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SEA TURTLES AS BIOLOGICAL TRANSPORTERS OF NUTRIENTS AND ENERGY FROM MARINE TO TERRESTRIAL ECOSYSTEMS

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Abstract. Our study quantified the nutrients and energy introduced into the nesting beach at Melbourne Beach, Florida, from distant foraging grounds by loggerhead sea turtles, *Caretta caretta.* The fate of eggs deposited into 97 nests was determined by monitoring nests throughout incubation. The organic matter, energy, lipid, nitrogen, and phosphorus content of fresh eggs, eggs at successive stages of development, hatchlings, and hatching remains were determined. From these analyses, we estimated the flow of energy and nutrients introduced into the 14 305 nests ($\sim 1.6 \times 10^6$ eggs) deposited in a 21-km stretch of Melbourne Beach in 1996. We quantified the amount of energy and nutrients incorporated into each of four pathways: ingested by nest predators; consumed by detritivores, decomposers, and plants; lost as metabolic heat or gases during embryological development and hatching; or returned to the ocean as hatchlings. Each nest introduced a mean of 688 g of organic matter, 18 724 kJ of energy, 151 g of lipids, 72 g of nitrogen, and 6.5 g of phosphorus into the beach. Twenty-five percent of the organic matter, 27% of the energy, 34% of the lipids, 29% of the nitrogen, and 39% of the phosphorus introduced into the nests returned to the ocean as hatchlings. Quantities of energy and nutrients transported by the turtles are comparable to quantities moved by other important biological transporters. Human activities have substantially altered the quantity of energy and nutrients transported, and the distribution of those nutrients on the beach. By introducing nutrients into beach ecosystems, sea turtles may help maintain stable dune systems that are critical to their reproductive success.

Key words: allochthonous flow; beach ecosystem; Caretta caretta; *energy flow; loggerhead sea turtle; marine turtles; Melbourne Beach, Florida; nesting beach; nutrient and energy transport; nutrient cycling and enrichment.*

INTRODUCTION

The availability of nutrients and energy within an ecosystem plays an important role in shaping the community dynamics of that system and can be influenced by the introduction of nutrients and energy from other ecosystems. These subsidies can result from biological transport when animals carry nutrients from one system to another (Likens and Bormann 1975), and can significantly impact the receiving system by influencing the distribution and abundance of organisms (Powell et al. 1991, Polis and Hurd 1996, Rose and Polis 1998), by impacting food web interactions (Polis and Hurd 1995), and by affecting the growth and nutrient composition of organisms (Onuf et al. 1977, Meyer and Schultz 1985).

The introduction of nutrients from other ecosystems can be particularly important in island and coastal communities. Both marine birds feeding at sea and macrophytes and carrion washing ashore were significant sources of marine-derived nutrients in the Great Barrier Reef and the Gulf of California (Heatwole 1971, Allaway and Ashford 1984, Polis and Hurd 1995, 1996). These introduced marine nutrients were found to increase faunal densities and affect food web interactions in the nutrient-stressed island and coastal communities. Additionally, Rose and Polis (1998) found that coyote distribution and abundance were significantly higher in coastal areas than in inland areas due to the introduction of nutrients from the sea. They summarized studies describing other terrestrial mammals that subsidize their diets by nutrients introduced into coastal communities from the marine ecosystem.

Sea turtles nest in temperate and tropical coastal and island communities throughout the world, and could serve as important biological transporters by moving nutrients and energy from marine foraging grounds to nesting beaches. All seven species of sea turtles migrate long distances from widely dispersed feeding grounds to congregate in large numbers at relatively small nesting beaches to reproduce (Meylan 1995). Because they consume little food during the migration and nesting period (Bjorndal 1997*a, b*), the energy and nutrients invested in reproduction originate in the marine feeding grounds, and are transported to the nesting beaches via the turtles. Perhaps the longest and most impressive migration is that of leatherbacks, *Dermochelys coriacea,* that feed on jellyfish near the Arctic circle and nest on tropical beaches (Bjorndal 1997*b*).

