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Simulated Hibernation of Sea Turtles in the Laboratory: I. Feeding, Breathing Frequency, Blood pH, and Blood Gases

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ABSTRACT Captive immature green (*Chelonia mydas*) and Kemp's ridley (*Lepidochelys kempi*) sea turtles were examined to determine if a hibernation-like state could be induced under controlled conditions. Both species demonstrated that they are able to acclimate to cold temperatures behaviorally. However, the two species appeared to respond differently to decreasing temperature. Whereas the green turtles tolerated the onset of cold water temperatures by reducing swimming activity, the ridleys became very agitated and active as they were exposed to temperatures below 20°C. Nevertheless, both species displayed semi-dormant behavior at temperatures below 15°C, coming to the surface to breathe periodically at intervals of up to three hours. At low temperatures, venous blood pO_2 and pCO_2 decreased, whereas venous blood pH increased. Feeding also decreased as either species was exposed to cold temperature: greens (at 15°C) and ridleys (at 20°C) decreased food consumption to 50% of control levels, and ceased feeding below 15°C. Thus, these species tolerated temperature drops and the associated hypophagia. They did not exhibit cold-stunning behavior, as has been observed in wild sea turtles exposed to rapid temperature drops, or prolonged periods of hibernation-like dormancy, as has been proposed for wild sea turtles during cold winter months. *J. Exp. Zool. 278:372–380, 1997.*

Temperature profoundly influences the physiology of reptiles. Their activity is depressed in cold weather and if the temperature is too low to survive in an active state, reptiles become dormant. Hibernation, or brumation, has been described for a number of reptilian species (Gregory, '82). Whereas hibernation can contribute to survival of temperate reptiles during cold periods, the significance of this behavior in tropical, subtropical, and migratory reptiles such as sea turtles is less well understood.

In temperate or subtropical areas, sea turtles are sometimes subjected to rapid, unanticipated temperature decline, resulting in what has been called cold-stunning (Witherington and Ehrhart, '89). A less well-known temperature response of sea turtles has been described as "hibernation." Sea turtles, which may have the behavioral option to escape cold water, were not known to hibernate during the winter until green, loggerhead, and Kemp's ridley sea turtles were discovered by fishermen (Felger et al., '76) and turtle biologists (Carr et al., '80) in what appeared to be dormancy. Carr and his coworkers dragged many chilled, torpid loggerheads and a few ridley turtles from the sea floor of Port Canaveral Ship Channel, Florida. Since there has been little documentation of sea turtle hibernation, and the behavior and physiology of this condition has never been described, there are still many questions regarding wintering adaptations in sea turtles that need to be addressed (Lutcavage and Lutz, '97). Lutz and Dunbar-Cooper ('87) concluded that severe physiological malfunctioning, including acidosis, occurs in loggerhead sea turtles rapidly taken from 30°C to 10°C and that this acute cold-stun state may be quite different from hibernation. When temperature decreases too rapidly (as presumably occurs in cold-stunning), sea turtles are unable to physiologically adjust to temperature changes, whereas a slower drop of temperature may enable sea turtles to prepare for survival at cold temperatures. No studies have been undertaken, however, to examine the behavioral and physiological responses of sea turtles to gradually decreasing temperature. We therefore examined the effects of gradual temperature declines on the be-

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havior of captive sea turtles with the objective of determining whether such gradual drops allow successful behavioral and physiological acclimation to low temperature.

MATERIALS AND METHODS

Animals

Ten immature green (*Chelonia mydas*) and ten immature Kemp's ridley (*Lepidochelys kempi*) sea turtles were used in the following experiments. The green sea turtles were hatched in Florida in 1982 and raised in the laboratory for 8 years. The Kemp's ridley sea turtles had been hatched at Padre Island National Seashore, Texas, in 1987 and were obtained from the National Marine Fisheries Service Galveston Headstart Program. These Kemp's ridleys had minor anatomical deformities (some with scoliosis and others with reduced front flipper size) which prevented their release to the wild; however, they ate and grew well in the laboratory.

Two cold-exposure experiments were performed. At the beginning of the first experiment, the green sea turtles were 8 years old, 7–11 kg body weight (BW), and 37–43 cm straight carapace length (SCL). The Kemp's ridley sea turtles were 3 years old, 5–13 kg BW, and 31–40 cm SCL. At the beginning of the second experiment, the greens ranged from 10–14 kg BW and 40–47 cm SCL, whereas the ridleys ranged from 9–12 kg BW and 33–42 cm SCL. A two-month reconditioning period elapsed between experiments, during which all animals were subjected to 26°C and daily feeding.

