ORIGINAL PAPER

Conservation implications of density-dependent predation by ghost crabs on hatchling sea turtles running the gauntlet to the sea

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Abstract Protecting eggs from predators is common practice in sea turtle conservation, but routine protection of hatchlings is not. Of 42 loggerhead hatchlings observed emerging from 10 nests on undeveloped Onslow Beach, North Carolina, 24 % were preyed on by ghost crabs. In experimental trials, ghost crabs similarly threatened and captured neonate freshwater sliders, supporting their substitution as proxy for threatened and endangered sea turtle hatchlings in field experiments testing density dependence. Exploiting natural long-shore variation in ghost crab density, we show that a 2.6-fold higher ghost crab density resulted in 5 times more nocturnal threat encounters with sliders and 3.4 times more slider captures. Sliders released in simulated group emergences experienced lower per capita capture risk by ghost crabs than solitary sliders, implying predator dilution. Non-independence of egg and hatchling depredation motivates consideration of merging sea turtle egg and hatchling stages when modeling and managing food web interactions.

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Introduction

Worldwide, sea turtles have experienced substantial and alarming declines in abundance over decades and centuries (Magnuson et al. 1990; Jackson 2001; Jackson et al. 2001; Bjorndal et al. 2010), establishing them as an important target of ocean wildlife conservation. Along with inducing high mortality in coastal oceans by exploiting sea turtles for food or culturally prized body parts and by inadvertently entangling them in fishing gear (e.g., Crouse et al. 1987), humans also can disrupt nesting success on ocean beaches sufficiently to challenge the sustainability of sea turtle populations via a variety of processes (Bjorndal et al. 2010; Bolten et al. 2011). For example, both people and animals whose populations are facilitated by people prey on sea turtle eggs (Clarke et al. 2000). Subsistence hunters once commonly captured adult females after emergence onto the beach for egg laying (Jackson 1997). When combined with beach development, climate change-induced sea level rise and increased frequencies of intense storms lead to loss of beach nesting habitat (Hawkes et al. 2009). Disorientation of hatchlings by beachfront lighting elevates mortality of hatchlings (Witherington and Bjorndal 1991a).

Despite recognition that predation by multiple species takes place on hatchlings between emergence from the nest and submergence into the sea, quantification of hatchling

depredation is rarely attempted. Qualitative observations have documented predation on hatchlings by the raccoon, red fox, feral cat, ghost crab (references and Latin names in Online Resource Table S1) and several birds. Simms et al. (2002), based on observations by Smith et al. (1996), estimated that 45–99 % of sea turtle hatchlings on Egyptian Sinai beaches are consumed by ghost crabs, and Rebelo et al. (2012) documented such high numbers of hatchling carcasses killed by ghost crabs but left recognizable on a green turtle rookery at Poilao in Guinea-Bissau that they suggested using this source to make annual surveys of green turtle sex ratio. Yet, only Conant (1991) has begun to evaluate factors that determine quantitative losses of hatchlings to ghost crabs. Conant (1991) observed ghost crab captures of loggerhead hatchlings on South Core Banks in North Carolina, estimating that 39 % of hatchlings were captured from nine emergences of <37 individuals, whereas 8 % were captured from five emergences of >91 individuals. She also documented increasing risk of ghost crab predation with greater time spent on the beach by a hatchling, indicating that predation is greater for nests located further from the ocean high-tide line. Nevertheless, the most recent recovery plan (NMFS and USFWS 2008) for the Northwest Atlantic population of the loggerhead sea turtle (*Caretta caretta*), for example, includes no recommended actions to control ghost crab predation on eggs or hatchlings and its only recommended action relating to mammalian predators on the beach specifies a goal of limiting mammalian predation on eggs to <10 %. Inattention to understanding factors that determine the quantitative levels of predation on hatchlings may be explained by the relatively low relative reproductive value of a hatchling as compared with older life stages of a sea turtle with a potential longevity of decades (Crouse et al. 1987; Bolten et al. 2011) and perhaps by an assumption that mortality during the few minutes in the dark that hatchlings spend exposed on the beach is unlikely to be high. Given the example of an observed decline of 43 % in nesting activity of loggerheads in Florida during the last decade (Witherington et al. 2009), there is ongoing need to re-evaluate each ongoing risk to loggerheads so as to implement appropriate management responses. Based on the similarity of sources of egg and hatchling risks among all species of sea turtles, understanding predation processes on loggerheads may by extension apply broadly to other more endangered sea turtles.

Here, we report on field observations quantifying multiple behaviors and the fates of loggerhead hatchlings and on field experiments exploring the intrinsic nature of the predation process by varying both predator (ghost crab) and prey turtle (a slider) densities. We chose ghost crabs (*Ocypode quadrata*) as predator because of their evident high densities and habitual predation on hatchling sea turtles. We chose cultured, juvenile red-eared, yellow-bellied sliders (*Trachemys scripta elegans*) as proxy prey for sea turtle hatchlings to avoid ethical concerns of subjecting a listed species to risk of mortality. We observed nocturnal emergences of hatchling loggerhead sea turtles on undeveloped Onslow Beach, counted hatchling numbers in each emergence, documented interactions between those hatchlings and predatory ghost crabs, quantified predation rates, and recorded times taken by hatchlings to travel from nest to submergence in the ocean swash. We then made use of sliders as proxies for sea turtle hatchlings to test whether risks of capture and threat approach vary with prey abundance, predator density, or both. Here, we address whether integrating observations on loggerheads as they interacted with ghost crabs with inferences about the nature of the predation process from experiments using sliders provides new scientific insights that motivate renewed management consideration of ghost crab predation.

Materials and methods

Onslow Beach observations of loggerhead nests and hatchlings

Onslow Beach, a largely undeveloped barrier island near Jacksonville, North Carolina, is owned by Marine Corps Base Camp Lejeune. The Marines use the island for amphibious training, while their civilian environmental team implements a management program to protect sea turtle nests (almost exclusively loggerheads) from vehicular injury, nest erosion and flooding, and egg predators. During nesting season, daily surveys of the entire ocean beach front at dawn identify the locations of each new nest. The environmental team moves any nest placed low enough on shore to run a high risk of erosion or flooding and any nest placed in the active military training zone to a portion of the island protected from human disturbance and to an elevation presumed to have low risk of erosion or flooding. The environmental team maps locations of every nest and places caging over and around the nest to inhibit entry by raccoons, foxes, and other mammalian predators and to advertise the location to prevent inadvertent vehicular or pedestrian passage over the nest.