When sea turtles nest, they introduce nutrients and energy in the form of eggs into the relatively nutrient-

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poor beach environment. Nesting aggregations at a single beach can be very dense and result in the concentration of tremendous quantities of nutrients from widely dispersed foraging grounds. For example, The Archie Carr National Wildlife Refuge together with adjacent beaches along the coast of Florida supports one of the largest loggerhead (*Caretta caretta*) nesting aggregations in the world (National Research Council 1990). Loggerhead sea turtles migrate there from foraging grounds that range up to 1500 km away from the nesting beach (Meylan et al. 1983). The nutrients consumed in these vast foraging grounds are then concentrated in ~120 km of beach on the east coast of central Florida, where ~28 000 nests (each with ~100 eggs) are deposited each year (Meylan et al. 1995).

Nutrients and energy contained in a sea turtle nest may follow several paths. For those eggs that successfully hatch, most of the nutrients return to the marine ecosystem in the form of hatchlings. However, a small portion of nutrients remains in the beach in the form of chorio-allantoic fluid and egg shells. Many nests also contain eggs at various developmental stages that fail to hatch. Nutrients that remain in the nest chamber will enter detrital and decomposer food chains through organisms such as bacteria, fungi, ants, fly and beetle larvae, and crabs (Dodd 1988). Nest contents may also be consumed by predators, such as ants, crabs, foxes, and raccoons, that prey upon incubating nests (Fowler 1979, Stancyk 1995), or be absorbed by plant roots that grow into nests and penetrate the shells of developing or decomposing eggs (Witherington 1986).

In this study, we quantified the nutrients and energy introduced into the nesting beach at the Archie Carr National Wildlife Refuge on the east coast of Florida, and determined to what extent they were incorporated into the following four pathways: (1) consumed by nest predators, (2) made available to decomposers, detritivores, and plants, (3) lost as metabolic heat or gases (e.g., CO_2 or N_2) during embryological development and hatching, or (4) returned to the ocean as hatchlings.

MATERIAL AND METHODS

Study site

Field work was conducted at the Archie Carr National Wildlife Refuge at Melbourne Beach, Florida (28.0° N, 80.5° W), from 5 June to 2 October 1996. The refuge includes 21 km of high-energy barrier island beach. This study was conducted on a 2.5-km portion of the beach located in the southern region of the refuge between Floridana Beach and Sebastian Inlet. This area has a typical dune habitat interspersed with houses and condominiums. The dune vegetation included sea oats (*Iniola paniculata*), sea grape (*Coccoloba uvifera*), and beach morning glory (*Ipomoea pes-caprae*).

Nest success

To trace the path of the nutrients and energy introduced into the beach by loggerhead sea turtles, 97 marked nests were monitored throughout their incubation period. Beginning on 5 June, 10 nests were marked per week for 10 weeks (until 9 August) with the exception of the fifth, seventh, and ninth weeks, in which nine nests were marked. We marked nests throughout the peak loggerhead nesting season and from the high tide line to the vegetation.

All marked nests were monitored daily throughout the incubation period, to observe any disturbance by nest predators, primarily raccoons, *Procyon lotor.* In the event that a nest was depredated, it remained exposed as left by the predator, until the end of the incubation period, when it was excavated and inventoried in the same manner as undisturbed nests.

Each nest was excavated three days after the hatchlings emerged from the nest, or 65 days after oviposition. Because the incubation period at Melbourne Beach is ~50 days, waiting 65 days ensured we would not disturb the nest prematurely. The following nest remains were quantified at each excavation: (1) the number of hatched and unhatched eggs, (2) the number of pipped eggs containing either dead or live hatchlings, and (3) the number of live and dead hatchlings remaining in the nest. Additionally, the number of eggs depredated by ghost crabs, *Ocypode quadrata,* was estimated by counting those eggs that had a small circular section of the eggshell removed. Generally, these eggs were almost hollow, and the remaining contents were desiccated. Finally, we noted how many eggs or eggshells had plant roots associated with them, and how many nests were infiltrated by plant roots.

All unhatched eggs were opened to determine the stage at which development had ceased. All eggs were classified as one of four stages or as unidentifiable. Stage 1 referred to those eggs in which no development was visible to the naked eye, whereas stages 2–4 corresponded to ~50%, 75%, and 100% of development (Miller 1985, Bouchard 1998). Unidentifiable eggs were decomposed to the extent that stage of development could not be determined.