Each species was randomly divided into two equal-sized groups (control and experiment) which were held in separate 2,000 gallon artificial seawater (Super Salt, Fritz Chemical, Grand Prairie, TX) raceways (7 m long by 1 m wide by 0.75 m deep) in two separate rooms of the Bioaquatics Facility of the Biology Department, Texas A&M University. Recirculating water was cleaned by ultraviolet-light sterilization, biological and particulate filtration, and regular vacuuming. Each turtle was kept isolated from the others by a plastic pipe divider. Chillers and reduced ambient temperature (room air-conditioning) were used to cool the water for the experimental groups. The experiments were conducted under U.S. Fish and Wildlife Service Permit #PRT-689914, State of Florida Permit #PRT-695140, and Texas Scientific Permit #SP480.

Temperature regime

In the first experiment, the water temperature in the experimental tank was reduced from 26°C to 11°C by decreasing 5–6°C every two weeks over an 8-week period and then raised gradually in similar increments back to 26°C over a subsequent 8-week period. Control groups of turtles were maintained at 23–26°C throughout the study. The photoperiod was maintained at 10 h light:14 h dark throughout the experiment. The second experiment used a similar protocol, but one of the Kemp's ridley sea turtles died after 48 h at 10°C. Although none of the other experimental turtles showed abnormal signs, the temperature for all experimental animals was then increased to 25°C over 48 hours and the experiment terminated. The timing of temperature changes is indicated in the figures.

Feeding and behavioral observations

The animals were fed a diet made from Purina Trout Chow (44.4% protein) and Pet-Tabs Plus vitamins bound into solid blocks with unflavored gelatin. The diet was weighed before feeding, at 4:00 PM every day. Turtles were allowed to eat for 15 min and leftover food in the raceways was estimated (to one-tenth of the fed ration) by observation. Behavior of each animal was observed each day at 10:00 AM (2 h after lights on). Breathing frequency (breaths per min) was measured for 15 min (in warm water) or for up to 4 h (from video tapes of turtles in cold water) as described by Davenport et al. ('82). A single breath was counted when a turtle lifted its head out of the water with its mouth opened for inhalation. At colder temperatures, breathing frequency was calculated by counting the number of single breaths taken by animals when they rose to the surface for a multiple breath episode. Single breaths in multiple breath episodes were summed to calculate breaths/h. Maximum submergence time was measured as the maximum number of minutes during which the animal remained entirely below the surface of the water. Swimming behavior at the surface or underwater, body posture at the bottom, and basking-like behavior at the surface in the afternoon were observed and recorded, but not measured quantitatively. Food consumption, breathing frequency, and submergence time were quantified every two weeks (except for week 4 in Experiment 1), allowing animals 7–10 days to acclimate to each temperature adjustment.

Blood analysis

In addition to behavioral observations, blood samples were taken from turtles in the first experiment at 2 weeks (prior to the initial tempera-

ture drop), 7 weeks (after 7 days at the initial 15°C, experimental animals only), 9 weeks (after 7 days at 11°C), 11 weeks (after 7 days at the second 15°C, experimental animals only), and 15 weeks (7 days after experimental animals were returned to control temperatures) for hematocrit, blood gas ($p0_2$ and pCO_2), and pH measurements. Blood samples were taken between 1000 and 1200 h, 18 h after the most recent feeding. Blood was removed within 5 min of capture. Turtles were restrained by hand and were generally inactive during blood sampling. Blood samples were taken from the cervical sinus into 10 ml syringes with lithium heparin through 21G 1½ inch needles (Owens and Ruiz, '80). After sampling, needles were immediately capped with a rubber stopper. These samples were maintained at 4°C and analyzed for pO_2, pCO_2, and pH within 30 min of sampling on a Corning 288 blood-gas analyzer. Values were then temperature-corrected to the body temperature of the sea turtles at sampling (Stabenau et al., '91). Samples for hematocrit determination were taken separately into heparinized microhematocrit tubes which were centrifuged immediately for hematocrit measurement.

Statistical analysis

Repeated-measures analysis of variance (ANOVA) was performed using the GLM procedure of the SAS program package (SAS Institute, Cary, NC) to determine if significant differences existed in food consumption, breathing frequency, and blood gases within treatment groups and between treatments over time. Significance was determined at the level of $P < 0.05$.

