

**Point of No Return: Determining Depth At Which Sea Turtle Carcasses Experience
Constant Submergence**

**EMMA A. SCHULTZ^{1,*}, MELISSA COOK², REDWOOD W. NERO³, RYAN J. CAILLOUET², JAYMIE
L. RENEKER¹, JAMES E. BARBOUR², ZHANKUN WANG^{4,5}, AND BRIAN A. STACY⁶**

*¹Riverside Technologies Inc., Southeast Fisheries Science Center, 3209 Frederic Street
Pascagoula, Mississippi 39567 USA [emmaschultz25@gmail.com, jrenerker@gmail.com];*

*²National Oceanic and Atmospheric Administration, National Marine Fisheries Service
Southeast Fisheries Science Center, 3209 Frederic Street Pascagoula, Mississippi 39567 USA
[melissa.cook@noaa.gov, ryan.caillouet@noaa.gov, james.e.barbour@noaa.gov];*

*³National Oceanic and Atmospheric Administration, National Marine Fisheries Service,
Southeast Fisheries Science Center, Building 1021, Stennis Space Center, Mississippi 39520
[woody.nero@gmail.com];*

*⁴NOAA's National Centers for Environmental Information, 1021 Balch Boulevard, Stennis Space
Center, Mississippi 39529 USA [zhankun.wang@noaa.gov];*

*⁵Northern Gulf Institute, Mississippi State University, 1021 Balch Boulevard, Stennis Space
Center, Mississippi 39529 USA [zhankun.wang@noaa.gov];*

*⁶National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office
of Protected Resources, Silver Spring, Maryland 20910 USA [brian.stacy@noaa.gov];*

**Corresponding author.*

ABSTRACT. – **At-sea mortality information is important for understanding the magnitude of threats to protected sea turtle species. When a sea turtle dies, it typically sinks, starts decomposing, and will eventually float to the surface if the carcass remains intact and enough internal gases accumulate. However, few data are available regarding the rate and duration of these processes to allow estimation of time since death once carcasses are recovered. Twenty-seven Kemp's ridley (*Lepidochelys kempii*) and 15 green sea turtle (*Chelonia mydas*) cold-stunned carcasses were placed in wire mesh, weighted cages at varying water depths (10–40 m) and temperatures (18.5–28.7 °C) in the northern Gulf of**

Mexico from June 2018 to October 2019. Cameras and temperature-depth-orientation recorders were used to document decomposition progression and carcass buoyancy. Decomposition rate was measured using corrected accumulated degree hours and values of observed time to float were compared to predictions based on lab and field experiments in previous research. Overall, carcasses did not float when deployed in waters >30 m when temperatures were <22 °C and carcasses tended to float sooner in ≤20 m depths especially if bottom temperatures were >24 °C. Green sea turtle carcasses floated in a variety of environmental conditions, but onset of positive buoyancy was not very predictable. Buoyancy of Kemp's ridley sea turtle carcasses was inconsistent, but float times were fairly predictable. We did not identify the exact depth at which sea turtle carcasses cannot generate enough gases to float, but that depth is likely very close to 40 m. Carcasses that became buoyant in ≥30 m depths tended to float for <24 hrs before sinking again and, therefore, it is unlikely that they have enough time to drift to shore. This information enhances our understanding of the likelihood of carcasses washing ashore and can be incorporated into carcass backtracking analyses to facilitate identification of mortality causes.

KEY WORDS. – Mortality investigation, carcass decomposition, submergence, carcass flotation, sea turtle stranding, endangered species

Sea turtles that wash ashore dead (i.e., strand) are the most visible indicator of mortality at-sea. Information gleaned from stranded sea turtles is used to identify mortality sources (especially anthropogenic causes), locate potential mortality hot spots (Nero et al. 2013, 2022), and study biology and ecology (Mancini et al. 2012; Foley et al. 2019; Ramirez et al. 2020). However, sea turtle strandings represent a minimum measure of actual mortality, can be quite variable over temporospatial scales, and observations derived from strandings are inherently biased by a number of factors (Koch et al. 2013; Cook et al. 2021). The location of mortality (e.g., distance from shore, shoreline characteristics) will greatly influence the likelihood of carcass discovery and reporting (Epperly et al. 1996; Hart et al. 2006; Cook et al. 2021). The probability of a carcass stranding also varies greatly depending on time of year, water

temperature, water depth, decomposition rate, and oceanographic (e.g., current and direction) and atmospheric conditions (e.g., wind) (Nero et al. 2013, 2022; Cook et al. 2021).

Juvenile and adult sea turtles are denser than seawater, making them negatively buoyant (Milsom 1975). In living sea turtles, buoyancy is controlled by adjusting the volume of air in the lungs (Milsom 1975; Milsom and Johansen 1975; Minamikawa et al. 1997). When a sea turtle dies from a sudden cause, such as forced submergence or a vessel strike, it typically sinks to the bottom, begins decomposing, and then floats to the surface if enough internal gases accumulate (Epperly et al. 1996). This order of events is evidenced by direct observations of sea turtles sinking at death and instances where sea turtles happened to be equipped with satellite transmitters when they died (Epperly et al. 1996; Nero et al. 2013). There are circumstances in which sea turtle may be neutrally or positively buoyant upon death, such as those that die at the surface with sufficient gas in their lungs or pathologic states where gas is entrapped in other compartments. For scenarios where sea turtles sink upon death, attaining positive buoyancy is crucial to studies involving dead stranded sea turtles because floating carcasses are the most likely to be discovered. The time required for a carcass to decompose and float depends on multiple variables, including water temperature, depth (influence of water pressure), integrity of the carcass, and likely biological characteristics such as diet and gut content (Higgins et al. 2007; Nero et al. 2013, 2022; Cook et al. 2020).