Based on these inventories, clutch size was determined for each nest by summing the number of hatched and unhatched eggs. To test the accuracy of these estimates, based on piecing together eggshell fragments, we inventoried nine nests of known clutch sizes ($\bar{X}$ = 109 eggs) and determined the counts to be accurate to ±5 eggs. Mean clutch size of nondepredated nests was used to estimate clutch size for raccoon-depredated nests.

Analysis of transported nutrients and energy

Collection and preparation of samples.—We quantified the organic matter (ash-free dry mass), energy, lipid, nitrogen, and phosphorus content in: (1) fresh eggs, (2) unhatched eggs at the four stages of development described above, (3) hatchlings found dead in the nest chamber, and (4) hatching remains, or shells and chorio-allantoic fluid remaining after a turtle hatched. Two fresh eggs were collected each week, one from each of two females, for 10 wk from 13 June through 11 August 1996. Samples of dead hatchlings and unhatched eggs remaining in each nest were collected: 23 hatchlings from 16 nests, 32 stage-1 eggs from 16 nests, 34 stage-2 eggs from 17 nests, 22 stage-3 eggs from 18 nests, and 28 stage-4 eggs from 17 nests. All eggs and dead hatchlings were weighed, placed in a 65°C drying oven, and dried to constant mass.

To collect the hatching remains (chorio-allantoic fluid and shells left behind by successful hatchlings), an additional 31 loggerhead nests were marked. Approximately three days before hatching, eggs were removed from these nests and placed into glass jars on aluminum egg holders. After the eggs hatched, all the fluid and shell remaining in the container was collected and dried to constant mass at 65°C. Hatchlings were released on the beach after their yolk sacs were internalized.

After drying, all samples were ground for nutrient and energy analyses. Because of the high lipid content of most samples, they were ground in a mill (C.W. Brabender Instruments, Incorporated, South Hackensack, New Jersey) with dry ice to ensure complete mixing. Because of their small size, hatchlings from the same nest were combined, as were hatching remains from eggs of the same nest. This ensured there would be sufficient sample to complete all nutrient analyses.

Nutrient and energy determinations.—In this paper, we define the term nutrient in a nutritional ecology sense, as representing nutritional components, not as elemental nutrients that cannot be further decomposed. Dry matter content was determined by drying subsamples overnight at 100°C. Organic matter content was then determined by combustion of the subsamples at 500°C for three hours. Energy content was determined with a Parr bomb calorimeter (Parr 1960); lipid content was determined through ethyl ether extraction using a Goldfisch apparatus (Association of Official Agricultural Chemists 1960). Nitrogen and phosphorus analyses were performed using a modification of the standard Kjeldahl procedure. Samples were digested for four hours at 400°C using 10 ml of H_2SO_4 and 2 ml of H_2O_2 (Gallaher et al. 1975). Nitrogen and phosphorus content of the digestate were determined with the Technicon Autoanalyzer II by semiautomated colorimetry (Hambleton 1977).

All analyses were performed in duplicate except for those of hatching remains. For the hatching remains, there was insufficient sample to run duplicates for the dry matter, organic matter, and energy determinations. Lipid determinations were not performed because of the small quantity of sample and the very low lipid content.

Data analyses and calculations.—Differences in energy and nutrient content among stages were evaluated with a nested ANOVA and Tukey's post hoc test using the Statistical Package for the Social Sciences (SPSS), version 7.5. Samples from the same nest were nested within stage because eggs and hatchlings removed from the same nest were not independent of one another. To determine the mean energy and nutrient values for each sample type, means were first calculated for eggs and hatchlings on a per nest basis. These means were then averaged to determine a value for each sample type.

The fate of the energy and nutrients introduced into the beach was calculated on a per nest basis (Table 1) using the results of the energy and nutrient analyses and the nest inventories. The nutrient and energy composition of different developmental stages were compared to assess if significant changes in composition occurred during development. Because no significant losses occurred in the first three stages, the energy and nutrient content for fresh eggs was used for all calculations involving eggs in stages 1–3. However, because the organic matter and energy content of stage-4 eggs were significantly less than those of fresh eggs, the values for stage-4 eggs were used in calculations for these components. The decision to use fresh-egg values for the earlier stages instead of stage-specific values is supported by the fact that oxygen consumption by loggerhead embryos increases slowly in the first portion of the incubation period, and exponentially in the latter part (Ackerman 1981). Thus, more energy and nutrients are metabolized in later stages of development, and substantial changes in composition would not occur until then.