RESULTS

Food consumption and weight gain

The results of the second experiment did not differ from the first. Only data from the first experiment are therefore presented in the figures. Figure 1 shows the mean amount of food consumed per kg body weight per day. Green turtles (Fig. 1a) and Kemp's ridley turtles (Fig. 1b) initially consumed all the food given. Feeding decreased significantly as animals were cooled, ceasing altogether in water below 15°C. Between 15° and 11°C, green turtles remained responsive to moving objects (e.g., they responded to the presence of the investigator or to nets in their tank), but paid no attention to the food which was presented. Between 15° and 11°C, Kemp's ridley turtles either tried unsuccessfully to grab food or ignored it altogether, remaining on the bottom. As with the green turtles, Kemp's ridleys stopped feeding below 12°C. Both green and Kemp's ridley turtles returned to levels of food consumption which were not significantly different from controls when returned to 25°C. Neither control nor experimental groups exhibited a significant change in mean weight over the duration of the experiments.

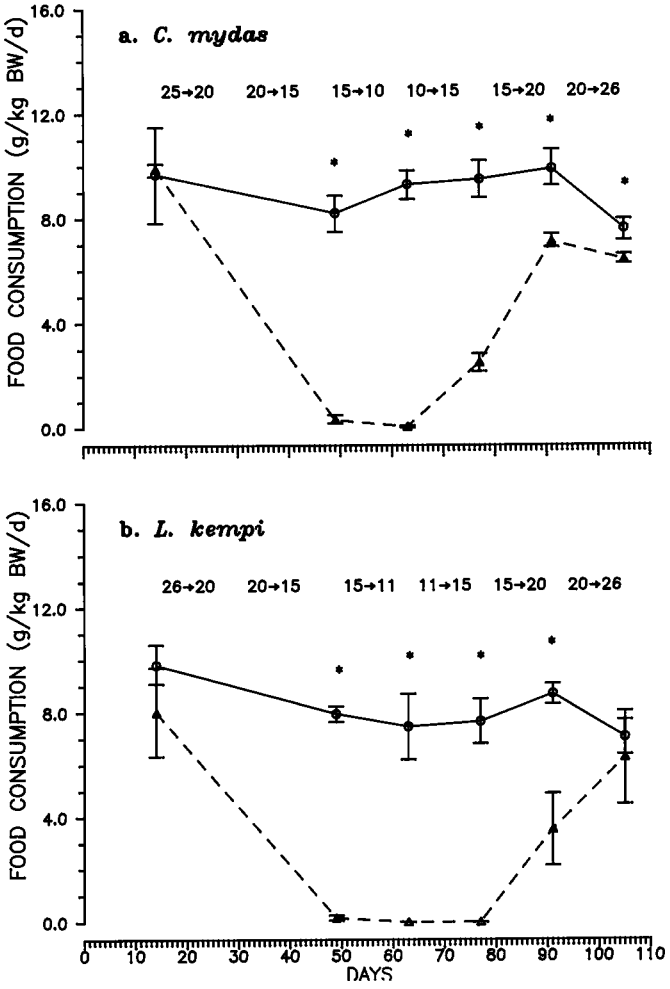

Fig. 1 Mean food consumption (grams of food consumed/kg body weight/day) in Experiment 1. Vertical bars represent standard errors of the mean. 1a) Green turtles, n = 5. 1b) Kemp's ridley turtles, n = 5. Asterisk denotes significant ($P < 0.05$) difference between control and experimental turtles on that date.

Behavior

Significant changes in breathing frequency (breaths/min) over the experimental period were observed in green turtles in both experiments. In warm water (>15°C), green turtles (Fig. 2a) swam actively and took a single breath with each emergence. Below 15°C, green turtles were very slug-

