, I first compare meiofaunal abundance in naturally predated nests relative to densities outside of nests; and secondly, quantify the temporal response of meiofauna to the resource pulse with an *in situ* experiment that mimics conditions of naturally predated sea turtle nests.

## **Materials and Methods**

### **Study site**

Sample collection and experiments were carried out during the turtle nesting season from December 2014 to February 2015 at Bhanga Nek (Fig. 2.1, see Chapter 2).

### **Meiofauna sampling**

Predated loggerhead turtle nests were sampled to assess the response of meiofauna to turtle nutrients. Predated nests were those nests that had been predated on by honey badgers, mongoose, ants, monitor lizards, domestic dogs, and ghost crabs (De Wet, 2012) and had clear signs of disturbance (egg shells laying at the surface, ghost crab burrows going to the nest chamber; Fig. 4.1). These predated nests were sampled by filling a 40 ml sample jar with sediment taken at 5, 20, and 40 cm depth, with control samples taken 2 m away from the nest, digging a hole and then sampling at the same depths. In total, 15 predated nests with adjacent controls were sampled.



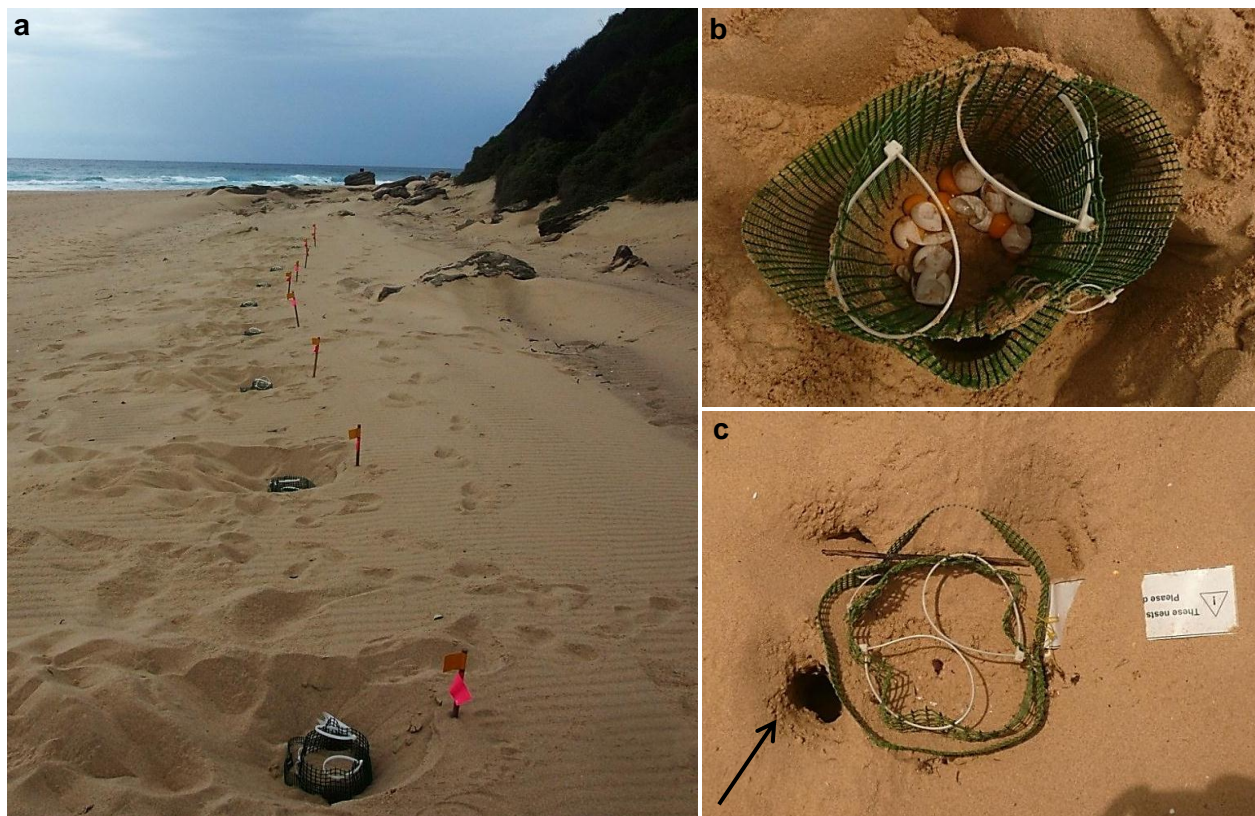
**Figure 4.1:** Examples of predated nests (a-b) with numerous egg shells visible at the sand surface; some nests were newly predated (c), and others were older (d).

### **Experimental design of *in situ* experiment**

The following experiment was designed to monitor changes in meiofauna communities in response to the decomposition of turtle eggs over time. Ten pseudo-nests in two treatments (5 controls and 5 experiments) were placed 2 m apart at the dune base (Fig. 4.2a) at Bhanga Nek. Each pseudo-nest comprised two baskets of 30 cm in diameter and 30 cm in depth. The inner basket, made of 1-mm mesh, was placed into an outer basket of 0.5-mm mesh that facilitated easy removal of the clutch out of the sand, with minimal disturbance to the surrounding sand (Fig. 4.3). Fifty eggs were collected from nesting female loggerhead (*Caretta caretta*) nests (5 eggs from 10 turtles) while they were laying eggs at night. Ten eggs were placed in each of the experimental baskets and the shell ruptured to mimic natural predator damage in a nest e.g., badger biting

into eggs or a ghost crab pinching through the egg shell. All baskets were placed into a pseudo-nest and then filled with sand (Fig. 4.2b.c).

Small (40 ml) sediment samples were taken daily by scraping the dry sand of the surface, removing the basket and then taking a sample at the surface, middle and bottom (5, 20, 40 cm depth, respectively) of the baskets to quantify the abundance of beach meiofauna in the baskets. These samples were preserved in 4 % formaldehyde and stained with Rose Bengal to facilitate identification (Rodriguez et al., 2001; Nozais et al., 2005; Sajan et al., 2010). The experiment was carried out for a period of 20 days, with a total of 630 samples obtained over three weeks.



**Figure 4.2:** (a) Pseudo-nests were placed at the dune base, 2-m apart, comprising an inner- and outer basket. (b) Pseudo-nests in the experiment treatment had 10 freshly broken turtle eggs added to the inner basket. (c) All baskets were then covered with sand. Subsequent predation by ghost crabs (*Ocypode ryderi*) was also evident, with the crab's burrow indicated by an arrow in c.