The energy and nutrients lost as metabolic heat and gases for unhatched eggs were calculated by subtracting the composition of each stage from the composition of fresh eggs (Bouchard 1998). For hatched eggs, the metabolic heat and gas loss was calculated by subtracting the energy and nutrient composition of hatchlings plus that of the hatching remains from the composition of fresh eggs.

Calculations on a per nest basis were extrapolated to estimate the energy and nutrient contribution of loggerheads to the terrestrial ecosystem for a 21-km stretch of beach located in the Brevard County portion of the Archie Carr National Wildlife Refuge. The mean energy and nutrient contribution per nest was multiplied by the total number of nests (14 305; L. M. Ehrhart, *personal communication*) deposited into the beach in 1996. The energy and nutrient contribution per area of beach was calculated by multiplying the beach length (21 km) by the width of beach into which eggs were deposited (11 m). The beach width is the maximum distance from dune to nest for the 97 nests monitored in our study.

RESULTS

A total of 10 608 loggerhead sea turtle eggs were deposited into 97 nests, with a clutch size of 109 ± 20.9 eggs (mean ± 1 SD, range of 56–152). Of those nests, 35% were depredated by raccoons, 48% were depredated by ghost crabs, 3% were disturbed by other

TABLE 1. Calculations used to determine path of energy and nutrients introduced into Melbourne Beach, Florida, on a per-nest basis.

Pathway of energy and nutrient flow	Calculations†
Introduced into beach	clutch size × ENC fresh eggs‡
Nest predators	
Raccoons	eggs eaten × (ENC eggs at stage when depredated − ENC hatching remains)
Ghost crabs	eggs eaten × (ENC fresh eggs − ENC hatching remains)
Detritivores, decomposers, and plants	
Hatched eggs	hatched eggs × ENC hatching remains
Unhatched eggs (stages 1–4)	(stage-1–3 eggs × ENC fresh eggs) + (stage-4 eggs × ENC stage-4 eggs)
Unhatched eggs (unidentifiable)	unidentifiable eggs × [(stage-1–3 eggs/[unhatched − unidentifiable eggs]) × ENC fresh eggs] + [(stage-4 eggs/[unhatched − unidentifiable eggs]) × ENC stage-4 eggs]
Pipped eggs	pipped eggs × (ENC hatchlings + ENC hatching remains)
Hatchlings trapped in nest	hatchlings × ENC hatchlings
Eggs killed by nesting turtles	eggs disturbed × ENC eggs at stage when disturbed
Remains from raccoon/ghost crab predation	eggs eaten × ENC hatching remains
Returned to ocean as hatchlings	introduced into beach − [(nest predators) + (detritivores, decomposers and plants) + (metabolic heat and gases)]

† The placement of sample type (i.e., eggs eaten, stage-1 eggs, or unidentifiable eggs) into an equation indicates that the number of that particular sample type in that clutch should be inserted.

‡ ENC represents the energy and nutrient composition of that sample type. Values for fresh eggs were used for all eggs in stages 1–3 and for the lipid, nitrogen, and phosphorus calculations for stage-4 eggs. Stage-4 values were used for the organic matter and energy calculations for stage-4 eggs. See Table 3 for the corresponding values.

nesting sea turtles, and 23% were invaded by plant roots. Forty percent of all eggs produced hatchlings that successfully emerged from the nest, whereas 34% of all eggs were destroyed by either raccoons, ghost crabs, or other nesting females (Table 2). Most unhatched eggs were classified as stage 1; the fewest were in stage 3 (Table 2). All data are expressed as means ± 1 SD. Hatching success per nest (percentage of eggs that hatched) was 42.5 ± 36.8% (range of 0–98.1), and emergence success (percentage of eggs that produced hatchlings able to leave the nest) was 41.0 ± 35.7% (range of 0–95.4). For those nests undisturbed by predators or other nesting turtles, hatching success on a per nest basis was 63.1 ± 29.0% (range of 0–98.1), and emergence success was 61.0 ± 28.4% (range of 0–95.4).

TABLE 2. Fate of eggs (*n* = 10 608) deposited in loggerhead sea turtle nests (*n* = 97) at Melbourne Beach, Florida.