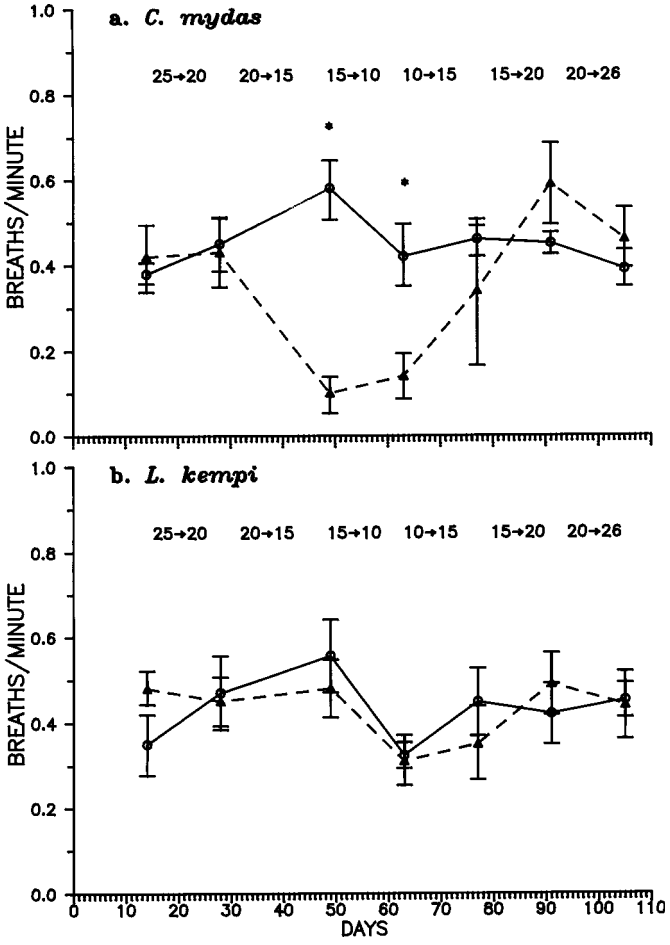

Fig. 2. Breathing frequency (breaths/min, mean ± SE) in Experiment 1. 2a) Green turtles, n = 5 (except on Day 91, when n = 4). 2b) Kemp's ridley turtles, n = 5 (except on Day 91, when n = 4). Asterisk denotes significant ($P < 0.05$) difference between control and experimental turtles on that date.

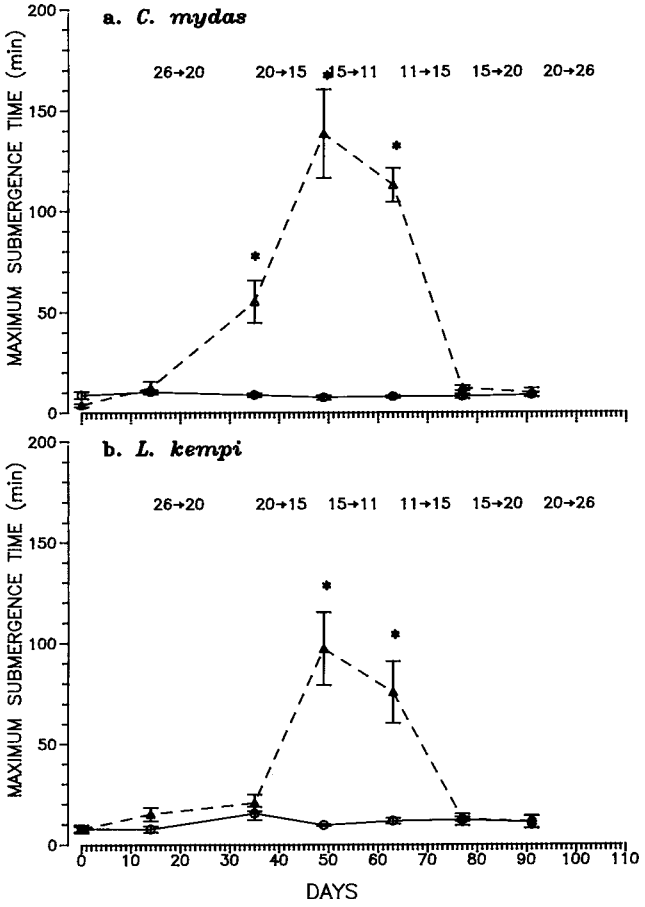

Fig. 3. Maximum submergence time (minutes, mean ± SE) in Experiment 1. 3a) Green turtles, n = 5 (except in experimental turtles on Days 35, 49, and 63 when n = 4). 3b) Kemp's ridley turtles, n = 5 (except in experimental turtles on Days 49 and 63 when n = 4). Asterisk denotes significant ($P < 0.05$) difference between control and experimental turtles on that date.

gish, closed their eyes, and dropped their heads down to the bottom. They often remained motionless on the tank bottom for extended periods, but did come to the surface to breathe at least once every 3 h. In contrast, breathing frequency of Kemp's ridley turtles did not differ between control and experimental animals at any time (Fig. 2b). Below 20°C, Kemp's ridley turtles remained active and stayed at the surface, although their breathing pattern changed from single breaths to multiple breaths after long periods (up to 2 h) of submergence. Unexpectedly, most Kemp's ridley turtles showed hyperactive responses, such as continuous movement of the front flippers, when they were exposed to water from 20°C to 15°C. These Kemp's ridley turtles remained active and stayed at the surface for a prolonged period of time, although their activity tended to become more labored in cold water. Below 15°C, however, Kemp's ridley turtles did decrease activity and remained submerged for up to 2 h. This prolonged submergence was not reflected in an alteration in breathing frequency, however, because of the multiple breaths ridleys took during each trip to the surface.