### **Meiofauna extraction**

In the laboratory, the meiofauna was extracted from the sediment by elutriation (Moens et al., 2002; 2005). Each sample was placed into a 2 L plastic bottle with filtered tap water (using a 45- $\mu\text{m}$  sieve) and vigorously shaken for 10 s. The water was then passed through a 1-mm and a 45- $\mu\text{m}$  mesh sieve. This procedure was repeated twice. The sediment and meiofauna retained on the 45- $\mu\text{m}$  mesh sieve were then placed into a sample jar (250-ml), immersed into a sugar solution (900 g.L<sup>-1</sup>; Heip et al., 1974) to detach the organisms from the sediment particles, and shaken for 10 s. After 10 min, the content was sieved again through a 45- $\mu\text{m}$  mesh sieve. Meiofauna was sorted from the 45- $\mu\text{m}$  fraction, counted, and identified to major taxa. Meiofaunal density was expressed as individuals per 40 ml<sup>-1</sup>.

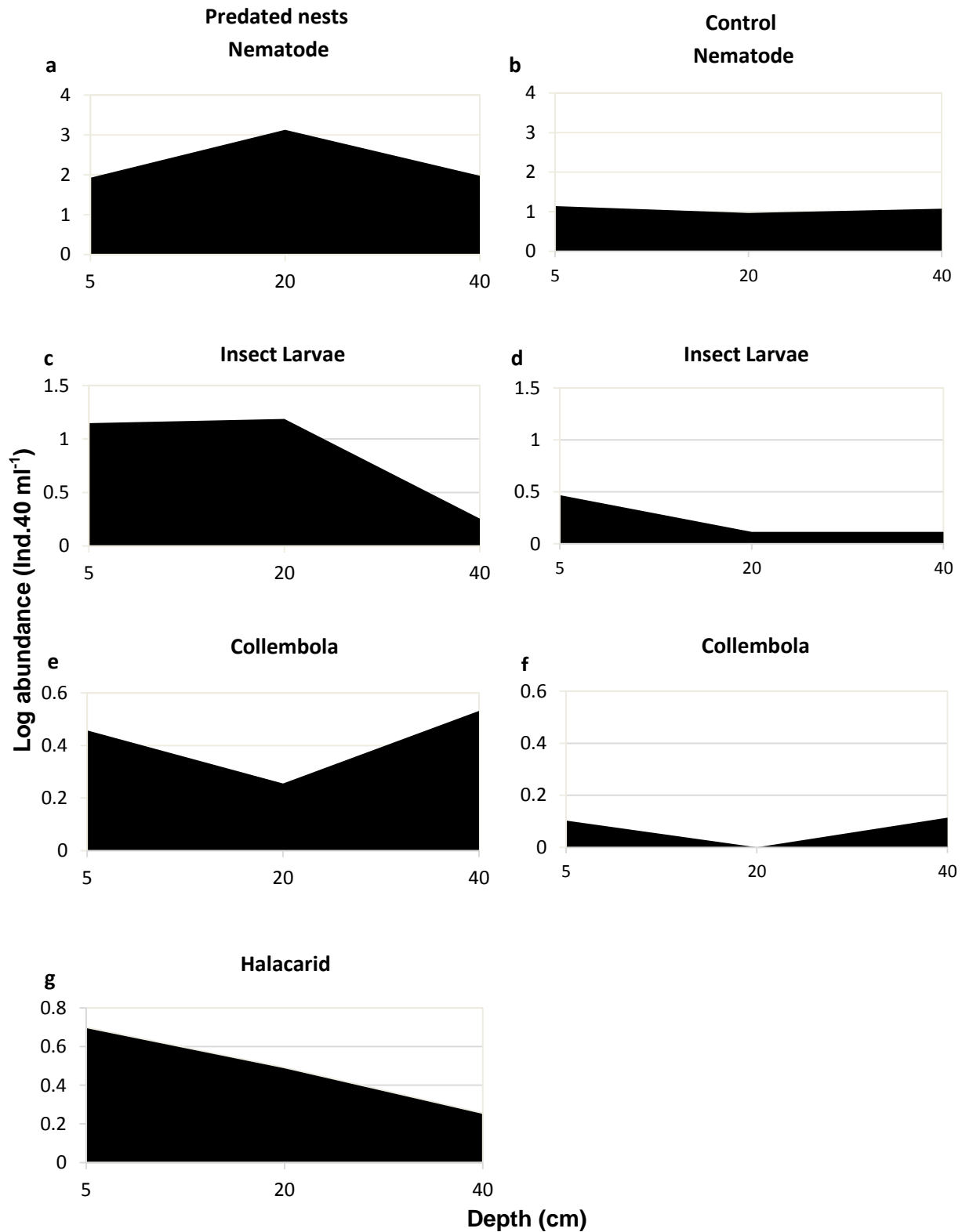
### **Statistical analysis**

Differences in meiofaunal abundance (no.40ml<sup>-1</sup>) and differences in higher taxa due to the presence/absence of sea turtle eggs and in predated nests were tested using Two-Way Analysis of Variance (ANOVA). In the analysis, meiofauna abundance was used as a response variable and treatment (control vs experiment) and depth (surface, medium and bottom) as the two factors. A Tukey post-hoc test was used for pair-wise comparisons among treatments. All data were log transformed to comply with the assumptions of normality and homoscedasticity. Statistical analyses were performed in R, version 3.0.2 (R Core Team 2013), and all statistical conclusions were drawn with a significance value of  $\alpha \leq 0.05$ .

## Results

### Meiofauna response in predated nests

Overall, meiofaunal diversity was higher in predated nests (n=4 taxa) than in the controls (n=3 taxa), and nematodes were the dominant taxon in both the predated nests and in the controls (Fig. 4.3). In the predated nests, collembola (7.4 %) and insect larvae (5.6 %) were the second-most numerous taxa, which was similar in the controls, with insect larvae (7.8 %) and collembolans (3.3 %) (Fig. 4.3). All taxa had decreased abundances with depth, except for collembolans that had similar abundances at 5 and 40 cm depth. In the controls, insect larvae had the highest abundance (after nematodes) which decreased with depth, followed by collembolans that had similar abundances at 5 and 40 cm depth (Fig. 4.3).