Fate of eggs	Total number	Percentage of total eggs
Hatched†	4429	41.8
Hatchlings emerged from nest	4268	40.2
Hatchlings live in nest	37	0.3
Hatchlings dead in nest	123	1.2
Pipped	155	1.5
Hatchlings live in shell	2	0.0
Hatchlings dead in shell	153	1.4
Unhatched	2464	23.2
Stage 1	1225	11.5
Stage 2	357	3.4
Stage 3	129	1.2
Stage 4	272	2.6
Unidentifiable	481	4.5
Raccoon predation	2972	28.0
Ghost crab predation	269	2.5
Disturbed by other nesting turtles	319	3.0

† Fifty-nine hatched eggs had plant roots growing within the shell.

For total lipid, nitrogen, and phosphorus content, there were no significant differences found between fresh eggs and developmental stages 1–4. The organic matter and energy content of fresh eggs was significantly different from those of stage-4 eggs (Table 3).

Each nest introduced a mean of 688 g of organic matter, 18 724 kJ of energy, 151 g of lipid, 72 g of nitrogen, and 6.5 g of phosphorus into the beach. Twenty-five percent of the organic matter, 27% of the energy, 34% of the lipids, 29% of the nitrogen, and 39% of the phosphorus introduced returned to the ocean as hatchlings (Fig. 1). The proportions of nutrients and energy that followed the remaining pathways varied (Fig. 1). For example, a greater proportion of nitrogen flowed to detritivores, decomposers, and plants than to nest predators, whereas the reverse was true for lipids. The results were extrapolated to the entire 21-km stretch of beach at the Archie Carr National Wildlife Refuge (Table 4).

DISCUSSION

Nutrient and energy pathways within Melbourne Beach

Nesting sea turtles introduce large quantities of nutrients and energy into beach ecosystems. These nutrients may be particularly important for dune vegetation and for terrestrial predator populations. At Melbourne

TABLE 3. Nutrient and energy composition of loggerhead sea turtle eggs and hatchlings.

	Mean (1 SD)					
Sample type	Egg or hatchling dry mass (g)	Organic matter per egg or hatchling (g)	Energy per egg or hatchling (kJ)	Lipids per egg or hatchling (g)	Nitrogen per egg or hatchling (g)	Phosphorus per egg or hatchling (g)
Fresh eggs (n = 20 eggs, 20 nests)	7.71^{a} (1.00)	6.30^{a} (0.86)	171.21^{a} (24.70)	1.38^{a,b} (0.28)	0.66^{a} (0.08)	0.059^{a} (0.008)
Eggs with stage 4 embryos (n = 28 eggs, 17 nests)	6.97^{a} (0.89)	5.41^{b} (0.56)	145.08^{b} (15.22)	1.47^{a} (0.17)	0.59^{a} (0.07)	0.066^{a} (0.014)
Hatchlings (n = 23 turtles, 16 nests)	4.93^{b} (0.66)	4.20^{c} (0.58)	113.53^{c} (17.18)	1.17^{b} (0.28)	0.47^{b} (0.06)	0.057^{a} (0.007)
Hatching remains† (n = 51 eggs, 31 nests)	1.51 (0.24)	0.71 (1.12)	14.90 (2.48)	···	0.107 (0.021)	0.002 (0.001)
$F_{5,102.7}$	25.419	23.113	26.612	7.578	16.068	2.183
P values	<0.001	<0.001	<0.001	<0.001	<0.001	0.062

Notes: See *Methods* for explanation of how means were calculated. The F statistic and P values are from nested ANOVAs comparing fresh eggs, eggs with stage-1–4 embryos, and hatchlings. Values for stage-1–3 embryos are not presented because they were not significantly different from fresh eggs. Different superscript letters within a column indicate significant differences between fresh eggs, eggs with stage-4 embryos, and hatchlings.

† Hatching remains were not included in the ANOVA.

Beach, 29–40% of all nutrients were made available to detritivores, decomposers, and plants, whereas nest predators consumed 26–31% of all nutrients (Fig. 1). These two groups constitute the primary terrestrial nutrient pathways in this study.