Both species exhibited significantly increased submergence time as water temperature decreased (Fig. 3). Increased submergence time was first apparent in green turtles (Fig. 3a) after temperatures dropped to 20°C, although during warming, submergence times at 15°C were not different from controls. Submergence time estimates were complicated in greens by their display of basking-like behavior, in which they floated with cara-

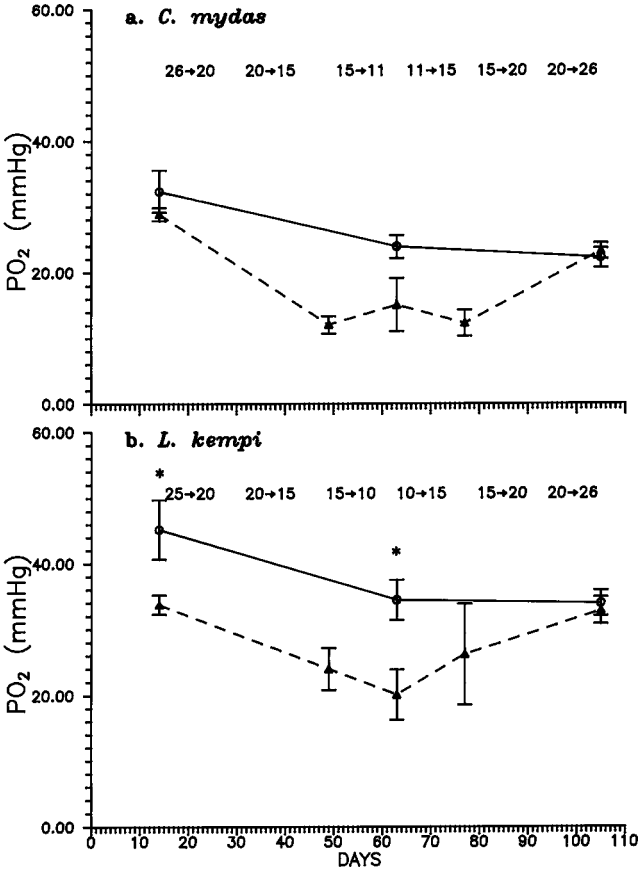

Fig. 4. Venous pO_2 (mm of mercury, mean ± SE) in Experiment 1. 4a) Green turtles, n = 5. 4b) Kemp's ridley turtles, n = 5. Asterisk denotes significant ($P < 0.05$) difference between control and experimental turtles on that date.

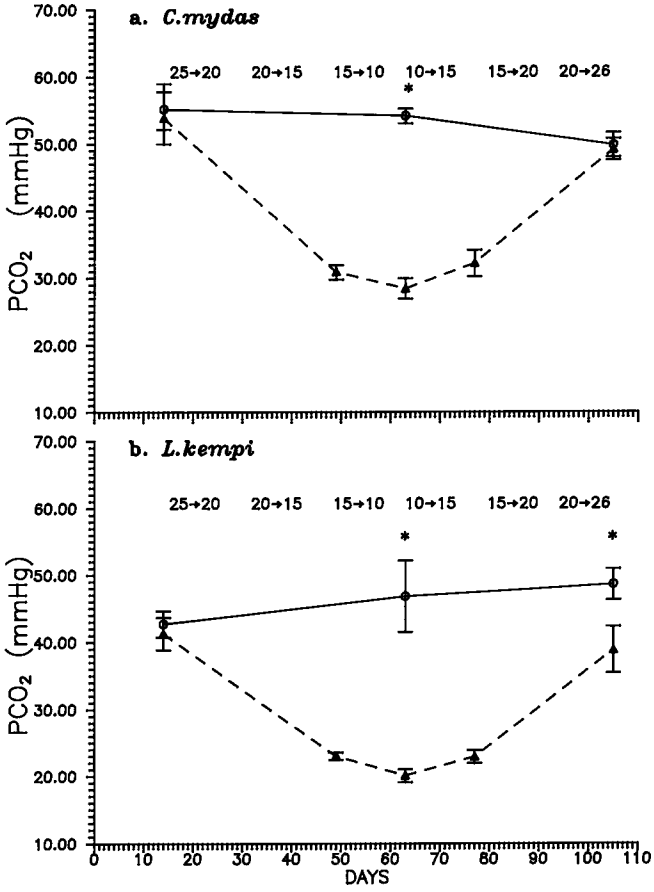

Fig. 5. Venous pCO_2 (mm of mercury, mean ± SE) in Experiment 1. 5a) Green turtles, n = 5. 5b) Kemp's ridley turtles, n = 5. Asterisk denotes significant ($P < 0.05$) difference between control and experimental turtles on that date.