Knowledge of nest locations and dates of egg laying allowed us to efficiently observe emerging loggerhead hatchlings and their interactions with predatory ghost crabs during late summer 2009. We deployed multiple pairs of identically trained nocturnal observers at nests approaching hatch (from day 55 onwards, based on historical incubation times for Onslow Beach loggerhead nests). Each observer pair was equipped with a stop watch, tape measure, and battery-powered flashlights with lenses covered by

translucent red plastic. We chose red filters and dim illumination to avoid using light waves and intensities that attract sea turtle hatchlings (Witherington and Bjorndal 1991b) and to use lighting predicted to fall outside the visible range for brachyurans like ghost crabs (Cronin and Forward 1988). For every emergence event, the observing pair recorded numbers of hatchlings in each emergence, fate of each hatchling (successful submergence into the ocean swash or capture by a predator—always a ghost crab), and the duration and linear distance of the track from nest to the sea. We also conducted surveys of active (as judged by crab tracks) burrows of ghost crabs around of each monitored nest (one transect on each side of every nest, separated from the nest by <0.5 m) during this late summer period (25 July through 13 August), when emergent hatchlings were observed. We surveyed ghost crab burrows in early morning (after crabs had terminated nocturnal activity and disappeared into burrows) and within 2 h of low tide. Surveys constituted counts in replicated 4-m wide transects from the top of the swash zone to the dense vegetation zone at the peak of the primary dune, which ended the ghost crab burrowing habitat. We divided the mean burrow counts by 4 to produce estimates of average numbers of active ghost crab burrows per linear m of shoreline. To characterize ghost crab densities in September 2009 across all of Onslow Beach except the military training zone and the northeastern zone closed to our access because of live ordnance passing overhead, we also conducted 5 more sets of 8 replicate burrow transects in each. Each set was composed of two groups (separated by 150 m) of 4 adjacent transects, and sets were located in each of 5 locations scattered across the island. In data reported here, we exclude counts of small burrows (<25-mm diameter), which correspond to ghost crabs less than 30 mm in carapace width, sizes generally too small to capture hatchlings (Conant 1991).

Experimental tests of density dependence in ghost crab predation on sliders

We first assessed whether the most apparent predator on hatchling sea turtles on the beach foreshore, the local ghost crab in North Carolina and the broader southeast U.S. (Stancyk 1979; Conant 1991; Stewart and Wynecken 2004), responded to juvenile red-eared, yellow-bellied sliders as if they were hatchling loggerheads. Sliders are freshwater turtles and this species is cultured for use in the pet trade. On July 26, 2009, after full nighttime darkness arrived, we sequentially introduced individual sliders to the beach foreshore by placing each one on the beach berm (the apex of the sloping foreshore) on Bogue Banks, a barrier island near Morehead City, North Carolina. For each of 8 sliders separated by 20 m, a single observer

retreated landward from the slider and remained stationary 5–7-m away, a separation distance at which we detected no indication of disrupting ghost crab behavior. The consequences of an undetected disruption of aggressive predatory behavior would render our observed rates of predation conservative (underestimates). Ghost crabs had already emerged from their burrows and were occupying the lower foreshore zone of the beach, especially the swash zone. The (tidally changing) swash zone is defined at any time as that portion of the ocean beach between the highest extent of wave penetration and the lowest level to which waves retreat as backwash. At intervals of about every 1–2 min for an 8-min trial, each observer briefly illuminated the targeted slider with red-filtered, dim light from a flashlight to observe any interactions with ghost crabs. Ghost crabs aggressively confronted and then captured sliders in a fashion analogous to the responses of these predators to emerging loggerhead hatchlings observed on Onslow Beach. After capture, the ghost crab held the turtle tight to its ventral surface and moved rapidly away from the foreshore and toward the burrows located higher on the beach. This directional transport facilitated our ability to retrieve each captured slider at the end of each observation period and each subsequent set of 8-min experimental trials, before any evident physical damage occurred to the turtle. Our recoveries of the captured sliders did not detectably disturb ghost crabs that remained in the swash zone and higher on the foreshore, yet we waited high on the beach for 10–15-min recording data before initiating each subsequent trial. The sliders used in our experiments were generally smaller, with mean carapace length of 32.5 mm (SE = 0.1; $n = 194$) and mean wet mass of 7.31 g (SE = 0.07; $n = 194$) than loggerhead hatchlings (with clutch means in carapace widths ranging from 43.4 to 47.6 mm and wet mass means from 19.0 to 24.4 g, as reported in McGehee 1990 for Merritt Island, Florida). Nevertheless, ghost crabs successfully captured the largest slider used in our study (carapace length of 48.4 mm, wet mass of 23.4 g, a size close to the highest mean loggerhead hatchling size), as well as many smaller sliders. Ghost crabs are known to prey on diamondback terrapins (*Malaclemys terrapin*) as well as sea turtle hatchlings (Arndt 1994) so we had expected them to recognize other small turtles as potential prey.

After confirming that ghost crabs captured juvenile sliders at night on the beach in a manner similar to their capture of hatchling loggerheads, we conducted experimental trial releases (emergences) on Bogue Banks beaches. We used cultured, juvenile, red-eared, yellow-bellied sliders as proxy for the threatened loggerhead hatchlings to explore whether risks of threat approach and of capture varied with ghost crab density on the beach and/or with numbers of turtles in a simulated emergence from the nest.