During decomposition, gases such as methane, ammonia, hydrogen sulfide, and carbon dioxide are produced by aerobic and anaerobic bacteria in the tissues and digestive tract (Zhou and Byard 2011). These gases are soluble in water and compressible. Generally, gases are more soluble under higher pressure and are less likely to produce bubbles (which create buoyancy) at greater depths. Gas laws state that at double the pressure, the same amount of gas produced occupies half the volume at a constant temperature (Levine 1978). For example, a carcass submerged 10 m in saltwater experiences double the pressure that it would at the surface and internal gas occupies half the volume. Therefore, at 10-m depth, twice the amount of gas must be produced to occupy the same volume at the surface. As related to buoyancy of carcasses, the volume of gases needed to float is the same, but the amount of gas required is doubled.

Temperature is another important factor in determining if a carcass will float (Higgins et al. 2007; Cook et al. 2020; Nero et al. 2022). Temperature typically decreases with depth below the mixed layer in the ocean (thermocline), which has two major implications for

decomposition: as temperature decreases, (1) the volume of gas also decreases (Charles' Law) and (2) the decomposition rate will nonlinearly decrease (Nero et al. 2022). Therefore, at certain combinations of depth and temperature, a carcass will not generate enough gases to float to the surface before its integrity is lost due to decomposition. Sea turtles that die and sink in such conditions will not float or drift ashore, and are unlikely to be discovered. Therefore, sea turtle mortalities that occur in areas where carcass submerge is beyond this threshold are not observed and documented as strandings.

Very little research is available regarding decomposition of sea turtle carcasses (Higgins et al. 2007; Santos et al. 2018; Cook et al. 2020; Nero et al. 2022). Moreover, information on flotation of human bodies as a proxy for sea turtle decomposition is largely anecdotal. The National Underwater Rescue-Recovery Institute states that humans that drown in -1 to 4 °C water will not surface unless the water temperature increases. They also state that 30 m is likely the depth at which pressure and temperature cause a human body to never surface (Sanders et al. 2005). A review by Moore et al. (2020) notes that increased pressure at depth along with cold temperatures hinder buoyancy of whale carcasses. The threshold depth from which a whale carcass will not resurface is estimated to be 100 m (Reisdorf et al. 2012; Smith et al. 2015). In a previous study of sea turtle decomposition, Nero et al. (2022) suggested that this depth for sea turtle carcasses is likely between 30 and 40 m (depending on water temperatures). This was based on extrapolation from observations made at shallower depths (<10 m) and gas law physics. In addition, Nero et al. (2022) derived a formula to predict the rate at which sea turtle carcasses will become positively buoyant (based on water temperature and depth) for application in a backtracking model. As the flotation parameter is crucial to understanding sea turtle strandings and detection of known or potential mortality sources, we sought to directly document decomposition at different depths and temperatures in order to better characterize carcass flotation and the conditions under which carcasses will not surface.

METHODS

Carcass Preparation and Monitoring. — Twenty-seven sea turtle (Kemp's ridley) carcasses used in this study were salvaged from 2017 and 2018 cold stun events by the Massachusetts Sea Turtle Stranding and Salvage Network (STSSN). Fifteen sea turtle (green)

carcasses were salvaged from a 2018 cold stun event by the Florida STSSN. Overall, the carcasses had a mean size of 25.6 cm straight carapace length (SCL) and a size range of 20.6–32.4 cm SCL. Non-decomposed sea turtles with no obvious external abnormalities were frozen (<0 °C) upon discovery by STSSN members and were kept frozen until needed for experiments. One day prior to deployment, carcasses were removed from the freezer and placed in coolers with ice-chilled water to slowly thaw over approximately 24 hr. Carcasses were individually identified using flipper tags placed on the front or rear flippers. Once thawed, if the carcass was still floating, air was expelled from the lungs by compressing the plastron 5–10 times until it sank. Air expulsion ensured that all carcasses were negatively buoyant at the beginning of deployment on the seafloor as time to float was the focus of this study.

Three wire mesh, weighted cages measuring 122 x 61 x 61 cm with a divider in the center were constructed to contain carcasses at depth on the seafloor. Carcasses were monitored using a GoPro^{®1} camera mounted on one end of each cage and by temperature-depth-orientation recorders (TDRs) within mesh net bags tied to the carapace of most (36 of 42) carcasses (Appendix A). Mesh bags with TDRs were secured using 4-mm braided polyethylene twine tied between the head and front flippers and around the inguinal region on both sides of the carcass. TDRs were only slightly positively buoyant and there was no evidence that attachment impacted carcass buoyancy or flotation. The cameras were set to photograph carcasses every hour during daylight hours. The TDRs recorded bottom temperature, depth, and pitch/roll approximately every 20 seconds to determine when and if the carcass floated off the bottom of the cage.

Study Sites and Deployment. — In June 2018, cages were initially deployed at 20-, 30-, and 40-m depths in the Gulf of Mexico (GOM) south of Mississippi (Fig. 1, labeled “A”); however, we suspect two cages were inadvertently encountered by shrimp trawlers. The 30-m cage was temporarily lost and recovered 58 days later by a commercial shrimper. The data from the TDR on the green sea turtle carcass and the photos from the GoPro[®] were recovered but the Kemp’s ridley and TDR fell out of a large hole in the cage. The 40 m cage was lost and never recovered. To reduce the potential for trawl interactions, the remaining cages were deployed in locations 10-, 15-, 20-, 30-, and 40-m deep near artificial reefs off the coast of Alabama during

¹ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

2019 (Fig. 1). We deployed a total of 18 cages during six deployment trips from June 2018 to September 2019. Each cage contained either one Kemp's ridley and one green sea turtle carcass in each compartment (initial five deployments) or two Kemp's ridleys in each compartment (final deployment; Table 1).