pace exposed and head and tail partly submerged. This behavior continued for 1–2 h at all temperatures, exclusively in the afternoon, often yielding a dry carapace. Kemp's ridleys again appeared more resistant to a drop in temperature (Fig. 3b), not showing a significant increase in submergence time until after temperatures dropped to 15°C.

Blood gases and pH

Venous pO_2 in experimental green turtles (Fig. 4a) was not significantly lower than controls at any temperature at which paired samples were available. Venous pO_2 in experimental Kemp's ridleys (Fig. 4b) differed from controls at the start of the experiment and at 11°C. Temperature had a significant effect on venous pCO_2 in both species (Fig. 5), as venous pCO_2 decreased dramatically over the temperature range between 26 and 11°C. ANOVA revealed that the effect of temperature on blood pH levels was also significant in both species (Fig. 6). For green turtles, blood pH increased by 0.014 units/C°; for Kemp's ridley turtles it increased 0.015 units/C°. Differences in hematocrit (data not shown) were not observed in green turtles over time or between experimental and control animals, whereas Kemp's ridley turtles showed a significant difference in hematocrit only between control and experimental animals at 11° (20.6% ± 0.9 SE for control vs. 13.4% ± 1.2 for experimental). Hematocrits for all turtles during the course of the experiment ranged from 10.0 to 33.8 % for Kemp's ridleys and 18.8 to 36.5% for green turtles.

DISCUSSION

The thermal biology of sea turtles has rarely been investigated, primarily because there are long-term sampling difficulties in the wild (Lutz and Dunbar-Cooper, '87). The present study attempted to overcome some of these difficulties by

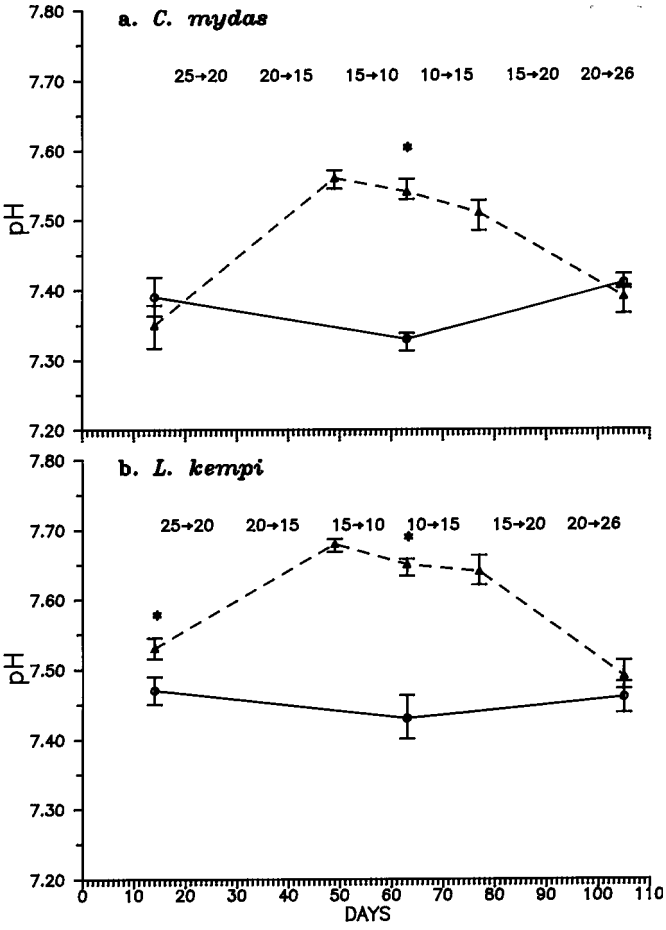

Fig. 6. Venous pH (mean ± SE) in Experiment 1. 6a) Green turtles, n = 5. 6b) Kemp's ridley turtles, n = 5. Asterisk denotes significant ($P < 0.05$) difference between control and experimental turtles on that date.