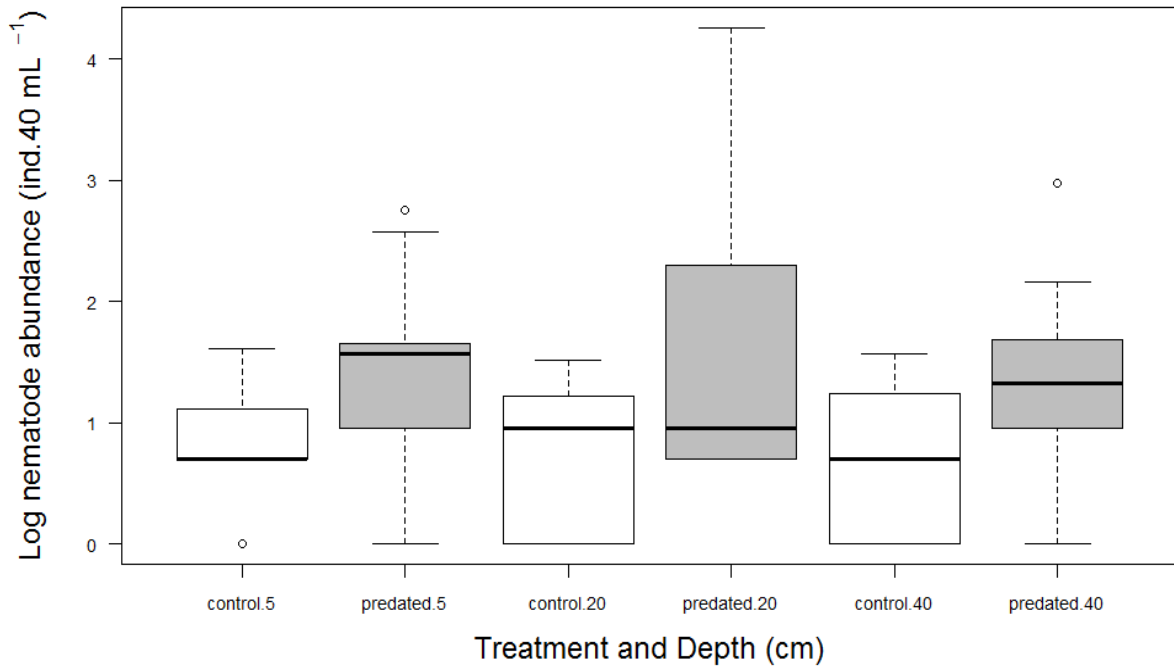
**Figure 4.3:** Kite diagrams of (Log) abundance of the major meiofaunal taxonomic groups in predated nests and controls: nematodes (a-b); insect larvae (c-d); collembolan (e-f); halacarid mites (g).

Meiofaunal ( $F_{5,84} = 5.991$ ,  $p = 0.0081$ ) and nematode ( $F_{5,84} = 3.641$ ,  $p = 0.005$ ) abundances in predated nests were significantly different to those in the controls (Table. 4.1, M1-2). Nematode abundance was higher in predated nests at 20 cm ( $1.8 \times 10^4$  ind. ml<sup>-1</sup>) than in the controls ( $6.4 \times 10^1$  ind. ml<sup>-1</sup>) (Fig. 4.4).

**Table 4.1:** Results of the two-way ANOVA tests for differences in the abundances of total meiofauna (AbT) and nematodes (AbN) for predated nests with different treatments (Treat: predated nests vs control) and at different depth (Depth: 5, 20, 40 cm). Only significant Tukey test results (\*  $p < 0.05$ ) are shown.

Model		<i>df</i>	<i>F</i>	<i>p</i>	Tukey	<i>p</i>
M1	AbT~Treat*Depth	$F_{5,84}$	5.991	<0.001*	Cont:20-Pred:5	0.0081*
					Cont:40-Pred:5	0.0026*
					Pred:20-Cont:20	0.0086*
					Cont:40-Pred:20	0.0027*
M2	AbN~Treat*Depth	$F_{5,84}$	3.641	0.005*	Cont:20-Pred:5	0.0081*
					Cont:40-Pred:5	0.0026*
					Pred:20-Cont:20	0.0086*
					Cont:40-Pred:20	0.0027*