Cages were left in place from six to 30 days to allow sufficient time for carcasses to float (Table 1), based on predictions from Nero et al. (2022). Carcasses deployed in colder, deeper water were predicted to take longer to float than those in warmer, shallower water (Nero et al. 2022). Upon retrieval, all carcasses were photographed and placed on the surface of the water to test their buoyancy. The change in pressure and temperature upon retrieval would expand any existing gas bubbles within the carcass, if it was not too decomposed. If the carcass did not float at depth but floated at the surface it would provide evidence that the depth/pressure and temperature influenced buoyancy status. Retrieved carcasses were characterized as either severely decomposed (soft tissue remaining) or skeletonized.

Decomposition Rate and Time to Float Calculations. — Decomposition rate was estimated using accumulated degree hours (ADH), a metric developed in forensic science to study postmortem events and submerged human bodies (Mateus and Pinto 2016). Accumulated degree hours measure thermal energy input into the carcass during decomposition and allows standardization of temperature on the rate of decay (Simmons et al. 2010). However, ADH (and decomposition rates) are not independent from temperature, so we applied a correction factor, the corrected temperature (T_c), to account for the non-linear relationship between decomposition and water temperature (Nero et al. 2022).

To derive the T_c , temperatures recorded by the TDRs for each carcass were used to calculate hourly mean water temperatures at depth. Then the equation,

$$T_c = \frac{2086.4}{0.246Te^2 - 21.52Te + 468.0}$$

from Nero et al. (2022) was applied to convert the recorded temperatures to the mean hourly T_c . The hourly T_c values were then summed from the time the carcass was deployed until the carcass was observed floating, giving the value for the corrected ADH to float (cADHf) for each floating carcass. If a carcass was not individually equipped with a TDR, the GoPro® photos were used to

identify initial float time and the temperatures from the TDR on the other carcass in the same cage was used for calculations. If only photo data was available, and carcasses floated or sunk overnight (too dark to capture images; $n=2$), then an estimated float or sink time of 0200 was used for calculations.

The thawing process also contributed to the thermal energy budget of the carcasses. To account for this addition, five TDRs were placed in the coolers prior to one of the deployments to record the temperature throughout the thawing process, which was then converted to T_c using the above formula. The cADH were summed for the duration of the thawing process for all five recorders (163.9–209.2 cADH) and the average (185.6 cADH) was added to all cADHf values.

Nero et al. (2022) provided a formula that predicts cADHf (Appendix B) for applications in backtrack modeling. We evaluated the performance of the formula by comparing the predicted cADHf and the actual cADHf determined from our field studies. In addition, we were interested in how long carcasses remained floating in the cage and when they ultimately degassed and sank. To characterize these steps, cADH values were summed from deployment to the time that the carcass sank (cADHs). The cADHf value for each carcass was then subtracted from this value to calculate the cADH that the carcass was buoyant (from time of float to time of sink, cADHb) (Appendix B).

RESULTS

As expected, flotation of carcasses was influenced by temperature and depth (Figs. 2, 3). We also observed differences between the two species. Kemp's ridley carcasses tended to float sooner (with less cADH) in depths ≤ 15 m (Fig. 2). All five green sea turtle carcasses floated in the 20-m cages regardless of temperature. They also floated in the 30-m cages once water temperatures increased above 22 °C (Fig. 3). One Kemp's ridley carcass floated in the 20-m cage at 23.5 °C during the first deployment in June 2018, but no other Kemp's ridley carcasses were observed floating until the September 2019 deployment. Only once, during September, when the average water temperature was 24.0 °C, did both the Kemp's ridley and green sea turtle carcasses float in the 40 m cage. Carcass flotation was not observed in any of the colder 40-m deployments (19.5–23 °C; $n=8$). Since we observed that both species were able to float at the 40-m depth, at least when water temperature averaged 24.0 °C, we are unable to conclude the depth at which sea turtle carcasses cannot generate enough gas to float.

During the final deployment in shallower waters (10, 15, and 20 m), when bottom temperatures ranged from 26.5–28.7 °C, two to four Kemp’s ridley carcasses floated (Fig. 2) in each of the cages. Kemp’s ridley carcasses had a higher correlation between depth and cADHf ($R^2 = 0.8398$) than the green sea turtle carcasses ($R^2 = 0.4655$) (Fig. 4). However, the linear fit for the green sea turtle carcasses was driven by the single data point of the carcass that floated in the 40-m cage. The correlation was negated if this data point was omitted ($R^2 = 0.0056$).

Overall, as water depth increased, the average duration carcasses remained buoyant tended to decrease (Appendix C). As carcasses decomposed, the amount of gases produced increased while the integrity of body tissues decreased due to decomposition and scavenging. Once buoyant, carcasses floated until they become so decomposed or scavenged that they could no longer trap gas inside their body. In some instances, at depth, carcasses built up some internal gases, but not enough to overcome the influence of pressure (depth) and thus, never floated. We observed four carcasses that did not float at depths of 20–40 m in the cages but floated upon retrieval at the surface as a result of gas expansion during ascent. There were also 11 instances (10–30 m) in which the carcasses floated in the cage but did not float at the surface. In these cases, by the time the cages were retrieved, the carcasses had decomposed to the state that internal gas was released as they were brought to the surface. Similar occurrences are likely under natural conditions when entrapped gas expands during surfacing and is released if the integrity of the carcass is insufficient to contain it.

In all instances but one, carcasses floated sooner than predicted (Fig. 4; Appendix C). The cADHf predicted using the Nero et al. (2022) equations were very close to actual values for Kemp’s ridley carcasses with only three of the 11 floating carcasses falling slightly outside of the ± 709 cADH error bound (Nero et al. 2022, Fig. 5; Appendix C). However, green sea turtle carcasses floated considerably earlier than predicted, most floating two times sooner (half of the predicted cADHf) (Fig. 5; Appendix C).