using long-term laboratory acclimated animals to determine whether imposed cold temperatures can induce a hibernation-like state. Below 15°C we observed a substantial decrease in swimming behavior in both species, even though both did come to the surface to breathe occasionally. In contrast, Schwartz ('78) reported that Kemp's ridley and green turtles displayed floating behavior around 10°C in outdoor tanks. This was in response, however, to a rapid drop of temperature from a cold front. The present experiments indicate that when temperature decreases are more gradual, uncontrolled torpor is avoided, and sea turtles are capable of acclimating to cold temperatures. No behavior resembling cold-stunning was observed in any of our animals.

Important differences were noted in the behavioral responses of these two species to cold temperatures. Green turtles cease all activity (except occasional trips to the surface to breathe) at temperatures below 20°C. Kemp's ridley turtles were clearly more active than the quiescent green turtles at 15° and 10°C although their movements became more labored at low temperatures. This activity in Kemp's ridley turtles is reflected in shorter submergence times at 20°C during cooling, but the differences between species were most notable in breathing frequency. Jackson et al. ('79), and Kraus and Jackson ('80) observed decreased breathing frequency with decreasing temperatures in immature green turtles. Breathing frequency of our green turtles also decreased with temperature, in association with substantial increases in submergence time. Although submergence time also increased in Kemp's ridley turtles as temperature decreased, this increase occurred at a lower temperature and no similar association of decreased breathing frequency with low temperature was observed. In both species, the breathing pattern changed from single breaths separated by short apneic periods at warm temperatures to multiple breaths separated by prolonged apneic periods at cold temperatures. However, in the more active Kemp's ridley turtles, the average number of breaths per minute (counting all breaths in multiple breath episodes) did not differ between control and experimental animals, even at coldest temperatures, suggesting that some characteristic of respiratory function other than breathing rate (e.g., tidal volume or oxygen extraction) may be more responsive to decreasing temperatures (Kraus and Jackson, '80; Lutz et al., '89). The more frequent breathing of Kemp's ridley turtles may reflect their reduced ability to maintain submergence and store oxygen in blood and tissues (Stabenau and Heming, '94).

The difference in behavioral response to cold between ridley and green turtles is interesting, as ridley turtles are known to range farther into temperate waters than the circumequatorial greens. The maintained swimming behavior of the ridleys may facilitate survival and movement in colder climates, thus extending this species' range. According to Schwartz ('78), young or hatchling green, loggerhead, and Kemp's ridley turtles can tolerate cold water longer than adults, suggesting that younger turtles are able to swim in cold water, whereas older turtles such as juveniles and adults may show depressed activity in cold water. Caution should be exercised, however, in comparing the behavior of our captive-raised ridleys to that of wild animals, as ours were slightly abnormal anatomically and had been raised in cap-

tivity on an artificial diet. It would thus be of great interest to repeat this comparative study with wild animals to determine whether ridleys display behavioral characteristics which make them more resistant to the effects of cold temperature. Interestingly, telemetric studies of wild juvenile Kemp's ridleys found active, directed movements when ambient temperatures were below 15°C (Standora et al., '89; Lutcavage and Lutz, '97).

Both species showed similar changes in blood gases during cold exposure. Prior research on acid-base status and blood gases in sea turtles has primarily focused on brief periods of imposed temperature alterations or submergence (e.g., Kraus and Jackson, '80; Butler et al., '84; Lutz et al., '89; Stabenau et al., '91). Additionally, most results were based on data collected from arterial blood. In contrast, turtles in the present study were subjected to a gradual temperature change, were allowed to voluntarily control their submergence time, and were sampled from the dorsal cervical sinus, yielding venous blood samples. Although arterial blood most accurately reflects the effects of alterations in breathing rate and lung ventilation on blood gas and acid-base status, Lutz et al. ('89), also collected blood from the dorsal cervical sinus because they found that arterial-cannulated loggerhead turtles showed abnormal behavior. In spite of differences in cold-exposure protocols, the venous blood gas changes observed in the present experiment were similar to those observed in previous studies on sea turtle cold exposure.