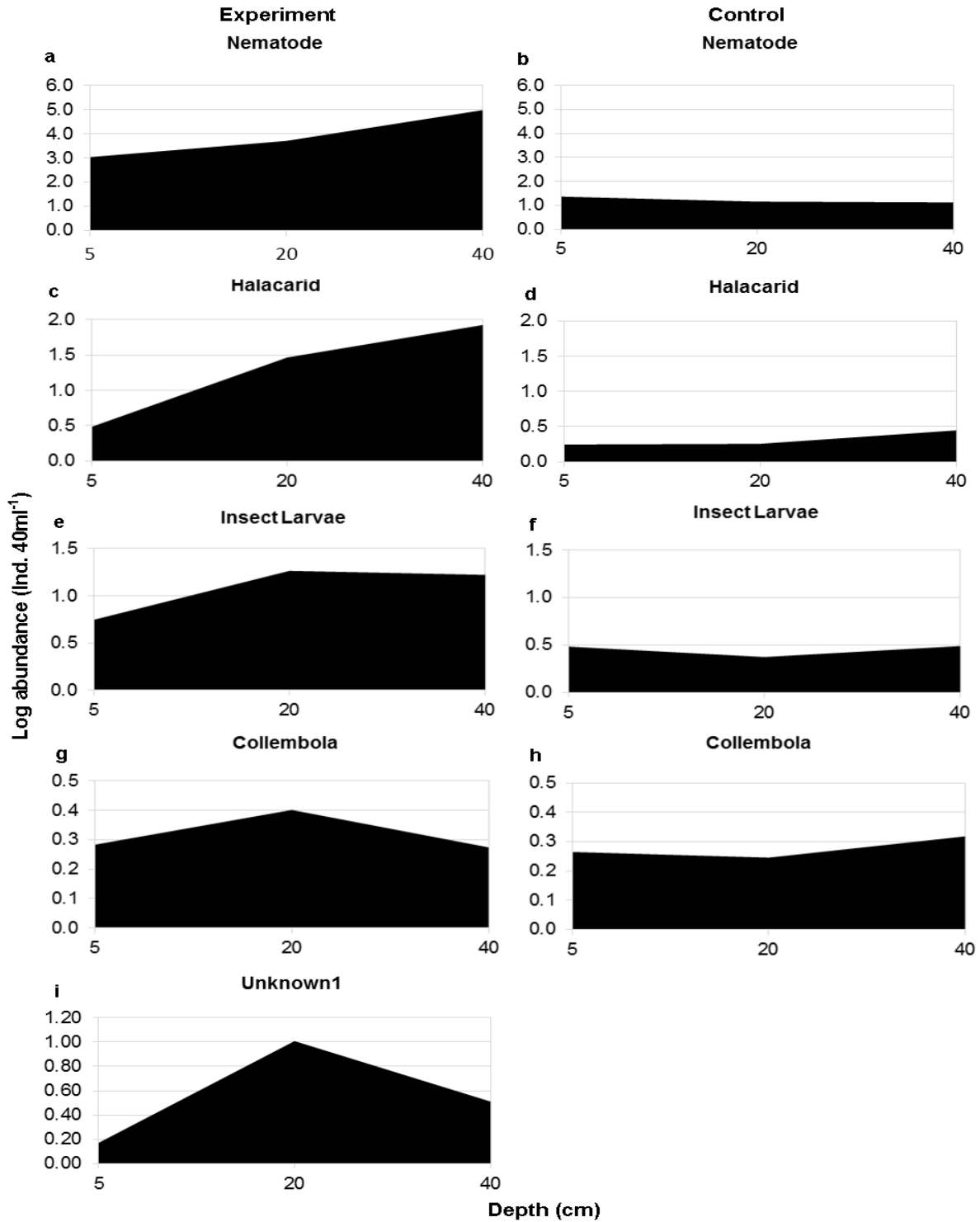


**Figure 4.4:** (Log) Nematode abundance (Ind.40ml<sup>-1</sup>) in predated nests (grey boxes) and controls (white boxes) at different positions (5, 20, 40 cm depth). Data are presented as medians (black line), inter-quartile range (box), first and fourth quartiles (whiskers) and outliers (dots).

## Meiofauna response in the *in situ* experiment

### *Overall response*

Species richness was higher in the experimental baskets (n=5 taxa) (Fig. 4.5) than in the control ones (n=4 taxa; Fig. 4.5). The meiofauna was dominated by nematodes, which were in all instances the most numerous group in both the experiment baskets and in the controls. Halacarid mites constituted the second most abundant meiofaunal group throughout the study period, followed by insect larvae and collembolans (Fig. 4.5).



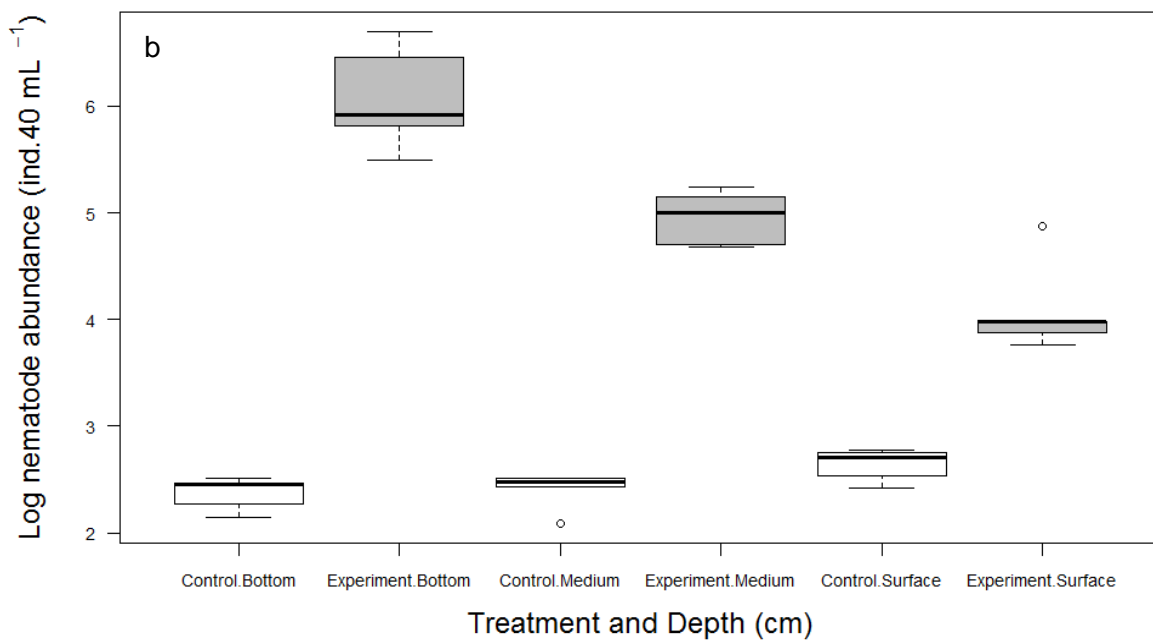
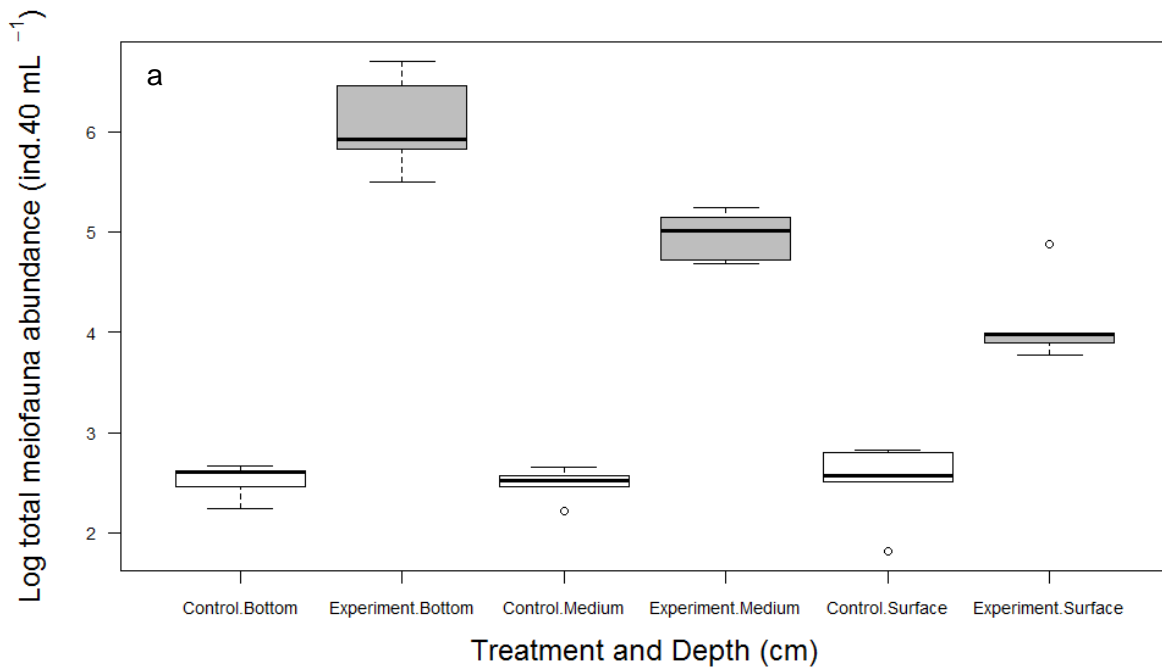
**Figure 4.5:** Kite diagrams of (Log) abundance of the major meiofaunal taxonomic groups in the experimental baskets and controls for the *in situ* experiment. (a-b: nematodes; c-d: halacarid mites; e-f: insect larvae; g-h: collembolans; i: unknown 1).