DISCUSSION

This study provides additional information on the important influence of temperature and depth on decomposition of submerged sea turtle carcasses and processes that affect their availability for discovery as shore-cast strandings. We demonstrate that carcasses can float from a depth of at least 40 m if the water temperature is ≥ 24.0 °C, thus the depth from which

submerged carcasses will not resurface regardless of temperature is somewhere beyond this threshold. These findings support the common assumption that sea turtle stranding data is biased towards animals that die in shallower waters and closer to shore. Furthermore, the probability of a carcass stranding is greatly influenced by bottom water temperatures, which vary temporally and spatially. These parameters should be considered along with other biases inherent to stranding data related to shoreline characteristics, survey effort, reporting probability, and other factors (Cook et al. 2021).

Under natural conditions, when a carcass floats, it rises to the surface and then begins to drift. The float time determines the duration for which the carcass will drift and thus influences its probability of washing ashore. Although the top of the cage prevented floating carcasses from surfacing in our study, if a carcass is buoyant enough to float off the seafloor, it will float at the surface if it remains intact. Therefore, the cADHb derived from our study estimates the maximum number of hours that a carcass may be able to drift after surfacing and can be used to gauge its likelihood of making landfall. We consider cADHb to be a maximum estimate of float time because actual duration may be affected by surface processes that erode carcass integrity, such as wave action and surface scavenging, which were not included in this study.

While both Kemp's ridleys and green sea turtles floated in the 40 m cage, their cADHb was only 361 and 683, respectively. This equates to about 12 and 23 hrs of available drift time based on average surface temperatures during summer and fall, the only seasons when bottom temperatures at this depth are warm enough to result in carcass buoyancy. A carcass would have to drift approximately 50–60 km to make landfall from such depths along the Alabama and Mississippi coast (Fig. 6), which is unlikely this time of year because prevailing wind patterns do not favor shoreward drift and scavenging rates are highest (Cook et al. 2021). Furthermore, the closest land masses are remote barrier islands, where probability of discovery and reporting is much lower than mainland beaches (Cook et al. 2021). Although we found that carcasses can float from depths as great as 40 m, it is unlikely that they would reach shore in our region of study. Nonetheless, beaching of carcasses from such depths may be possible in other regions where 30–40 m depth contours are much closer to shore.

Our results also highlight the potential for considerable inter-individual variability in key postmortem processes under natural conditions and warrant caution when deriving estimates for real-world applications, such as backtracking analyses. Validation and

parameterization of a previously published backtracking model (Nero et al. 2022) was a major impetus for this study. In our earlier decomposition research under controlled conditions, we observed that green sea turtle carcasses floated more quickly than Kemp's ridleys, but with much less disparity than found in the current study (Reneker et al. 2018; Cook et al. 2020). We previously concluded that decomposition rates were sufficiently similar between the species to treat them identically in our backtracking model (Nero et al. 2022). However, our current results under field conditions indicate considerable interspecies differences in the overall time and ability of submerged carcasses to float. Green sea turtle carcasses tended to float less predictably and under a wide range of environmental conditions, including waters as cold as 18 °C (all 20-m deployments) and in 30-m depths once temperatures were >22 °C. In contrast, Kemp's ridley carcasses were more likely to float when submerged in comparatively warmer (≥ 23 °C) and shallow areas (≤ 20 m); and none floated when placed at 30 m. The increased rate at which green sea turtles reach positive buoyancy under a wider breadth of conditions suggests that species differences should be considered in the future refinement of backtracking model parameters.

It is notable that during the 9 September 2019, deployment when both species floated in the 40 m cage, neither of the Kemp's ridleys in the 20-m and 30-m cages floated, despite the bottom temperatures being the same or warmer. It was also the first deployment where all three green sea turtles at various depths (20, 30, and 40 m) floated. One possible contributing cause of differences in buoyancy among individuals is internal gas volume. We sought to control this variable using consistent plastron compression prior to deployment; however, differences in gas volume with the lungs and digestive system are possible and may have contributed to these differences. Species differences in overall ability and time to float may be linked to differences in diet and gastrointestinal anatomy and physiology. The primarily herbivorous green sea turtle has a relatively longer intestine and digests plant matter by hindgut fermentation (Bjorndal 1979), which may lead to accelerated postmortem gas production and buoyancy as compared to the carnivorous Kemp's ridley. There also may be considerable differences in the amount of digesta present within the gut at the time of death. Many cold stunned green sea turtles from Florida commonly contain abundant digesta (Foley et al. 2007); whereas some Kemp's ridley cold stunned carcasses have very little gut contents (Innis et al. 2009).

Scavenging by benthic fauna and small fish, as observed in GoPro® images, also may have contributed to the species differences. Upon retrieval, in almost all instances, the green sea turtle carcasses were more intact than the Kemp's ridleys. Green sea turtles may have been less susceptible to scavenging by some benthic fauna because they tended to float sooner and for longer durations. Some Kemp's ridleys had little remaining soft tissue upon retrieval and would no longer contain gas, thus scavengers certainly affected buoyancy in our study. Notably, our cages excluded larger scavengers that could not fit through the 5 x 2.5 cm openings and are relevant to the fate of carcasses under natural conditions. Additional study of marine scavenging under various conditions is needed.

While the focus of our study was decomposition and buoyancy, subsurface drift is another significant consideration in the study of carcass dispersal in aquatic environments. We observed very little lateral movement in sea turtle carcasses until they began to become buoyant (Supplementary Materials). Although we acknowledge that the cage floor may have interfered to some degree, we feel that lateral movement would have been detected, especially if it were significant. This observation suggests that a sea turtle carcass is likely to surface and begin drifting very near to its mortality location, as was assumed in our previously published drift model in Nero et al. (2022).