We defined a threat approach as a close approach of a ghost crab to within about 4 cm of a slider followed by a varying period during which neither predator nor prey moved. Such threat approaches preceded capture, which occurred after the stationary turtle re-initiated movement. Ghost crabs appeared to be cued into responding to a slider by the turtle's movement, perhaps because ghost crabs recognize turtle prey by sound and vibration (Horch 1971; Popper et al. 2001). Although each capture for which we observed the complete set of initial interactions with the slider included a threat approach, we avoided double counting in tallying threat approaches and captures by not including among threat approaches those that led to captures in our study. Threat approaches that failed to lead to a capture were terminated by our intervention ending the set period of observation. Because of behavioral differences, such as slower crawling rates and occasional stopping by sliders, potential biochemical differences between loggerheads and sliders that may elicit differential predator responses, and possible artifacts associated with the presence of human observers and short pulses of red light, such uses of proxy species cannot provide reliable estimates of absolute rates of predation. Nevertheless, use of proxies can, with cautious interpretation and some uncertainty, provide insights into the nature of the predation process (testing potential dependence on predator and prey densities here).

After release at the top of the berm, sliders moved toward the ocean, which meant downslope on the foreshore like sea turtle hatchlings, although movement was not always continuous, direction of movement not consistently perpendicular to the shoreline, and rate of movement visibly slower than that of loggerhead hatchlings on Onslow Beach. To standardize observations of slider interactions with ghost crabs for analyses, we recorded all interactions within 8-min trials, the maximum time required among 42 loggerhead hatchlings observed on Onslow Beach to transit from nest to ocean submergence. We rejected the alternative of defining an emergence trial as the complete journey into the sea for this comparative risk approach because the times required for sliders to reach the swash would have extended far beyond what loggerhead hatchlings exhibited. Comparing risks for a fixed time period standardizes our metric across different treatments and avoids using behavioral data pooled across varying, indeterminate, and non-representatively long durations of turtle occupation of the foreshore beach. Nevertheless, the interruption of the process of sliders moving to the sea motivated us to record not only capture events but also threat approaches to reflect our interruption of a process potentially leading to eventual capture. We conducted analyses of threat approaches and captures separately, as well as pooled. In addition, our risk assessment is done only in the foreshore, where ghost crabs congregated, not partly on the back beach where nests

occur and actual emergence takes place. Thus, the predation risk that we measure is an index of comparative risk, allowing contrasts between density treatments. It is not a measure of actual risk to hatchlings for this reason and for the reason that slider behaviors differed from true hatchlings.

To test the effects of varying ghost crab (predator) density and emergence counts (solitary vs. groups) of sea turtle hatchlings (using sliders as proxy prey), we first scouted Bogue Banks beaches to locate nearby areas that differed naturally in abundance of ghost crab burrows, an indicator of ghost crab abundance (Wolcott and Wolcott 1984). We successfully identified two stretches of beach about 2.5-km apart that differed in burrow density by more than a factor of two. We confirmed by conducting formal counts of active burrows along replicate vertical transects (see methods above) that this burrow abundance difference persisted across all three dates on which we conducted our experimental turtle releases (26 July, 23 and 28 September 2009). For each replicate night, we chose different locations within both the East high-density site and the West low-density site at which to conduct our slider releases. Among nights, site locations varied across 1 km in the East and 150 m in the West. By dividing into two teams trained to use the same protocol and maintaining cell phone contact, we thereby replicated trials in time and space simultaneously.

For three nights of experiments, each team, one in the East and the other in the West sites, established a set of five contiguous 4 × 4-m plots arranged along a vertical transect extending from the mid swash zone up into the mid intertidal zone. We marked the corners of each plot with orange surveyors' flags. During the first 2 h of complete darkness, one member of each team used red-filtered flashlights to count all ghost crabs in each plot at intervals of every 10–15 min, to determine whether differences in active burrow counts between study sites accurately reflected differences in densities of ghost crabs active on the beach after dark. Most observed ghost crabs were relatively large (>3 cm carapace width), within the size range capable of consuming loggerhead hatchlings (Conant 1991).

During the first 2 h of full darkness, each team of four observers simultaneously conducted identical experimental trial releases, one set in the East and the other in the West site, to test whether per capita risk of capture and threat approach varied significantly with ghost crab density. Each team of four observers first introduced individual sliders to positions at the top of the berm that were separated by 20 m. Each observer was responsible for observing a separate replicate turtle. Each observer retreated landward about 5–7 m from the slider and every 1–2 min for each 8-min trial used the red-filtered light to scan for and record

any interactions between the slider and ghost crabs. After completing 4–5 sets of solitary turtles, we subsequently introduced sliders in groups of 8, 20, or 40 individuals to positions at the top of the berm and followed the same procedure used for individual sliders to document any incidence of capture or threat approach with any of the sliders in the group. We spread out individual sliders within simulated group emergences over a distance of about 1 m along the berm, a spread that rapidly increased to about 3 m as they approached the swash zone, matching the approximate scale of horizontal spread among loggerhead hatchlings within an emergence on Onslow Beach. Inclusion of trials with multiple sliders mimicked a mass emergence of sea turtle hatchlings, allowing us to test whether per capita risk of capture or threat approach by a ghost crab varies between isolated turtles and those in group emergences during the dash to the sea. Our entire period of experimentation lasted only <2 h. Each trial used fresh sliders to avoid differences arising from re-use and problems of pseudoreplication, with the exception that a small fraction (less than about 20 %) of sliders comprising the group releases had been previously used in solitary trials. In those cases, we selected sliders that displayed the same high level of activity in the holding trays as sliders not yet used to insure crawling when placed on the beach. In all our analyses using simulated group release data, the trial not the slider is the experimental unit.

We based our choices of numbers of sliders to include in mock emergences on published emergence size distributions for loggerheads and green (*Chelonia mydas*) sea turtles on Cyprus over 2 years (Glen et al. 2005). The average emergence size for loggerheads was 11 in 1997 and 6 in 1999, with 1–5 hatchlings the most frequently occurring size class of emergences, accounting for 12 % in 1997 and 22 % in 1999 of the total numbers of hatchlings. The largest emergence for loggerheads fell in the 61–80 size class in 1997 and 41–60 size class in 1999. For greens, average emergence size was 9 in 1997 and 7 in 1999, with 1–5 hatchlings the most frequently occurring emergence size, accounting for 16 % in 1997 and 20 % in 1999 of the total numbers of hatchlings. Our own observations of emergence sizes for loggerheads on Onslow Beach (given in the "Results") confirm a high frequency of small numbers, ranging from 1 to 15, but we lacked opportunity to observe larger emergences.