There was a significant difference between meiofaunal ( $F_{5,24} = 96.97$ ,  $p < 0.001$ ) and nematode ( $F_{5,24} = 122.3$ ,  $p < 0.001$ ) abundances in the experiment baskets compared to that in the controls (Table. 4.2, M3-4). The results of the Tukey tests showed that abundances at both the bottom and medium depth positions were significantly different (Table 4.2) compared to those of the controls. Average meiofauna abundance in the experiment baskets ranged from 34 207.9 to 1017 702.2 ind.40 ml<sup>-1</sup>, and in the control baskets from 0.8 to 113.6 ind.40 ml<sup>-1</sup>. Nematodes in the experiment baskets reached extremely high abundances (Fig. 4.6), four orders of magnitude higher than the controls, with a mean abundance exceeding  $1 \times 10^6$  ind.40 ml<sup>-1</sup> at the bottom depth (40 cm), compared to the controls that had a maximum abundance of  $1 \times 10^2$  ind.40 ml<sup>-1</sup> at the surface position (depth = 5 cm).

**Table 4.2:** Results of the two-way ANOVA tests for differences in the abundances of total meiofauna (AbT) and nematodes (AbN) for the in situ basket experiment with different treatments (Treat: experiment vs control) and at different positions (surface, medium, bottom depths); Only significant Tukey test results (\*  $p < 0.05$ ) are shown.

<b>Model</b>		<b>df</b>	<b>F</b>	<b>p</b>	<b>Tukey</b>	<b>p</b>
M3	AbT~Treat*Pos	$F_{5,24}$	96.97	<0.001*	Exp:Bot-Cont:Bot	<0.001*
					Exp:Med-Cont:Bot	<0.001*
					Exp:Surf-Cont:Bot	<0.001*
					Cont:Med-Exp:Bot	<0.001*
					Exp:Med-Exp:Bot	<0.001*
					Cont:Surf-Exp:Bot	<0.001*
					Exp:Surf-Exp:Bot	<0.001*
					Exp:Med-Cont:Med	<0.001*
					Exp:Surf-Cont:Med	<0.001*
					Cont:Surf-Exp:Med	<0.001*
					Exp:Surf-Exp:Med	0.0080*
					Exp:Surf-Cont:Surf	<0.001*
					M4	AbN~Treat*Pos
Exp:Med-Cont:Bot	<0.001*					
Exp:Surf-Cont:Bot	<0.001*					
Cont:Med-Exp:Bot	<0.001*					
Exp:Med-Exp:Bot	<0.001*					
Cont:Surf-Exp:Bot	<0.001*					
Exp:Surf-Exp:Bot	<0.001*					
Exp:Med-Cont:Med	<0.001*					
Exp:Surf-Cont:Med	<0.001*					
Cont:Surf-Exp:Med	<0.001*					
Exp:Surf-Exp:Med	0.0030*					
Exp:Surf-Cont:Surf	<0.001*					

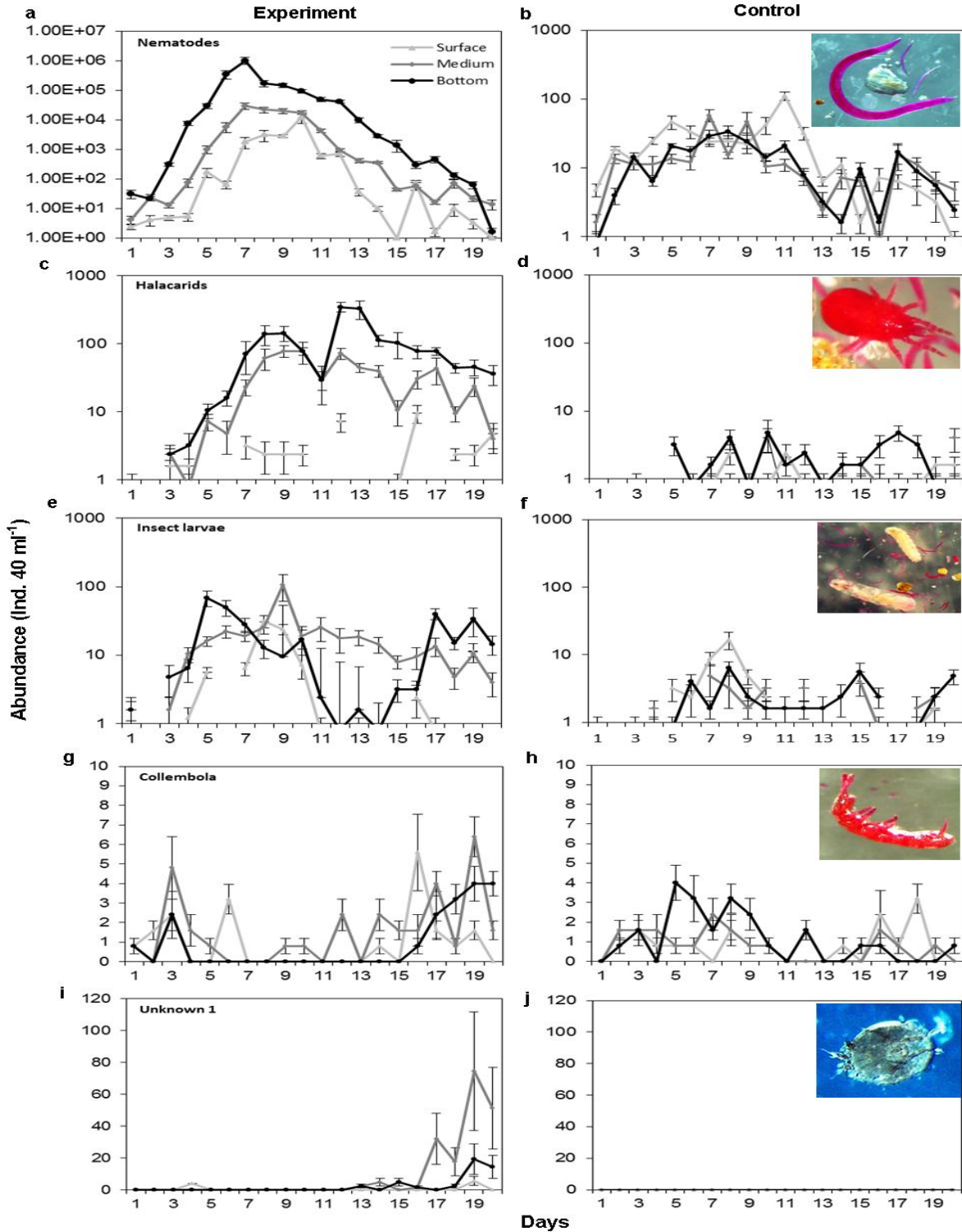
Exp= Experiment; Cont= Control; Pos= Depth position: surface (Surf: 5 cm), medium (Med: 20 cm) or bottom (Bot: 40 cm).