Kemp's ridleys comprise ~78% of strandings in Mississippi while green sea turtles make up only 3% (Howell et al. 2021). By applying the corrected temperature and results from this study, our findings suggest that the majority of stranded Kemp's ridley carcasses recorded by the Mississippi STSSN likely died in waters <20 m, within or just outside the Mississippi Sound. The backtracking projections depicted in Nero et al. (2013) also support this idea as the majority of mortality locations were predicted to come from depths ≤ 10 m primarily within state waters. Even in water depths as shallow as 20 m, the majority of the Kemp's ridley carcasses did not float during most of the deployments. Individual variability of carcasses may have affected these results, but these trends were consistent throughout all deployments, even as bottom temperatures began to warm. Under controlled conditions, Nero et al. (2022) documented numerous instances of Kemp's ridleys floating in 2–10 m of water in temperatures between 14–33 °C. Those results suggest carcasses can become buoyant in colder temperatures if the water depth is <10 m. Sea turtles that sink upon mortality and do not resurface will never

be documented by the STSSN, providing justification for continued research in these areas to inform true at-sea mortality estimates.

Here we provide in-situ data for carcass decomposition and buoyancy at varying water depths and temperatures throughout the year. Individual variability was noted, but in general, carcasses tended to float sooner in shallower, warmer environments as expected. We show that in cooler and deeper waters, there are many instances in which carcasses are not able to float and that significant species difference exist that should be considered depending on the species composition of strandings within the area of interest. The threshold at which sea turtle carcasses are not able to overcome the depth/pressure constraint is likely very close to 40 m, however, carcasses may surface from this depth if water temperature is $\geq 24^{\circ}$ C. This information can help determine likely origins of stranded animals, investigate known and potential mortality sources, and inform uses of other data derived from stranded sea turtles.

ACKNOWLEDGMENTS

This study was authorized under U.S. Fish and Wildlife Service permit number TE 676395-5. No live animals were killed or harmed for this cadaver study. We would like to thank many staff and volunteers from the Massachusetts and Florida Sea Turtle Stranding and Salvage Networks for salvaging and shipping carcasses during several seasons (2017 and 2018). Without their dedication and response effort this study would not have been possible. We also thank Kendall Falana, Michael Hendon, Jason Letort, Canh Nguyen, Peter Nguyen, and Bryan Wescovich for their assistance with vessel operations and deployment assistance. This research was supported with Sea Turtle Early Restoration Project funds administered by the Deepwater Horizon Natural Resource Damage Assessment Regionwide Trustee Implementation Group. This study was also partially supported by NCEI and NOAA grant 363541-191001-021000 (Northern Gulf Institute) at Mississippi State University. We thank the editor and two reviewers for their constructive feedback to improve this manuscript.

LITERATURE CITED

- BJORNDAL, K.A. 1979. Cellulose digestion and volatile fatty acid production in the green turtle, *Chelonia mydas*. *Comparative Biochemistry and Physiology--Part A: Physiology* 63:127–133
- COLEMAN, A.T., PITCHFORD, J.L., BAILEY, H., AND SOLANGI, M. 2016. Seasonal movements of immature Kemp's ridley sea turtles (*Lepidochelys kempii*) in the northern gulf of Mexico. *Aquatic Conservation* 27:253–267. doi: 10.1002/aqc.2656
- COOK, M., RENEKER, J.L., NERO, R.W., STACY, B., HANISKO, D.S., AND WANG, Z. 2021. Use of drift studies to understand seasonal variability in sea turtle stranding patterns in Mississippi. *Frontiers in Marine Science* 8:659536. doi.org/10.3389/fmars.2021.659536
- COOK, M., RENEKER, J.L., NERO, R.W., STACY, B.A., AND HANISKO, D.S. 2020. Effects of freezing on decomposition of sea turtle carcasses used for research studies. *Fishery Bulletin* 118:7
- EPPERLY, S.P., BRAUN, J., CHESTER, A.J., CROSS, F.A., MERRINER, J.V., TESTER, P.A., AND CHURCHILL, J.H. 1996. Beach strandings as an indicator of at-sea mortality of sea turtles. *Bulletin of Marine Science* 59:289–297
- FOLEY, A.M., SINGEL, K.E., DUTTON, P.H., SUMMERS, T.M., REDLOW, A.E., AND LESSMAN, J. 2007. Characteristics of a green turtle (*Chelonia mydas*) assemblage in northwestern Florida determined during a hypothermic stunning event. *Gulf of Mexico Science* 25:4
- FOLEY, A.M., STACY, B.A., SCHUELLER, P., FLEWELLING, L.J., SCHROEDER, B., MINCH, K., FAUQUIER, D.A., FOOTE, J.J., MANIRE, C.A., AND ATWOOD, K.E. 2019. Assessing *Karenia brevis* red tide as a mortality factor of sea turtles in Florida, USA. *Diseases of Aquatic Organisms* 132:109–124
- HART, K.M., MOORESIDE, P., AND CROWDER, L.B. 2006. Interpreting the spatio-temporal patterns of sea turtle strandings: going with the flow. *Biological Conservation* 129:283–290
- HIGGINS, B., CANNON, A., AND GITSCHLAG, G. 2007. Sea turtle decomposition study. Unpubl. report, National Marine Fisheries Service, Southeast Fisheries Science Center, Galveston, TX 19 pp.
- HOWELL, L., STACY, B., HARDY, R., SCHULTZ, E., COOK, M., WANG, Z., KEENE, J., LAWRENCE, M., SOLANGI, M., MOORE, D., AND MORGAN, T. 2021. Northern Gulf of Mexico sea turtle strandings: A summary of findings and analyses from 2015–2019. Department of