Our decision to recover all the sliders after each trial and prevent any from being consumed or harmed by ghost crabs required running the mass release treatments last after all trials on solitary sliders because recapturing the sliders involved substantial disruption of the ghost crabs as we chased down ghost crabs that carried turtles and searched for crawling sliders for 30 min. To test for potential bias in the group trial results associated with passage of time during the evening and potential previous exposure of ghost crabs to solitary sliders, we conducted logistic regressions on the fate of solitary sliders (threat approaches plus captures) as a function of time of trial. This analysis was made possible by our use of 4–5 sets of trials with solitary sliders on each night of experimentation. To conduct a comprehensive assessment of effects of turtle density (simulated individual vs. group emergence), predator density (sites of low vs. high ghost crab abundances), and their interaction on turtle fate (no encounter, threat approach, or capture by a crab), we conducted a G-test applying a log-linear model to the corresponding three-way table of frequencies of outcomes of independent emergence trials (Sokal and Rohlf 2012).

Results

Onslow Beach observations of loggerhead nests and hatchlings

Linear distance between loggerhead sea turtle nests and the moist wrack line, indicating the top of the previous swash zone at high tide, ranged from 3 to 53 m on Onslow Beach in 2009, as measured during the egg hatching season. Excluding those nests that were relocated so as to restrict our analyses to characterize choices made by nesting turtles, the average linear distance to the top of the high-tide swash for 29 nests laid in 2009 was 17.8 ± 2.1 m (SE). We spent 85 person-nights of nest observation on Onslow Beach beginning on July 14 and ending on September 23, 2009. From five separate hatching events, successful tracking of 21 individual hatchling sea turtles from the nest to submergence in the ocean swash revealed an average ($\pm$SE) distance covered of 13.0 ± 1.5 m, taking an average of 5.3 ± 0.3 min at an average rate of 2.4 ± 0.2 m min^{-1}. The longest time between emergence from the nest to submergence was 8 min, exhibited by two hatchlings. Out of a total of 42 loggerhead hatchlings emerging from 10 separate nests (1–15 per nest) in darkness from 22:25 to 03:53 h during the period of July 23 to September 13, 2009, our observation teams were able to follow the fate of each hatchling, of which ten were captured and killed by ghost crabs. Emergence sizes were 1, 2, 2, 2, 2, 3, 5, 5, 5, and 15. Ghost crab predation occurred on hatchlings emerging from only three nests: capturing both turtles from an emergence group of 2, 3 from one group of 5, and all 5 from another group of 5. The observed rate of predation (24 %) by ghost crabs documents the fate of hatchlings when emerging in small numbers, which is common for loggerheads (Glen et al. 2005; Adam et al. 2007). Ghost crabs were the only predators observed to capture or directly threaten loggerhead hatchlings despite confirmation by direct observation of bobcats (*Lynx rufus*),

feral cats (*Felis catus*), gray (*Urocyon cinereoargentus*) and red (*Vulpes vulpes*) foxes, opossums (*Didelphis virginiana*), and numerous raccoons (*Procyon lotor*) on Onslow Beach, as well as potential avian predators. Densities of active ghost crab burrows from transects located around the ten nests from which we successfully collected data on predation rate on loggerhead hatchlings averaged 0.20, ranging from 0.01 to 0.72, per linear m of shoreline. These burrow densities surrounding the monitored nests were relatively low compared with our identical systematic sampling during September 2009 of ten stretches covering all of Onslow Beach except the military training and ammunition overflight zones during September 2009, which yielded means of 0.39–3.25 active burrows m^{-1}, averaging 1.60 medium- and large-sized crabs.

Experimental tests of density dependence in ghost crab predation on sliders

Average numbers of active burrows and average counts of nocturnally active ghost crabs per linear m of shoreline differed between the East and West sites on Bogue Banks during the experimentation dates (Fig. 1). For each metric, the East sites averaged 2.6 times the ghost crab density at the West sites. *Ocypode quadrata* emerged from burrows around dusk and moved down toward and into the swash, where gills are wetted, so either summing burrow or nocturnal crab counts per m of shoreline quantified their
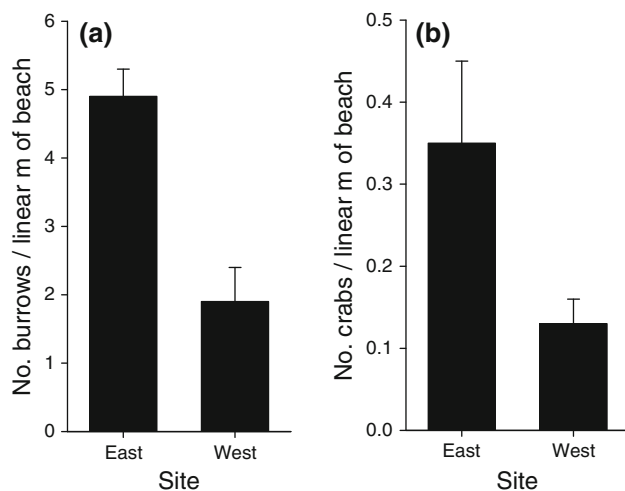
relative potential predation risk to sea turtle hatchlings. Crabs displayed a strong tendency to occupy the lowest of the contiguous 5 plots, which extended into the swash zone, and contained 17 of 33 total crabs pooled across sites and dates. Ghost crabs occasionally appeared even lower than our lowest plot.