Other studies have established that pO_2 in reptilian blood decreases at lower temperatures (Wood, '84; Glass et al., '85; Lutz et al., '89). Such a decrease reflects an expected drop in tissue oxygen consumption by cold animals, and is consistent with an observed increased affinity of hemoglobin at low temperatures (Stabenau and Heming, '94; Lutz et al., '89). Venous pO_2 levels in the present study were generally lower at 10°C, but not significantly compared to paired controls (greens) or Day 0 samples (ridley's). Although tissue extraction of O_2 is impossible to estimate in our animals without arterial pO_2 values, we expect that tissue oxygen consumption in our turtles is substantially reduced at lower temperatures, as in other reptiles (Bennett and Dawson, '76). A decrease in ventilation, coupled with decreased 0_2 consumption, thus results in minor changes in venous pO_2. Venous, pCO_2 levels in our study displayed a more dramatic decrease at low temperatures, also previously observed for sea turtles (Kraus and Jackson, '80; Lutz et al., '89). It has been proposed that sea turtles and other ectotherms alter their ventilation rates at low temperatures to regulate blood pCO_2 and consequently maintain a constant alkalinity difference between blood and water (Kraus and Jackson, '80). In the present study, both species of sea turtle experienced a significant drop in pCO_2 at coldest temperatures. Changes in ventilation frequency, as we measured it, thus do not account for observed alterations in $pC0_2$. Similar observations exist for other reptilian species (Milsom, '90). Whereas the decline in pCO_2 may be due in part to a direct effect of temperature on CO_2 solubility, additional information on other aspects of respiratory function (e.g., lung ventilation or tissue buffering, tissue CO_2 production) is required to determine the cause of the pCO_2 decline (Lutz et al., '89).

Associated with the decreased pCO_2 at low temperatures was an expected increase in blood pH. The magnitude of this increase in pH ($\Delta pH/\Delta T$ = 0.014–0.015) was very similar to that noted in other sea turtle studies (Kraus and Jackson, '80, Lutz et al., '89), and close to that of neutral water ($\Delta pH/\Delta T = 0.17$), indicating that constant relative alkalinity is being maintained in animals given relatively long acclimation periods. Kraus and Jackson ('80) suggested that greater variability in low temperature pH values in green turtles acclimated to 15°C for 1 day was due to a diminished ability to regulate blood pH below the normal temperature range of green turtles. We found no indication, however, that either of our species exhibited increased variability in pH values below 20°C, indicating that the relatively long (weeks) period of acclimation in the present study enabled turtles to make the necessary physiological adjustments to precisely regulate pH at cold temperatures.

Hibernation, as described for wild turtles, occurs in response to temperatures below 15°C (Felger et al., '76; Carr et al., '80; Ogren and McVea, '81) and should result in dramatic behavioral changes, including prolonged dormancy. We did not observe activity which would qualify as hibernation under existing reptilian definitions; turtles came up to breathe after a maximum of 2–3 h at the colder temperatures. "Hibernating" sea turtles captured by fisherman or trawled by nets were covered by mud or an algae film, which gave investigators the impression that the animals had been immobile on the bottom. However, since no one has directly observed dormant turtles in the water for a prolonged time, we question if

sea turtle dormancy is similar to that of freshwater turtles (e.g., prolonged periods of apnea). In addition, the inference that sea turtles have been in hibernation because algae has grown on their carapace (Felger et al., '76) is not conclusive. In confined situations (as in our tanks) turtles readily develop algal growth on their carapace when exposed to adequate light.

From our laboratory experiments, we hypothesize that sea turtles in cold water will be semi-dormant, periodically coming to the surface to breathe, as has been suggested for hibernating water snakes (Wasser, '90). Both species we examined are commonly found in water shallow enough to enable them to rest on the bottom (Lutcavage and Lutz, '97). However, based solely on our laboratory experiments we cannot exclude the possibility that under natural conditions sea turtles hibernate, as do freshwater turtles or other reptilian species. Interestingly, all captured sea turtles suspected of being in hibernation were immatures, which were possibly recent residents in the area. This leads us to believe that if hibernation occurs, age classes would be juveniles or subadults and that hibernacula would be limited to certain geographical areas.

In conclusion, the present study showed that captive immature green and Kemp's ridley sea turtles exhibited depressed activity in cold temperature. Lowered metabolism and activity may be advantageous to the animals, which must survive prolonged hypophagia or cold water. Both species clearly demonstrated that down to approximately 10°C they are able to acclimate to cold temperature behaviorally and physiologically. Additionally, the two species appear to have distinct behavioral responses to reducing temperatures. These responses appear to be related to ecological differences between the species. More field observations are needed to determine if these dormant periods are regular components of sea turtle life cycles or only an accidental and irregular occurrence resulting from unusual cold exposures in certain geographical areas.

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