Nutrients and energy derived from sea turtles can directly impact plant ecology when plant roots invade nest chambers. At Melbourne Beach, loggerhead nests were concentrated near dune vegetation ($\bar{X} \pm 1$ SD = 2.2 ± 3.0 m from dune, Wood and Bjorndal 2000). Twenty-three percent of nests were invaded by plants with roots growing both within and around eggs, as found in other studies (Lazell and Auger 1981, Witherington 1986). Studies on the eggs of diamondback

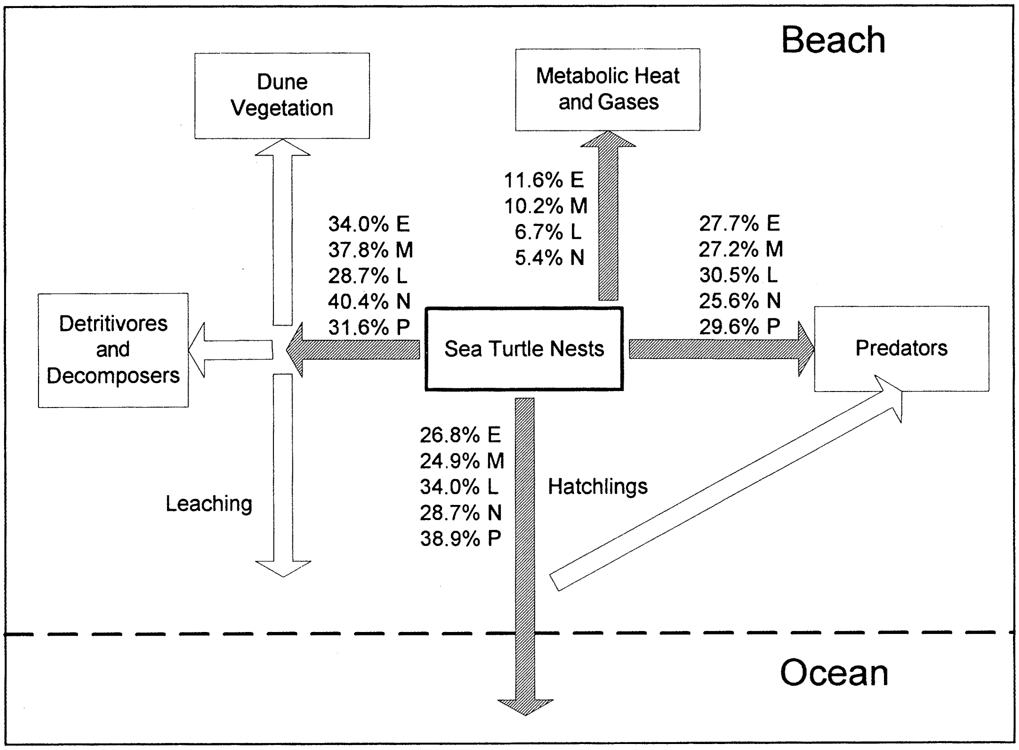

FIG. 1. Movement of nutrients and energy introduced into nests at Melbourne Beach, Florida, by loggerhead sea turtles. Values are percentages of energy (E) and each nutrient (M = organic matter, L = lipids, N = nitrogen, and P = phosphorus) that followed each pathway. Shaded arrows indicate pathways for which values have been determined. Open arrows indicate pathways for which the quantities of nutrients and energy have not been estimated.

TABLE 4. Fate of nutrients and energy deposited into 14 305 loggerhead sea turtle nests in a 21-km stretch of beach in Brevard County, Florida, in 1996, assuming a mean emergence success of 41% per clutch.

Variable	Total introduced into beach	Total not returned to ocean as hatchlings		
		Total	Total/m of beach	Total/m^2 of beach†
Organic matter (g)	9 841 840	7 391 222	352	32
Energy (kJ)	267 846 820	196 063 872	9336	849
Lipids (g)	2 160 055	1 425 636	68	6
Nitrogen (g)	1 029 960	734 361	35	3
Phosphorus (g)	92 983	56 813	3	0.3

† Using beach width of 11 m.

terrapins, *Malaclemys terrapin,* demonstrated that at least one dune grass, *Ammophila breviligulata,* has the ability to absorb nutrients from turtle eggs (Stegmann et al. 1988).