Per capita risks of both capture and of threat approach (terminating before possible capture by our trial-ending intervention) for releases of solitary sliders were higher during the standardized 8-min trials where ghost crab density was naturally greater on the East site (Fig. 2). Specifically, the 2.6-fold higher ghost crab density produced 5 times more threat approaches to and 3.4 times more captures of solitary sliders by ghost crabs. Separate analyses also revealed lower per capita risks per min during the 8-min emergence trial of both capture and threat approach by ghost crabs in groups of 8–40 sliders than for solitary sliders (Fig. 3). Average total numbers of threat approaches and of slider captures per 8-min emergence trial did not vary detectably between emergence trials involving a solitary turtle and those using larger emergence groups. No other potential turtle predator was detected interacting with the experimental animals during these trials, perhaps discouraged by the presence of human observers. Neither loggerhead hatchlings evacuating nests on Onslow Beach nor the sliders moving toward the sea on the foreshore of Bogue Banks appeared to attract ghost crabs from any substantial distance away from any
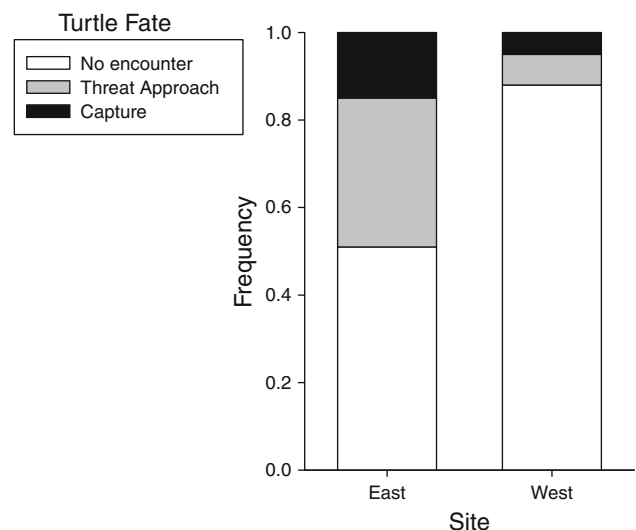

Fig. 1 Mean (+1 SE) abundance of (**a**) active crab burrows ($n = 19$) and of (**b**) nocturnally emerged ghost crabs ($n = 18$) per linear m of beach shoreline at each study site (East and West), pooled across all three sampling dates. For each response variable, the difference in means between sites was very highly significant ($P < 0.001$), as determined by separate fully factorial, two-way ANOVAs (in neither ANOVA, was the DATE main effect or the SITE × DATE interaction significant ($a \geq 0.05$))

Fig. 2 Frequencies of solitary turtle releases falling into each fate category, pooling simulated emergence trials across all three dates to compare sites of high (East) and low (West) ghost crab density. Replication involves both time (3 nights) and space (replicate pairs of different high-density sites ranging over 1 km and low-density sites ranging over 150 m). A significant difference in distributions of trial outcomes existed between sites ($\chi^2 = 14.3$ with 2 degrees of freedom; $P = 0.0008$), with by inspection more threat approaches and captures at the site (East) with higher ghost crab density
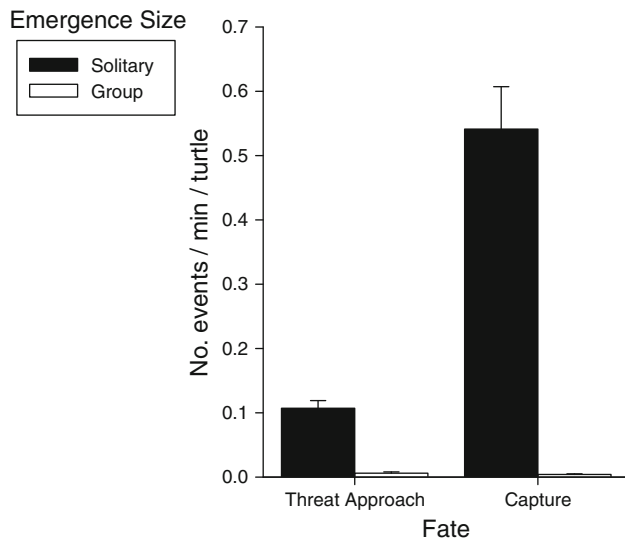
Fig. 3 Per capita risks of aggressive events per minute comparing turtles in simulated emergences of solitary (1 individual) versus group (of 8, 20, or 40 individuals) releases pooled across sites. Frequencies of threat approach and capture per trial (data not shown) did not differ between solitary and group emergence releases ($\chi^2 = 0.491$ with 2 degrees of freedom; $P = 0.782$). However, the per capita risk for both threat approach and capture (data illustrated) were significantly lower for turtles in groups, as determined by separate Wilcoxon tests (for threat approaches: $P = 0.0007$; and for capture: $P = 0.0178$)

Table 1 Results of simulated hatchling emergence trials displaying slider fate (numbers of trials with no turtle–ghost crab encounter vs. numbers exhibiting at least one aggressive encounter, defined as turtle capture or threat approach by a crab) as a joint function of emergence size (solitary vs. a group of 8, 20, or 40 turtles) and ghost crab density (East site with 2.6 times the crab density of the West site)

Simulated emergence	Fate	Site	
		East	West
Solitary	No encounter	21 (0.51)	37 (0.88)
	Aggression	20 (0.49)	5 (0.12)
Group	No encounter	6 (0.54)	7 (0.78)
	Aggression	5 (0.46)	2 (0.22)

Numbers in parentheses depict proportions of emergence trials falling into each fate category for each emergence size × site (ghost crab density) combination. In log-linear analyses, the interaction between site (ghost crab density) and turtle fate was not independent of whether the simulated emergence was a solitary individual or a group of 8–40 ($P = 0.0037$)

observed narrow cone of straight-line tracks toward the ocean, although lack of continuous illumination of the study areas prevented quantification of all ghost crab movements.

Logistic regressions on outcomes of successive trials (up to five each night) using solitary sliders tested whether the frequency of aggressive encounters (captures plus threat approaches) varied with time and thus with the temporal sequence of simulated emergence trials during the night-time experimental period. The best fit regression ($n = 83$) failed to demonstrate a time (sequence) effect ($P = 0.24$), nor did logistic regressions on any data subset (by date, or by West or East sites separately). Consequently, the sequence of when treatments were offered did not bias the results of the mass release, which came last in the sequence.