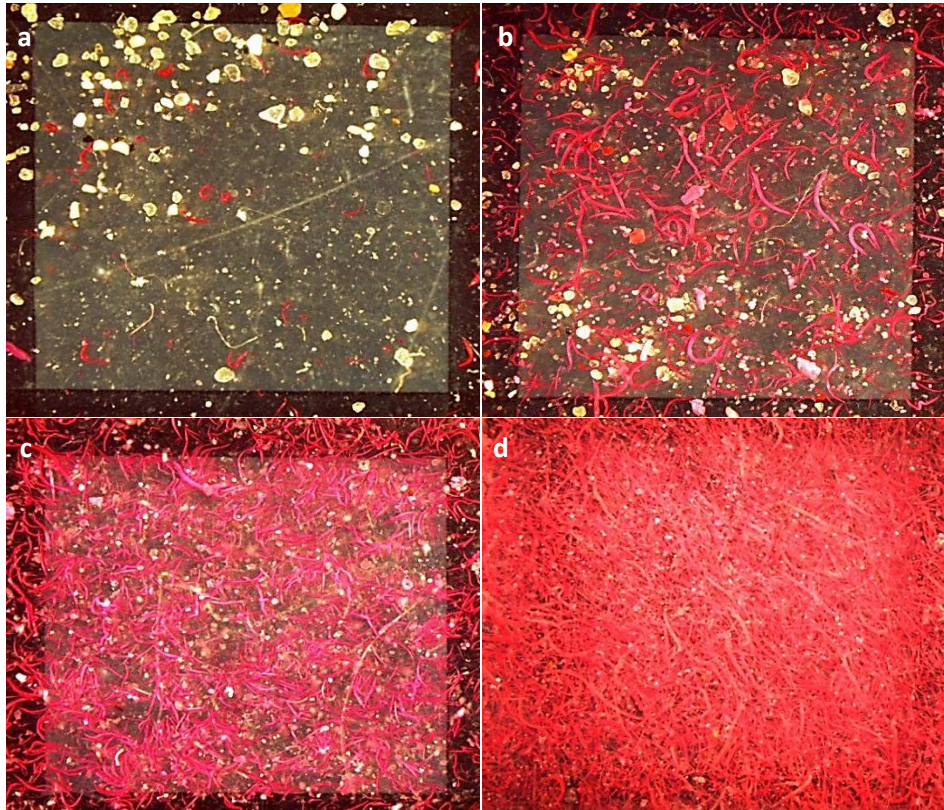
**Figure 4.6:** Mean abundance of (a) total meiofauna and (b) nematodes over three weeks in the *in situ* basket experiment with different treatments (experiment vs control), and depths (surface: 5 cm), medium: 20 cm, and bottom: 40 cm). Data are presented as medians (black line), inter-quartile range (box), first and fourth quartiles (whiskers) and outliers (dots).

### **Temporal response**

Strong temporal variability was found among meiofauna taxa (Fig. 4.7). Nematodes appear within a day and abundances reached a maximum after 7 days (Fig. 4.8), followed by insect larvae (9 days), halacarid mites (12 days) and collembolans and unknown taxon 1 (19 days). Maximum nematode numbers were observed after seven days and thereafter, their abundance declined to reach control treatment abundances (<100) after 20 days.



**Figure 4.7:** Mean abundances ( $\pm$  SE) of major meiofauna taxonomic groups in the experiment baskets (with turtle eggs: left panel) and control baskets (without turtle eggs: right panel) over the sampling period for the in situ experiment. (a-b nematodes; c-d halacarid mites; e-f insect larvae; g-h collembolan; i-j Unknown1).



**Figure 4.8:** Illustration of the temporal response in nematode abundance to turtle eggs. Photographs show one square (1 cm<sup>2</sup>) of a petri dish of nematodes extracted from sediment samples taken after (a) 2 days, (b) 4 days, (c) 6 days and (d) 7 days.



## Discussion

I predicted that meiofaunal abundance would increase in response to egg decomposition over time. When predated nests were sampled, I found that abundances were significantly higher in the presence of the broken eggs compared to in the surrounding sand (control). However, it was not clear if there was a temporal response to the nutrient inputs, how long the response lasted, and if there was a succession in taxa that responded to the broken egg nutrients. The *in situ* experiment provided answers to these questions, clearly demonstrating that there was a very strong (four orders of magnitude increase in abundance) but short-lived (one week for nematodes; three weeks for all taxa) response by the meiofauna, with a succession in the dominant, responding taxon over time. Against these results, I concluded that the predated nests sampled in the first part of this study were older than a week because relatively low abundances were found in the samples compared to those attained in the basket experiment. It also illustrates that time since the nest was predated (or since the food resource was made available) is an important factor to account for when quantifying the effects of nutrient inputs (turtle eggs, or other food resources) on the abundance of beach meiofauna. Our hypothesis and prediction therefore holds true, except that the localized increase in meiofauna abundance is temporary, and that they disperse soon after exploiting the resources.

Numerically, nematodes were the most abundant meiofauna group in all samples, which is not surprising since nematodes are generally the dominant taxon in marine and high shore meiofauna (McIntyre, 1969; McLachlan, 1980b; Dye et al., 1981). These results concur with other studies that have reported increased meiofauna abundance (dominated by nematodes) in response to pulses of: macrophyte wrack inputs (Inglis, 1989; Koop and Griffiths, 1982; Jedrzejczak, 2002; Bohorquez et al., 2013); surf diatoms (Netto and Meneghel, 2014); and horseshoe crab eggs (Hummon et al., 1976; Botton and Loveland, 2011), but abundances were not as high as those recorded in the present study. Additionally, mites were the second-most dominant meiofauna taxon, which is in accordance with other results found for South Africa (Nozais et al., 2005).

Colonization of the artificial and natural nests showed that not all meiofauna taxa invaded the nest at the same time. Nematodes responded rapidly to the inputs of turtle egg nutrients, with increased numbers after the second day and maximum numbers being recorded after seven days. Insect larvae were highest after nine days, while collembolans were highest after 12 days. Several studies which investigated the effects of macrophyte wrack on meiofauna have found similar results where nematode numbers increased dramatically after nine days (Inglis 1989; De Goede et al., 1993; Jedrezejczak, 2002).