Dune plants can survive under low-nutrient conditions, but require significant amounts of nitrogen, phosphorus, and potassium for high production (Kachi and Hirose 1983, Hawke and Maun 1988). By supplying high concentrations of nutrients during the spring and summer, sea turtle eggs may increase plant production. Secondarily, increased plant growth rates and nutrient concentrations in the leaves and stems may influence the distribution of herbivores (Onuf et al. 1977).

In addition to plants, nutrients derived from sea turtles also directly impact predators that consume eggs and hatchlings. In this study only egg predators were quantitatively assessed, although hatchlings en route to the ocean were also consumed by predators, such as raccoons, ghost crabs, and night herons, *Nyctanassa violacea* and *Nycticorax nycticorax.* Once hatchlings reach the ocean, avian predators feeding at sea may consume them and transport those nutrients back to the terrestrial system (Witherington and Salmon, 1992). Because hatchling predation on the beach and in offshore waters was not quantified in this study, the contribution of nutrients and energy to the beach ecosystem by loggerheads was underestimated.

Some of the nutrients and energy consumed by predators was transferred into the dune environment through predator movements (McLachlan 1991). Defecation by predators as they move, as well as the decomposition of predator carcasses, redistributes the nutrients throughout the dune. These processes make nutrients and energy derived from sea turtles available to a greater percentage of the vegetation. Both this indirect acquisition of nutrients by plants, and the direct acquisition through root penetration into nests, can positively influence vegetative dune succession and plant growth. In this way, sea turtles may play a role in stabilizing the dune and thus their own nesting environment.

Extrapolations to other sea turtle nesting beaches

To extrapolate the results of this study to other loggerhead nesting beaches, variation in nesting parameters that influence nutrient and energy flow must be considered. For example, the percentage of nests depredated among years and among beaches can vary from zero to nearly 100% (Talbert et al. 1980, Witherington 1986, National Research Council 1990, Johnson et al. 1996). Measures of emergence success incorporate variation in predation as well as other factors influencing hatchling production (e.g., weather). In this study, mean emergence success per nest was 41%. This is slightly lower than the 50–80% typically found among other sea turtle nesting beaches (National Research Council 1990). It is also lower than other values found at Melbourne Beach in 1993 and 1994 (69% and 53% respectively, Johnson et al. 1996) and in 1985 (75%, Witherington 1986). The difference in emergence success was primarily due to increased raccoon nest predation in this study.

Equations that estimate the nutrient and energy contribution per nest for a given emergence success allow us to extrapolate the results of this study to other beaches. These lines can be generated between values of the nutrient and energy contribution for a nest with 0% emergence success (nutrient and energy content of fresh eggs multiplied by mean clutch size) and 100% emergence success (hatching remains multiplied by the mean clutch size).

The relative distribution of these nutrients and energy, however, cannot be extrapolated directly to other sea turtle species because the nesting patterns of different species will influence the flow of energy and nutrients. For example, green turtles, *Chelonia mydas,* at Melbourne Beach nest farther into the dune than do loggerheads, and may contribute more nutrients to dune vegetation (Witherington 1986).

Significance of nutrient and energy transport by sea turtles

Beaches are transition ecosystems between marine and terrestrial environments. Thus, nutrients and energy in beach food webs can come from a variety of sources (McLachlan 1990). Studies have quantified some of these sources including surf diatoms (Lewin and Shaefer 1983), macrophytes of stranded wrack (Hayes 1974, McLachlan and McGwynne 1986), carrion (McGwynne 1980), groundwater and rain (McLachlan 1990), and, now, sea turtles (this study).

When sea turtles nest they deposit large nutrient loads into beach ecosystems. For example, in recent years, a 36-km stretch of beach at Tortuguero, Costa Rica, averaged 80 000 green turtle nests with a mean clutch size of 112 eggs (Bjorndal and Carr 1989, Bjorndal et al. 1999). Even denser nesting is found among olive ridley, *Lepidochelys olivacea,* nesting aggregations known as arribadas. In 1984, along 880 m of beach at Ostional, Costa Rica, three of five arribada nesting events numbered 47 200 nests, 74 900 nests, and 130 000 nests with a mean clutch size of 107 eggs (Cornelius et al. 1991). It is likely that these nesting sea turtle populations contribute even greater quantities of energy and nutrients than were measured in this study.