G-test results using a log-linear model of how slider fate varied with simulated emergence group size and ghost crab density first revealed no significant three-way interaction among turtle density, ghost crab density (site), and turtle fate (no encounter, threat approach, or capture). Of the three possible tests of conditional independence, the interaction between site (ghost crab density) and turtle fate was not independent of whether the simulated emergence was a solitary individual or a group of 8–40 ($P = 0.0037$), whereas the other two conditional independence combinations were non-significant. Because there are three levels of turtle fate, we decomposed the significant conditional

independence test on this factor using subsequent, orthogonal, log-linear models (first comparing no encounter to either threat approach or capture and, secondly, comparing threat approach to capture). These tests revealed that all of the significant difference between the site by fate frequencies across different levels of turtle density (solitary vs. groups of 8–40) are explained by differences in the relative frequency of no encounter versus aggressive encounters (either threat approach or capture: $P = 0.00048$): The relative frequencies among simulated emergence trials of threat approach versus capture were not significantly different ($P = 0.888$). In the higher ghost crab density site (East) slightly fewer than half of all slider releases produced aggressive encounters (48.8 % for lone turtles and 45.5 % for groups of turtles), while at the lower crab density site (West) fewer than one-fifth of slider releases exhibited aggressive encounters (11.9 % for lone turtles vs. 22.2 % for groups of turtles). This twofold higher frequency of simulated emergences resulting in aggressive encounters for groups of turtles than for solitary turtles at the site with lower ghost crab density but not also at the site with higher ghost crab density explains the significant conditional independence (Table 1).

Discussion

Our study was motivated by a concern that sea turtle conservation may be improved by further evaluation of predation risk to hatchlings, especially from predatory ghost crabs. This resulting research merges new quantitative observations of ghost crabs, loggerhead hatchlings, and ghost crab predation on the hatchlings and qualitative documentation of vertebrate predators on a natural beach

with results of experimental testing on proxy hatchlings for two forms of density dependence in the ghost crab–hatchling predator–prey process. The new insights arising from our results suggest that management of ghost crabs, directly or indirectly, may offer benefits to sea turtle fitness. Specifically, we conclude that further quantification of these density-dependent processes could motivate inclusion of additional and modified recommendations for recovery actions for loggerheads (NMFS and USFWS 2008) and, by extension, other threatened and endangered sea turtles.

Our demonstration that per capita predation risk for small turtles running the gauntlet to the sea is reduced when they exit the nest in groups of 8–40 individuals and rush simultaneously instead of making solitary runs reveals an important form of density dependence. These results complement Conant's (1991) observations of 39 % predation rates on loggerhead hatchlings emerging in groups of <37 individuals as compared with 8 % in emergences of >91 individuals to imply that per capita risk of ghost crab predation generally declines with increasing emergence size over the full range of actual emergences. Such density dependence can best be explained by applying the predator dilution hypothesis (Wrona and Dixon 1991) and assuming that larger numbers of hatchlings approaching the ocean swash saturate the predation potential of a finite number of ghost crabs occupying the length of swash zone shoreline that is penetrated by a group of nest-mates. Emergent loggerhead nest-mates on Onslow Beach took straight-line paths from nest to the sea, fanning out over less than about 3 m at the top of the swash. On South Core Banks, loggerhead nests extended to greater distances from the ocean, in part because of relocation by the National Park Service to higher ground, leading to wider spread among nest-mates reaching the swash zone (Conant 1991). Ghost crabs that successfully captured a hatchling in our study carried it off, moving toward burrows higher onto the beach. This process alone, even without adding in handling and consumption time, lasts long enough compared with the short duration of the hatchlings' rush to the sea (an average of 5 min for loggerheads on Onslow Beach) that it would be virtually impossible for any individual ghost crab to be able to actually consume multiple hatchlings from a single emergence group and unlikely for any crab to make multiple kills. We documented no ghost crab consuming just the turtle eyes and then abandoning the victim, which does occur and was documented but rare in Conant's (1991) study. If common, this practice would allow ghost crabs to kill even more hatchlings, including multiple nest-mates.

The observed crawling speed of loggerheads of 2.4 m min^{-1} on Onslow Beach is similar to the mean speed (3.1 m min^{-1}) measured for leatherback hatchlings in Costa Rica (Tomillo et al. 2010) and approaches the range

(2.7–3.4 m min^{-1}) measured for loggerhead hatchlings in emergence events with <37 individuals in North Carolina (Conant 1991). Thus, the observed low likelihood of a single ghost crab capturing more than a single slider or loggerhead from a given simulated or actual emergence may apply generally to sea turtle hatchlings. Smith et al. (1996) showed that the congeneric ghost crab *Ocypode cursor* in Cyprus would capture just one green or loggerhead hatchling from an emergence. While observing in darkness using only pulses of light every 1–2 min, we failed to document any nearby ghost crab moving laterally into the turtles' path to the sea and thereby replacing crabs that had already made captures. Consequently, the most parsimonious explanation for why hatchlings lessen their individual risk of ghost crab capture by emerging from the nest in larger groups invokes the concept of predator dilution (Wrona and Dixon 1991). Declining risk of hatchling depredation with increasingly large aggregations of hatchlings during nest emergence may reflect not only benefits of joint efforts in breaking through the top crust over the nest but also an evolutionary response to predation risk on hatchlings crossing the beach. This suggestion is analogous to the evolutionary explanation for nesting female ridley sea turtles forming nesting arribadas to overwhelm predators on the beach (Bernardo and Plotkin 2007).