- Commerce, National Marine Fisheries Service, NOAA Technical Memorandum NMFS OPR-69, 110 p.
- INNIS, C., NYAOKE, A.C., WILLIAMS, C.R., III, DUNNIGAN, B., MERIGO, C., WOODWARD, D.L., WEBER, E.S., AND FRASCA, S., JR. 2009. Pathologic and parasitologic findings of cold-stunned Kemp's ridley (*Lepidochelys kempii*) stranded on Cape Cod, Massachusetts, 2001–2006. *Journal of Wildlife Diseases* 45:594–610
- KOCH, V., PECKHAM, H., MANCINI, A., AND EGUCHI, T. 2013. Estimating at-sea mortality of marine turtles from stranding frequencies and drifter experiments. *PLoS One* 8:e56776
- LEVINE, I.N. 1978. *Physical Chemistry*. University of Brooklyn: McGraw-Hill, 1013 pp.
- MANCINI, A., KOCH, V., SEMINOFF, J.A., AND MADON, B. 2012. Small-scale gill-net fisheries cause massive green turtle *Chelonia mydas* mortality in Baja California Sur, Mexico. *Oryx* 46:69–77
- MATEUS, M. AND PINTO, L. 2016. Report on the accumulated degree days and post mortem submersion interval for an infant drowning accident. *Journal of Forensic Investigation* 4:3
- MILSOM, W.K. 1975. Development of buoyancy control in juvenile Atlantic loggerhead turtles, *Caretta caretta*. *Copeia* 1975(4):758–762.
- MILSOM, W.K. AND JOHANKSEN, K. 1975. The effect of buoyancy induced lung volume changes on respiration frequency in a chelonian (*Caretta caretta*). *Journal of Comparative Physiology* 98:157–160.
- MINAMIKAWA, S., NAITO, Y., AND UCHIDA, I. 1997. Buoyancy control in diving behavior of the loggerhead turtle, *Caretta caretta*. *Journal of Ethology* 15:109–118.
- MOORE, M.J., MITCHELL, G.H., AND ROWLES, T.K. 2020. Dead Cetacean? Beach, Bloat, Float, and Sink. *Frontiers in Marine Science* 7:333. <https://doi.org/10.3389/fmars.2020.00333>.
- NERO, R.W., COOK, M., COLEMAN, A.T., SOLANGI, M., AND HARDY, R. 2013. Using an ocean model to predict likely drift tracks of sea turtle carcasses in the north central Gulf of Mexico. *Endangered Species Research* 21:191–203
- NERO, R.W., COOK, M., RENEKER, J.L., WANG, Z., SCHULTZ, E.A., AND STACY, B.A. 2022. Decomposition of Kemp's ridley *Lepidochelys kempii* and green *Chelonia mydas* sea turtle carcasses and its application to backtrack modeling of beach strandings. *Endangered Species Research*
- PARSONS, G.R. AND HOFFMAYER, E.R. 2005. Seasonal changes in the distribution and relative

- abundance of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the north central Gulf of Mexico. *Copeia* 2005:914–920
- RAMIREZ, M.D., AVENS, L., GOSHE, L.R., SNOVER, M.L., COOK, M., AND HEPPELL, S.S. 2020. Regional variation in Kemp’s Ridley sea turtle diet composition and its potential relationship with somatic growth. *Frontiers in Marine Science* 7:253. doi: 10.3389/fmars.2020.00253
- RENEKER, J.L., COOK, M., AND NERO, R.W. 2018. Preparation of fresh dead sea turtle carcasses for at-sea drift experiments. NOAA Technical Memorandum NMFS-SEFSC-731. 14pp. doi:10.25923/9hgx-fn38
- REISDORF, A., BUX, R., WYLER, D., BENECKE, M., KLUG, C., MAISCH, M., FORNARO, P., AND WETZEL, A. 2012. Float, explode or sink: postmortem fate of lung-breathing marine vertebrates. *Palaeobiodivers. Palaeoenviron.* 92, 67–81.
- SANDERS, J., WHITTINGTON, J., AND WILLIAMS, M. 2005. Body float information. National Underwater Rescue-Recovery Institute, 2 pp.
- SANTOS, B.S., KAPLAN, D.M., FRIEDRICHS, M.A., BARCO, S.G., MANSFIELD, K.L., AND MANNING, J.P. 2018. Consequences of drift and carcass decomposition for estimating sea turtle mortality hotspots. *Ecological Indicators* 84:319–336
- SHAVER, D.J., HART, K.M., FUJISAKI, I., RUBIO, C., SARTAIN, A.R., PENA, J., BURCHFIELD, P.M., GAMEZ, D.G., AND ORTIZ, J. 2013. Foraging area fidelity for Kemp’s ridleys in the Gulf of Mexico. *Ecology and Evolution* 3:2002–2012.
- SIMMONS, T., ADLAM, R.E., AND MOFFATT, C. 2010. Debugging decomposition data—comparative taphonomic studies and the influence of insects and carcass size on decomposition rate. *Journal of Forensic Sciences*. 55:8–13. doi.org/10.1111/j.1556-4029.2009.01206.x
- SMITH, C.R., GLOVER, A.G., TREUDE, T., HIGGS, N. D., AND AMON, D. J. 2015. Whale- fall ecosystems: recent insights into ecology, paleoecology, and evolution. *Annual Review of Marine Science* 7: 571–596. doi: 10.1146/annurev-marine-010213-135144
- ZHOU, C. AND BYARD, R.W. 2011. Factors and processes causing accelerated decomposition in human cadavers—an overview. *Journal of forensic and legal medicine* 18:6–9

Received: 10 September 2021

Revised and Accepted: 25 January 2022

Handling Editor: Jeffrey A. Seminoff

Table 1. Summary of Kemp’s ridley and green sea turtle carcass deployments. Refer to Fig. 1 for cage locations. Floated in cage indicates whether or not carcass floated at depth over the course of that deployment. Bold Y indicates instances where carcass floated in cage. G=Green sea turtle, K=Kemp’s ridley sea turtle, Y=Yes, N=No, Unk=Unknown, * indicates cage that was returned by fisherman, – indicates that cage was never recovered.