To assess the significance of energy and nutrient transport by sea turtles in an ecosystem perspective, we should determine what percentage of the total beach nutrient budget is provided by sea turtles. However, no nutrient budget has been constructed for Melbourne Beach, or any other sea turtle nesting beach. Energy and nitrogen budgets have been determined for a few beach ecosystems (McLachlan et al. 1981, Cockcroft and McLachlan 1993, Heymans and McLachlan 1996), but it is difficult to compare nutrient inputs by sea turtles to these budgets because they deal principally with the surf and intertidal zones, whereas sea turtles primarily nest in the dune and fore dune areas. One study at Port Elizabeth, South Africa, did incorporate dune ecosystem dynamics in a beach energy budget and determined that carrion washing ashore contributed 2155 $kJ \cdot m^{-1} \cdot yr^{-1}$ (per meter refers to a linear stretch of beach) to the dune, insects blown onto the beach supplied 497 $kJ \cdot m^{-1} \cdot yr^{-1}$, and unspecified sources deposited 2468 $kJ \cdot m^{-1} \cdot yr^{-1}$ (McLachlan et al. 1981). Although at Melbourne Beach, some sea turtle nutrients were leached back into the marine system or consumed by ghost crabs in the intertidal zone, the energy that was not returned to the ocean as hatchlings, 9336 $kJ \cdot m^{-1} \cdot yr^{-1}$, far exceeds that introduced into the dune by the sum of the above mentioned sources, 5120 $kJ \cdot m^{-1} \cdot yr^{-1}$. Therefore, the energy introduced by sea turtles appears to be a major source for dune ecosystems.

No studies have specifically described and quantified the introduction of nitrogen into coastal dune environments. However, McLachlan and McGwynne (1986) quantified algal wrack as a nitrogen source for beaches as a whole. They determined that wrack contributed 14 000 g of $N \cdot m^{-1} \cdot yr^{-1}$ to a South African beach, an input that far exceeds that contributed by sea turtles, 35 g of $N \cdot m^{-1} \cdot yr^{-1}$. However, the nitrogen in sea turtle eggs and hatchlings is available to a wider range of organisms and is a higher quality resource for most animals than is the nitrogen in algal wrack. Indeed, McLachlan and McGwynne (1986) determined there was no net accumulation of nitrogen from the wrack in the beach, indicating the majority was recycled into the marine system.

Loggerhead sea turtles transport quantities of energy and nutrients comparable to quantities moved by some biological transporters, such as fish and birds, and less than others (Durbin et al. 1979, Meyer and Shultz 1985, Deegan 1993). However, direct quantitative comparisons are not the most effective way to compare energy and nutrient contributions by different animals because the receiving environments are often quite different, either in type (e.g., aquatic, terrestrial) or in nutrient concentration. Sea turtles may introduce less total nutrients than some transporters. However, because they deposit dense packages of high quality nutrients and because the beach is generally a nutrient-poor ecosystem, sea turtle nutrients may have a greater impact on the nesting beach than larger quantities introduced by other biological transporters into different ecosystems.

Human impact on the movement of nutrients and energy on sea turtle nesting beaches

Humans affect the fate of energy and nutrients through harvest of sea turtle eggs, introduction of feral predators, sea turtle management programs, beach development, and reductions in the size of nesting populations. The harvest of sea turtle eggs by humans removes nutrients from nesting beaches whereas predators introduced by humans (feral dogs, cats, and pigs) substantially alter nutrient and energy flow to nest predators. Management programs can either decrease the nutrients available to terrestrial ecosystems by protecting nests from predation, or substantially redistribute nutrients by relocating all clutches into hatcheries. Development along sea turtle nesting beaches can influence both the introduction and distribution of nutrients in the beach because structures such as seawalls can preclude nesting, and the presence of artificial lighting discourages nesting in those lighted areas and increases nesting density along darker stretches of beach (Witherington 1992).

Humans have influenced the quantities of energy and nutrients transported by sea turtles by substantially reducing the size of, and in some cases causing the extinction of, sea turtle nesting populations (National Research Council 1990, King 1995, Ross 1995). Thus, the present magnitude of energy and nutrient transport by sea turtles does not represent past levels, and we must be conscious of the "shifting baseline syndrome" (Jackson 1997) in our evaluation of the role of sea turtles as biological transporters. In the past, energy and nutrients transported by sea turtles played an even greater role in beach ecology than they do today.

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