The second form of density dependence revealed by our slider experiments implies that risks of threat approaches to and captures of loggerhead hatchlings are likely to increase with increasing ghost crab density on the nesting beach. This conclusion can have important conservation implications wherever ghost crab predation on hatchlings is judged to be unacceptably intense and where management practices could be implemented to directly or indirectly expose hatchlings to lower ghost crab densities. The documented loss of 24 % of loggerhead hatchlings to ghost crabs on Onslow Beach during hatching season in 2009 may seem high enough to invoke management interventions, given that management actions are called for in the loggerhead recovery plan when predation on eggs by mammals exceeds 10 % (NMFS and USFWS 2008). However, this figure must be interpreted in the context of both density-dependent processes revealed by our slider experiments. Specifically, we presume that this 24 % rate of predation on emergences averaging only 4.2 hatchlings would not also apply to the fate of a mass emergence, given our experimental demonstration that per capita risk of captures by ghost crabs is lower from emergence groups of 8–40 than for solitary hatchlings and the conforming Conant (1991) observations at even higher emergence sizes. Because of predator dilution, we would expect much less predation on hatchlings during mass emergences, which do occur (Conant 1991; Glen et al. 2005; Adam et al. 2007)

but simply did not during the 85 person-nights of our observations. Dribbles of fewer than five hatchlings are the most frequent emergence size in our data set and in Glen et al.'s (2005) observations on Cyprus. In addition, sizes of emergences are lower for relocated nests (Adam et al. 2007). Relocation is widely practiced, and done regularly on Onslow Beach to avoid direct military training impacts on nests. Nevertheless, the majority of hatchlings is likely to emerge in larger groups, as observed by Glen et al. (2005) in Cyprus, suggesting, based on emergence size alone, that hatchling losses to ghost crabs on Onslow Beach in 2009 were substantially <24 %.

At this point, our discussion lacks consideration of implications of the other demonstrated form of density dependence—the enhanced predation rate where ghost crab density was higher. Ghost crab densities surrounding the monitored nests on Onslow Beach were relatively low, averaging 0.2 active burrows per linear m transect, compared with an average (Fig. 1) of 1.9 (West site)—4.9 (East site) on Bogue Banks during our experiments and 0.39–3.25 (mean of 1.6) across Onslow Beach areas during our sampling in September 2009. Peterson et al. (2006) reported ghost crab burrow densities to range from 1 to 25 per linear m transect across Bogue Banks in 2001–2003, conforming with the relatively high densities documented on our East and West sites. Thus, nearby beach stretches of Onslow Beach were characterized by ghost crab burrow densities 8 times higher than where we measured hatchling depredation rates and Bogue Banks beaches have even higher crab densities. Because our sampling on Bogue Banks revealed that ratios of burrow counts between two stretches of beach matched ratios of numbers of emergent crabs at night, we can conclude that counts of recently active burrows accurately reflect ghost crab density differences between areas. In our slider experiments on Bogue Banks, an estimated 2.6-fold higher crab density in the East site produced an estimated 3.4 times greater predation on proxy hatchlings, approximating the direct 1:1 proportionality that would be predicted by a simple predator dilution process. Nevertheless, we cannot extrapolate from this experiment to suggest that per capita hatchling predation on these neighboring areas of Onslow Beach would be 8 times the 24 % documented around the 10 nests under observation, a mathematical impossibility anyway. Our log-linear conditional tests of slider fates exploring the nature of the significant G-test results revealed that the effects of ghost crab density on incidence of aggressive encounters with turtles were not independent of density of turtles in the emergence. This significant conditional interaction prohibits us from extrapolating experimentally derived, average predation rates on simulated emergence groups of 1 and 8–40 turtles to predation rates on a set of emergences in which the majority of individual hatchlings

may have emerged in a group of as many as 80 individuals, based on Conant's (1991) and Glen et al. (2005) observations on loggerheads. Despite this inability to extrapolate from the slider experiments to scale up hatchling depredation rate to a distribution of emergence sizes extending to 80 or more, the effect of nearly an order of magnitude higher ghost crab density would clearly be expected to elevate hatchling depredation on small emergences above the observed 24 % from monitored nests on Onslow Beach. The net effects on hatchling depredation of including larger emergences and far higher ghost crab densities more characteristic of Onslow Beach and Bogue Banks cannot be estimated from our slider experiments because of the significant conditional interaction that prevents additivity of the two forms of density dependence. Nevertheless, an eightfold higher number of ghost crabs in the swash zone could render predator saturation inoperable for a far wider range of emergence sizes, indicating a potential for high enough average predation rates to motivate management actions to protect hatchlings from ghost crabs.

Although we observed only loggerhead hatchlings and neonate slider proxies for sea turtle hatchlings, the egg stage and the short beach-based hatchling stage are sufficiently similar across all sea turtles that the density-dependent processes in ghost crab predation on the sea turtle proxy reported here may be universally applicable to sea turtles. Ghost crabs of the genus *Ocypode* are nearly ubiquitous in warm-temperate and tropical sandy beaches worldwide, being common from North and South America to Australia and the Mediterranean (McLachlan and Brown 2006). Furthermore, ghost crabs consume hatchlings of other species and other geographic populations of sea turtles (e.g., Stancyk 1979; Conant 1991; Smith et al. 1996; Tomillo et al. 2010), and our documentation that ghost crabs readily captured a neonate terrestrial slider along with knowledge that they take diamondback terrapins as well (Arndt 1994) confirms their catholic diet (Wolcott 1978) including many small turtles. Consequently, our slider results revealing that per capita risk of predation is lower in emergence sizes of 8–40 individuals than for solitary turtles and increases with ghost crab density can probably be extended to loggerheads and other sea turtles.

Our interpretation that a 24 % predation rate on loggerhead hatchlings by ghost crabs may be an underestimate because crab densities were atypically low by an order of magnitude around the nests monitored at Onslow Beach motivates further testing by field quantification of ghost crab predation on sea turtle hatchlings. Confirmation of high rates of ghost crab predation in excess of 10 % may imply need for management interventions. Possible actions include direct removals of ghost crabs or indirect removals achieved by exploiting food web interactions. Even the minimal food web including those vertebrate and

invertebrate predators that may affect sea turtle demography via direct or indirect interactions with either eggs or hatchlings has sufficient complexity on southeastern U.S. beaches (Fig. 4), however, to render ineffective some predator management options. For example, Barton and Roth (2008) describe the unanticipated consequences of raccoon removal done to reduce their predation on loggerhead eggs in Florida. After trapping out raccoons, ghost crab abundances increased dramatically through release from predatory control, and the few remaining raccoons that avoided traps consumed more sea turtle eggs than the