Deployment Date	Deployment Duration (d)	Cage Location (Depth)	Average Actual Bottom Temperature (°C)	Green/Kemp’s Ridley Floated in Cage (Y/N)	Floated at Retrieval? (Y/N)	Condition Code at Retrieval
11 March 2019	14	20 m-B	18.5	G-Y ; K-N	G-Y; K-Y	G-3; K-3
	30	30 m-B	18.5	G-N; K-N	G-N; K-N	G-3; K-5
	30	40 m-B	19.5	G-N; K-N	G-Y; K-N	G-3; K-3
7 May 2019	22	20 m-B	20.5	G-Y ; K-N	G-N; K-N	G-3; K-5
	22	30 m-B	21	G-N; K-N	G-Y; K-N	G-3; K-3
	22	40 m-B	21	G-N; K-N	G-N; K-N	G-3; K-5
20 June 2018	7	20 m-A	23.5	G-Y ; K-Y	G-Y; K-Y	G-3; K-3
	65*	30 m-A	23	G-Y ; K-Unk	G-Unk; K-Unk	G-Unk; K-Unk
	-	40 m-A	22.5	G-Unk; K-Unk	G-Unk; K-Unk	G-Unk; K-Unk
28 June 2019	20	20 m-B	23	G-Y ; K-Unk	G-N; K-N	G-5; K-5
	20	30 m-B	22.5	G-Y ; K-N	G-N; K-N	G-5; K-5
	20	40 m-B	23	G-N; K-N	G-N; K-N	G-5; K-3
9 September 2019	9	20 m-B	25.5	G-Y ; K-N	G-N; K-N	G-5; K-5
	9	30 m-B	24.0	G-Y ; K-N	G-Y; K-N	G-3; K-5
	9	40 m-B	24.0	G-Y ; K-Y	G-Y; K-Y	G-3; K-3
25 September 2019	6	10 m	28.6	K-Y ; K-Y ; K-Y ; K-Y	K-N; K-N; K-N; K-N	K-5; K-5; K-5; K-5
	6	15m	28.7	K-Y ; K-Y ; K-Y ; K-Unk	K-N; K-N; K-N; K-N	K-3; K-3; K-5; K-5
	6	20 m-B	26.5	K-Y ; K-Y ; K-Unk; K-N	K-Y; K-N; K-Y; K-Y	K-3; K-3; K-3; K-3

Figure Captions

Figure 1. Cage deployment locations. Sites are labeled with depth in meters. Locations labeled “A” were only used for the first deployment in June 2018. Locations labeled “B” were used for all other deployments at those depths. The 10-m and 15-m sites were utilized during the final deployment in September 2019.

Figure 2. Kemp’s ridley sea turtle carcass flotation at varying depths and bottom temperatures over the course of deployments at varying depth and temperature combinations. Data points for the three highest bottom temperatures are slightly offset for easier visualization since four Kemp’s ridley sea turtles were deployed at each of these temperatures.

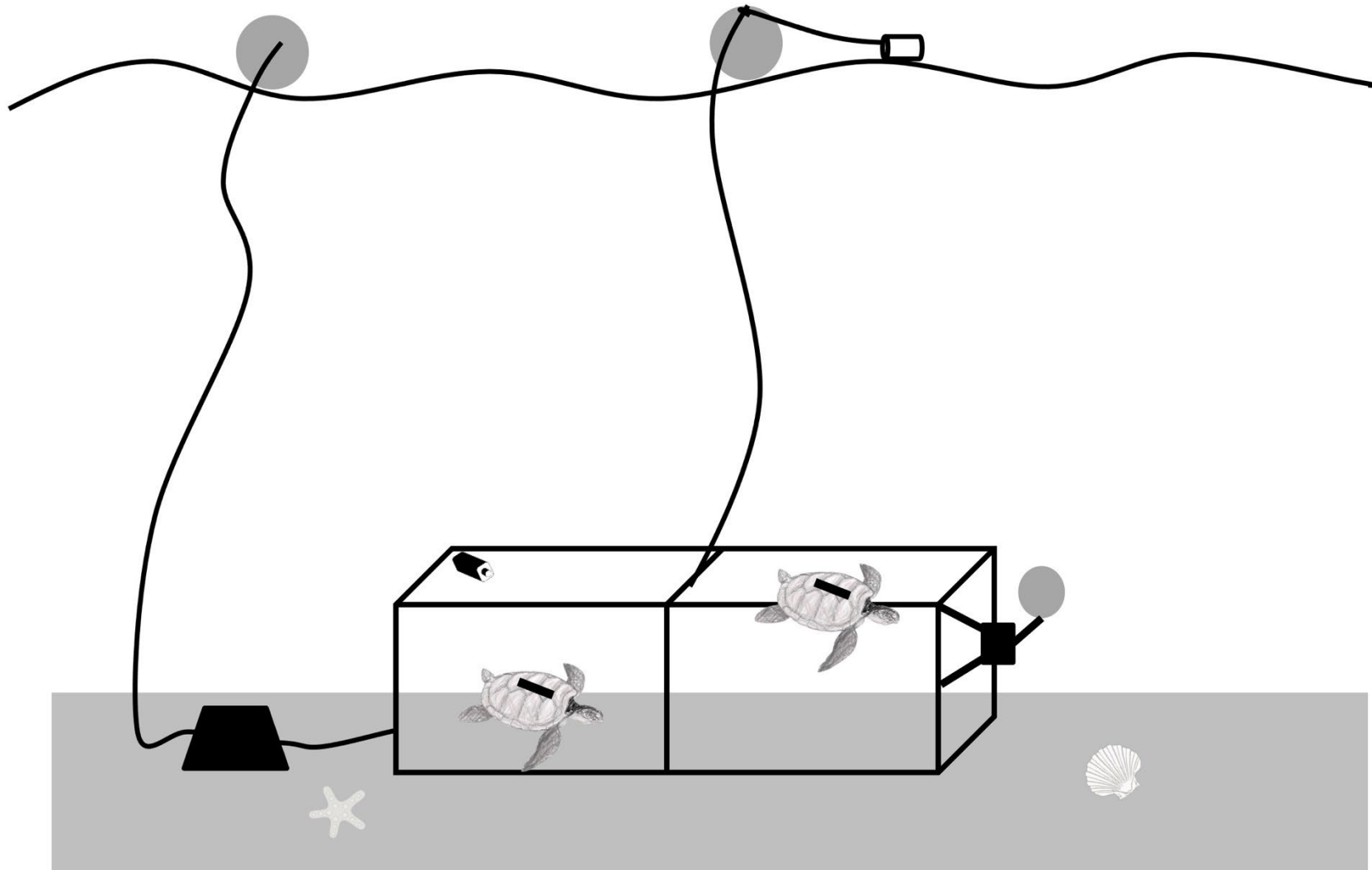
Figure 3. Green sea turtle carcass flotation over the course of deployments at varying depths and bottom temperatures.