While the distribution of intertidal meiofauna is largely determined by sediment particle size, oxygen, and salinity (McIntyre, 1969; Heip et al., 1985; Coull, 1999; Vincx et al., 1990; McLachlan and Brown, 2006), high shore meiofauna in the present study was influenced by food availability. This is illustrated by the fact that in the *in situ* experiment, meiofauna was most abundant in the deepest samples (~20 - 40 cm depth, medium and bottom positions), where the eggs were placed at the bottom of the baskets. This is not surprising as loggerhead sea turtles deposit their eggs between 29.5 (top of nest) and 54 (bottom) cm (Dodd, 1988). Thus, the meiofauna (those taxa that responded to turtle nutrients) in the present study appears to be concentrated more at the depths where most nutrients were available.

Studies investigating the effects of resource pulses on consumers have reported aggregative and reproductive responses (Yang et al., 2008, 2010). Yang et al. (2010) defined aggregative responses as "mechanisms of numerical recruitment driven by the immigration of mobile consumers from surrounding populations, while reproductive responses are mechanisms of numerical recruitment driven by locally increased reproduction". Aggregative responses to resource pulses appear to be generally faster than reproductive ones that are often delayed (Yang et al., 2008). However, it is possible that the combination of reproductive and aggregative consumer strategies may allow even larger numerical increases, which may have been the case in this study. A study by Hummon et al. (1976) investigating the response of meiofauna to horseshoe crab eggs found that meiofauna density increased in the presence of eggs and that both juvenile and gravid adult nematodes were present. Applying this principle here means

that part of the aggregation process could be attributed to successful reproduction in the presence of sea turtle eggs. This is especially true since reproduction and development in nematodes is temperature dependent (fecundity is higher at higher temperatures) and nematodes have continuous and short generation times (days or weeks; Gerlach, 1971; Heip et al., 1985; Giere, 2009; Tahseen, 2012). Thus, it is possible that in this study, temperature in the sediment may have increased over time as the nutrients decomposed and decayed which in turn may have stimulated meiofaunal activity and initiated reproduction.

The strong aggregation of meiofauna from decomposing loggerhead eggs suggests that they use turtle nutrients directly. However, the possibility cannot be excluded that the initial utilization of turtle eggs is by bacteria which are then ingested by the meiofauna (Koop and Griffiths, 1982; Jedrzejczak, 2002). This is especially true because bacteria usually have a higher standing stock than meiofauna (Koop and Griffiths, 1982; McLachlan and Brown, 2006) and meiofauna are common grazers of bacteria (Jensen, 1987; Moens and Vincx, 1997; Leduc and Probert, 2009). Gheskiere et al. (2004) found that bacterivorous nematodes have a high colonization capability, short generation times and can thus rapidly exploit microhabitat created by the pulse resources, and are hence typical enrichment opportunists. A study by De Goede et al. (1993a) investigating the trophic structure of nematodes in a primary succession of a sand-forest area found shifts in nematode feeding groups at different successional stages. The initial stages of succession were dominated by omnivorous nematodes while bacterivorous nematodes reached highest densities in the fermentation horizon (as organic matter decomposes), which demonstrates that changes in nematode species depends on the physiological tolerance of the species to fluctuations in micro-climatological conditions (such as fluctuating temperature and moisture (De Goede et al., 1993b). Another study by Wall et al. (2002) reported that epistrate feeders (grazers of bacteria, fungi and unicellular algae) were the dominant nematode trophic group of a succession at a beach site.

Although this study demonstrated that sandy beach high shore meiofauna is subsidized by sea turtle eggs, many subsequent questions have emerged. Future research should investigate the relationship between sea turtle nest temperatures and meiofauna

(nematode) reproductive output. Also, similar studies on the effect of turtle-derived nutrients should focus on identifying nematodes to species level and investigate changes in feeding groups related to succession and different stages of decomposition. Further research would benefit assessing the response of meiofauna to turtle eggs at different levels on the beach (high shore, intertidal), as some turtle species nest closer to the water line. Also, little information is available on the interactions between meio- and macrofauna: future work should investigate if nematodes feed directly on the egg nutrients or indirectly by ingesting bacteria that fed on the eggs, and assess if meiofauna are a link to higher trophic levels.

This study is the first to have investigated the effects of sea turtle-egg nutrients on the meiofauna of sandy beaches. The results showed a clear link (whether direct or indirect) between pulses of turtle eggs and the abundance of meiofauna. This strongly suggests that high shore sandy beach meiofauna uses sea turtle-derived nutrients as a food source. The accumulation of thousands of eggs from sea turtles during the nesting season, many of which are predated (De Wet, 2012), thus has the potential to lead to a large scale temporal aggregation of meiofauna, particularly, nematodes. Turtle eggs may not be the main feeding item of meiofauna but consumers of this pulsed resource probably display an opportunistic feeding behaviour, changing their habits depending on the availability of food. This is particularly likely on sandy beaches where food items are very erratic. Sea turtle nesting takes place every year, and it can thus be suggested that recurring resource inputs from sea turtles on sandy beach ecosystems are likely to become part of a predictable pattern of background resource variability. During these times, consumers aggregate and reproduce when a resource pulse occurs and then disperse when resources are depleted (Yang et al., 2008; Spiller et al., 2010). This in turn may indicate that shifts between alternative stable states of high and low resource availability may occur (Holt et al., 2008). Furthermore, it is possible to extrapolate the findings of this study and suggest that any organism (e.g., fish, crabs) utilizing beaches for mass spawning/nesting events may constitute a significant pulse of nutrients influencing meiofauna populations. Consequently, natural predation of turtle eggs may benefit (provided it is not excessive) beach faunal communities and participate in sandy beach nutrient cycling.

**Chapter 5: General Conclusions: Ecological role and function  
of sea turtles in sandy beach ecosystems**

## **Introduction**

Resource availability is the main abiotic factor structuring faunal communities (Polis and Hurd, 1996), and is rarely constant in natural environments. Instead the frequency and magnitude of resource supply is highly variable, often resulting in alternative states of low and high resource availability (Ostfeld and Keesing, 2000). Flows of nutrients across habitats can strongly influence populations and community dynamics in many ecosystems (Polis & Hurd, 1996; Polis et al., 1997; Cross et al, 2006). One of the best examples of drastic changes in resource availability is caused by resource pulses (Hiltunen and Laakso, 2013), which are ephemeral events of increased resource availability of large magnitude and short duration (Yang, 2006; Yang et al., 2008, 2010). The present study suggests that sea turtle eggs represent a pulsed resource that subsidizes sandy beach faunal communities.