previously larger population had done, presumably because the enhanced numbers of ghost crabs penetrated the turtle nest cavities more frequently and left odor trails that attracted follow-up raccoon entry and egg consumption (Barton and Roth 2008). The documentation in our experimental emergence trials that proxy hatchling losses to predatory ghost crabs increase with increasing abundance of the crabs implies that removal of raccoons where they are controlling ghost crab densities (Barton and Roth 2008) would probably lead indirectly through trophic effects to increased rates of ghost crab predation on
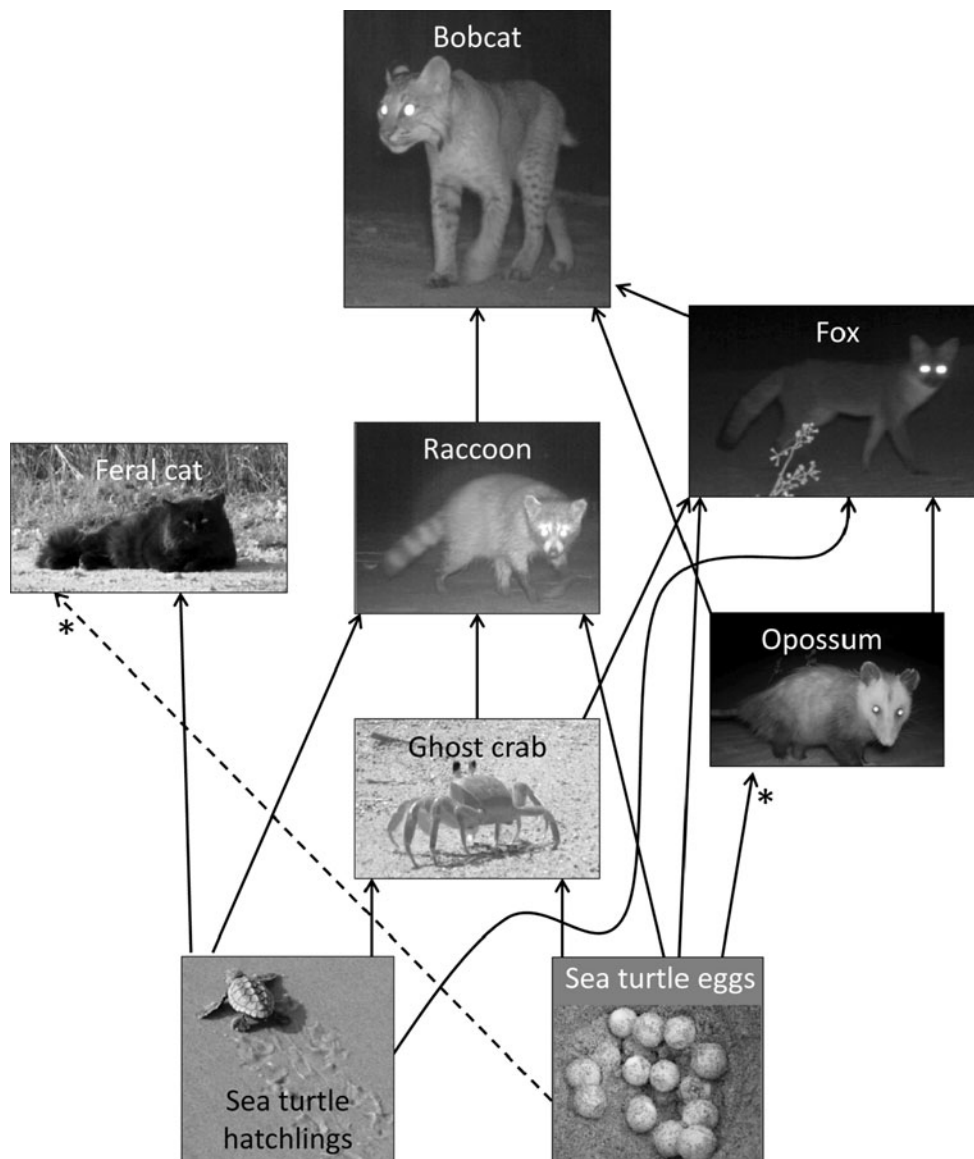

Fig. 4 The web of interactions between loggerhead eggs and hatchlings versus their predators versus the apex predator (bobcat) on Onslow Beach, NC. All images except the egg photo were captured on Onslow Beach (image credits: sea turtle eggs: OCEANA/ Houssine Kaddachi; feral cat: Kacy Ray; all others BMV; see Online Resource Table S1 for Latin names of predators and literature

citations used to construct this food web). *Asterisks* indicate opportunistic egg predators that depend on other species, such as raccoons or foxes, to excavate and provide access into a turtle nest. *Solid arrows* indicate documented predation. *Broken arrow* indicates suspected and likely predation

hatchlings. Our Fig. 4 illustrates the food web interactions that create interdependence of raccoon and ghost crab predation. This example reveals how simultaneous consideration of all strong food web interactions that affect both the egg and hatchling stages of sea turtles on ocean beaches is necessary to develop viable management interventions to protect sea turtles.

When mortality rate (risk) at one life stage is not independent of risk at a previous stage, this density dependence challenges the standard practice of applying stage-based demographic modeling to project sea turtle population growth under adoption of alternative management options (e.g., Crouse et al. 1987; Bjorndal et al. 2010; Bolten et al. 2011). Such interactions would arise if, for example, elevated nest predation increasing egg mortality (Barton and Roth 2008) or relocation of nests (Adam et al. 2007) decreased average size of emergences and led to higher predation on hatchlings by ghost crabs. Such destabilizing feedbacks represent examples of many possible density-dependent demographic interactions between life stages, as mediated by food web interactions. The widely used simple stage-based demographic projection modeling does not readily handle density dependence, even within a life stage (Caswell 1989). Yet, stage-based demographic projections may still be effective in developing quantitative comparisons of alternative management scenarios if a combined egg and on-beach hatchling life stage is used. For example, Crouse et al. (1987) merged these two life stages into a single one for their matrix modeling that showed that no amount of improved protection of early life history stages on the beach could possibly compensate for losses of prime reproductive-aged loggerheads to drowning in shrimp trawls. To apply this approach more broadly to modeling alternative conservation actions to protect the early life stages of sea turtles, however, more field studies are needed to quantify strengths of the food web interactions among the full suite of vertebrate and invertebrate predators on turtle nesting beaches.

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