Figure 4. The corrected accumulated degree hours to float (cADHf) for Kemp’s ridley and green sea turtle carcasses that floated at varying depths. The thawing decomposition factor of 185.6 cADH was added to the observed cADHf.

Figure 5. Comparison of the predicted and observed cADHf for Kemp’s ridley and green sea turtle carcasses that floated at varying depths. The predicted cADHf is represented by the white bars. The error bars represent the error range of ± 709 cADH calculated in Nero et al. (2022). The striped bars denote the observed cADHf for green sea turtle carcasses and the gray bars denote the observed cADHf for Kemp’s ridley carcasses. The thawing decomposition factor of 185.6 cADH was added to the observed cADHf.

Figure 6. Bathymetry map of offshore waters of Mississippi and Alabama (depths contours are provided in meters).

1 **Appendix A.** Schematic diagram of sea turtle carcasses deployed in a cage on the seafloor to document carcass time to float at various
2 water depths and temperatures.
3



4

5 **Appendix B.** Time to float prediction spreadsheet. Blue highlighted areas are for data input. Green highlighted boxes are calculated
6 output.
7
8 See pdf document

9 **Appendix C.** Deployment date, depth, and water temperature for all carcasses that floated during deployment. Observed corrected
 10 Accumulated Degree Hours to float (cADHf) includes thawing decomposition factor (185.6 cADH). Predicted cADHf was calculated
 11 from predictive equation in Nero et al. (2022) and Appendix B. A negative value for observed vs. predicted cADHf indicates that the
 12 carcass was observed floating before predicted. * Indicates that the observed cADHf was within the error range of ± 709 cADH from
 13 the predicted value. cADHs is the total number of cADH when the carcass sank (s). cADHb is the sum of cADH between float time
 14 and sinking (when the carcass was buoyant (b)), > indicates that the carcass did not sink before retrieval or data collection loss but had
 15 accumulated at least that many cADH at that time.

16
 17

Species	Deployment Date	Actual Water Temperature °C	Depth (m)	Observed cADHf	Predicted cADHf	Observed vs Predicted cADHf	cADHs	cADHb
Cm	3/11/19	18.5	22.6	1011.8	3308.9	-2297.1	3521.52	2509.72
Cm	5/7/19	20.5	22.5	1573.7	3298.75	-1725.1	>5041.88	>3468.19
Cm	6/20/18	23.5	21	1490.2	3146.5	-1656.3	>3809.5	>2319.32
Cm	6/20/18	22.5	32.5	1353.8	4313.75	-2960.0	2074.19	720.44
Cm	6/28/19	23	22.1	1624.8	3258.15	-1633.3	3754.31	2129.5
Cm	6/28/19	22.5	31.5	1546.2	4212.25	-2666.0	2184.83	638.59
Cm	9/9/19	25.5	23	1020.5	3349.5	-2329.0	3650.59	2630.06
Cm	9/9/19	24	32	1339.3	4263	-2923.8	>5098.97	>3759.72
Cm	9/9/19	24	39.5	4091.1	5024.3	-933.1	4774.58	683.45
Lk	6/20/18	23.5	21	3573.8	3146.5	*427.26	>3809.5	>235.74
Lk	9/9/19	24	39.5	4391.0	5024.3	*-633.24	4751.66	360.65
Lk	9/25/19	28.6	10.6	1492.2	2090.9	*-598.67	3721.05	2228.82
Lk	9/25/19	28.6	10.6	1414.9	2090.9	*-676.05	3493.7	2078.85
Lk	9/25/19	28.6	10.6	1685.7	2090.9	*-405.19	2885.84	1200.13
Lk	9/25/19	28.6	10.6	1376.2	2090.9	-714.7	4438.25	3062.05
Lk	9/25/19	28.7	15.4	1842.8	2578.1	-735.29	4663.65	2820.84
Lk	9/25/19	28.7	15.4	2424.9	2578.1	*-153.2	3742.58	1317.68
Lk	9/25/19	28.7	15.4	1359.0	2578.1	-1219.13	4622.36	3263.39
Lk	9/25/19	26.5	23.3	3308.2	3380.0	*-71.8	3928.17	620.02
Lk	9/25/19	26.5	23.3	2904.8	3380.0	*-475.15	3134.04	229.24

18 **Supplementary Material.** Individual cage time-lapse photos from GoPro[®] mounted in each
19 cage as well as Temperature-Depth-Orientation Recorders (TDR) graphs collected from
20 devices attached to Kemp's ridley and green sea turtle carcasses. Cage deployments
21 occurred offshore of Mississippi and Alabama. Reported Accumulated Degree Hours
22 (ADH) include the thawing decomposition factor (185.6 cADH) and were corrected for
23 temperature (c). Observed temperature differences recorded by TDRs on the same
24 deployment were due to instrument accuracy $\pm 1^{\circ}\text{C}$.
25
26 See pdf document