Sandy shores generally strongly rely on allochthonous subsidies to fuel beach food webs (McLachlan and Brown, 2006). Sea turtles represent one source of such subsidies because they introduce nutrients on beach ecosystems when they come ashore to nest and deposit eggs into the sand. It is expected that the drastic community responses to resource pulses should be heightened in oligotrophic systems where resources are inherently scarce.

The present study aimed to identify the effects of turtle-introduced nutrients on beach ecosystems. This was done by exploring three objectives: quantifying the nutrients inputs of sea turtles eggs into South African sandy shores; identifying potential pathways of turtle-derived nutrients through the beach food webs; and quantifying the meiofaunal response to turtle egg nutrients over time.

### **Sea turtle nutrient inputs to sandy beach ecosystems**

Chapter 2 demonstrated that sea turtles make significant nutrient contributions to sandy beaches, which are then potentially available for uptake by beach food webs. In South Africa, 554,025 loggerhead and leatherback sea turtle eggs are deposited on sandy shores annually. Of those nutrients, 37,521,567 kJ remain in the beach ecosystem, with

the greatest proportion introduced by the thriving loggerhead population, although leatherbacks introduced more nutrients per individual female. These nutrients are introduced over a small temporal scale (90 days), with most eggs being deposited in the loggerhead high nest density. beach Given how exceptionally well beaches are known to remineralise and recycle nutrients (Rocha, 2008), it is expected that beach food webs would be able to consume these turtle nutrients. The next question is, which fauna and which of the three food webs?

### **Pathways of turtle-derived nutrients through beach food webs**

In spite of showing (Chapter 2) that sea turtles introduce large quantities of nutrients into the beach ecosystem, there was little evidence (Chapter 3) that the majority of beach fauna accessed these nutrients directly. It is possible that only high shore mobile fauna have access to the nutrients since turtle lay their eggs at the base of the dune and intertidal species that are less mobile and restricted to the lower part of the beach, do not get access/are not in contact with turtle nutrients. Contrary to ghost crabs that are highly mobile, and responded to the increase in turtle nutrients in the high nesting density beach, but not observed on the low nesting density beach. This is not surprising since ghost crabs are opportunistic feeders comprising several trophic guilds, and are able to change their diet depending on the food availability of the habitat (Lucrezi and Schlacher, 2014). The study could also suggest that trophic guild influences the response to turtle nutrients. High shore scavengers, ghost crabs, showed a strong response whereas suspension feeders (*Emerita*) and intertidal scavengers (*Bullia*) did not. Nematodes (bacterivorous) had no direct overlap with turtle egg signature but this study (Chapter 4) suggests that they may be indirectly feeding on turtle nutrients. Furthermore, the results could actually suggest that the high shore communities (meiofauna, microbial loop and insects) are so efficient in utilizing and recycling turtle resources that all nutrients are consumed and do not reach the lower shore intertidal communities. This links to the very potential of beaches to recycle and remineralise nutrients (McLachlan and Brown, 2006; Rocha, 2008) or that the signal gets diluted in the groundwater and is not detectable.

Although stable isotope analysis is a powerful tool to identify trophic pathways of nutrients, this study could have benefitted from sampling other trophic pathways such as vertebrate predators (honey badgers, mongooses), coastal insects (beetles, flies), fishes, and microbes, to identify other potential pathways of turtle-derived nutrients. Lastly, this study also generated more questions than it has answered: do turtle nutrients leach in the water table of the beach? What is the spatial scale of turtle nutrients? If ghost crabs have a broad diet, what are the other sources that contribute to the stable isotope signature (potentially macrophytes, carrion)?

### **Meiofauna response to turtle egg nutrient inputs**

Studies on sandy beach subsidies have largely concentrated on the effect of allochthonous wrack inputs on macrofauna (Stenton-Dozey & Griffiths, 1983; Jeckzejczak, 2002; Dugan et al., 2003; Olabarria et al., 2007). The present study is the first to quantify the effect of sea turtle nutrients on sandy beach meiofauna. The results (Chapter 4) clearly demonstrated that there was a strong and short temporal response to turtle-derived nutrients by high shore meiofauna. Meiofauna aggregated rapidly in response to increased nutrient availability, with dramatic increase in abundance after 7 days. Thereafter, their abundance declined and the animals dispersed (presumably) when presumably most of the nutrients were utilized and only egg shells were left. This pattern, of numerical response of consumers to pulsed resources followed by depletion of the pulsed resource, is usually seen as the first most conspicuous effect of resource pulses on consumer populations (Ostfeld and Keesing, 2000). Similar studies have found identical patterns, whereby meiofauna abundances increase in response to nutrient subsidies (such as surf diatoms; Netto and Meneghel, 2014, and horseshoe crab eggs; Botton and Loveland, 2011). This would give further evidence at how successful meiofauna is to process nutrients. However, the main question that emanated from the study is whether meiofauna directly or indirectly incorporate turtle egg nutrients. Future studies should take this into consideration when investigating the effects of resource pulses on sandy beach meiofauna. Future studies could also sample the microbial food web and (attempt to) identify nematodes to species level.



## **Concluding remarks**

The present study aimed to identify the effects of turtle-introduced nutrients on beach ecosystems. This work is the first to have quantified sea turtle nutrient inputs to beach ecosystems in South Africa. It has shown that sea turtles accumulate great amounts of energy and nutrients that are introduced into sandy beach ecosystems as a pulsed resource that can subsidize beach food webs.

Sea turtles provide important ecological roles in marine ecosystems including: maintaining healthy seagrass beds and, coral reefs and a balanced food web; providing key habitats for other marine life (epibionts); and serving as prey species, consumers, or competitors, and engineers of the physical environment. From this study, it has been demonstrated that sea turtles also play a key ecosystem function in coastal environments as vectors of nutrients, providing marine-derived resources from nutrient-rich foraging grounds to nutrient-poor beach ecosystems. Furthermore, this research showed how successful beaches (and their associated fauna) are in cycling nutrients, further supporting the conservation of sea turtles and their nesting habitat.

This work suggests that sea turtles provide supporting services (those that are necessary for the production of all other ecosystem services), and that such mobile link species are critical for connecting ecosystems by cycling nutrient from marine to coastal ecosystems. It is very complex to quantify goods and services at an ecosystems scale. There are still gaps in our understanding of goods and services including, inter-dependences, inter-variability, and vulnerabilities, and further studies are required to understand the full extent of their ecological role and function in coastal ecosystems.

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