

A COMPARISON OF STABILITY IN SWIMMING LOGGERHEAD
(*Caretta caretta*) AND GREEN (*Chelonia mydas*) SEA TURTLE POSTHATCHLINGS

by

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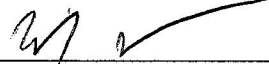
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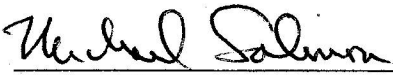
This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Jeanette Wyneken, Department of Biological Sciences, and has been approved by the members of her supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

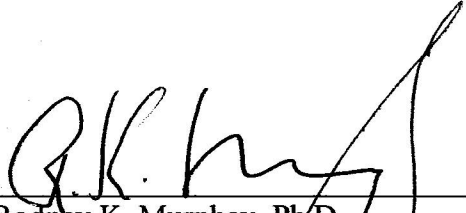
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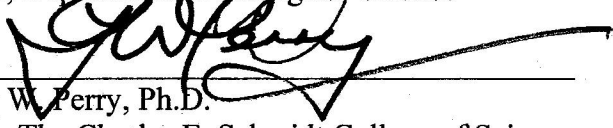

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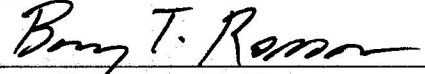

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ABSTRACT

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(*Caretta caretta*) and green (*Chelonia mydas*) sea turtle
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Posthatchling green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles overlap ecologically but differ morphologically. This study compared hydrodynamic stability between the two species during swimming to test for functional differences in body shape. Flipper movement paths, four stability measures (yaw, pitch, heave, and sideslip), and the relative positions of the centers of buoyancy and gravity were compared between species. Both centers of buoyancy and gravity lie in the anterior body; their positions relative to one another differed with species, but showed no functional consequences. Neither species demonstrated substantial yaw, sideslip, or pitch. Both experienced upward heave with the flippers' downstroke and downward heave with the upstroke; however phase relationships differed between these limb and body motions.

No differences were found between the two species. Despite obvious morphological differences, loggerheads and green turtles were similarly stable during swimming, suggesting that the species use different mechanisms to achieve stability.

A COMPARISON OF STABILITY IN SWIMMING LOGGERHEAD
(*Caretta caretta*) AND GREEN (*Chelonia mydas*) SEA TURTLE POSTHATCHLINGS

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Introduction

Animals moving through aquatic habitats can be exposed to a wide range of potentially destabilizing external forces, such as turbulence, or self-generated forces as are buoyancy or movement (Webb, 2002; Bartol et al., 2003). As a result, motion extraneous to an animal's direction of travel can be produced, including translational movements such as heave (vertical displacement), sideslip (lateral displacement), and surge (antero-posterior displacement), as well as rotational movements such as pitch (head up/down rotation about the transverse axis), yaw (left/right rotation about the dorso-ventral axis), and roll (rotation about the longitudinal axis; Figure 1) (Webb, 2002). Although many animals generate a controlled measure of instability to facilitate starting, stopping, and changes in direction (Weihs, 1993; Webb, 1997), instabilities that generate motion extraneous to the direction of travel can increase locomotor costs (Fish, 2002). Aquatic animals can resist such destabilizing forces and achieve stability by damping perturbations and correcting disturbances (Weihs, 1993; Webb, 2002). This stabilization can be produced actively through body movements, but can also be generated passively via a range of morphological features such as overall body dimensions or the presence of keel-like structures projecting from the body.

The marine turtles represent an intriguing group in the context of aquatic stability due to their locomotor habits, distinctive body plan, and range of morphological variation. Because they spend much of their lives migrating, including travel between

nursery areas and among developmental habitats (Musick & Limpus, 1997; Bolten et al., 1998; Bowen et al., 2005), and seasonal travel between feeding and breeding grounds (Plotkin, 2003), the costs of extraneous locomotor movement could be significant to sea turtles. Thus, mechanisms to enhance aquatic stability might be expected in this lineage (Fish, 2002). For example, with the incorporation of the trunk skeleton into a rigid shell, features of shell structure might convey enhanced stability in some species. Alternatively, species with less stabilizing shell form might adjust their limb motions so that stability is essentially similar even across turtles with different shell morphologies.

Some previous observations of swimming in sea turtles have described patterns related to their hydrodynamic stability. For example, Walker (1971) suggested that the dorsoventral forelimb flapping of sea turtles should be accompanied by pitching movements, but did not find such movements in the slowly swimming adult-size animals he examined. In contrast, Davenport et al. (1984) found pitching movements during routine swimming in juvenile green turtles (*Chelonia mydas*), and pitching became more pronounced during vigorous swimming. Both roll and yaw, on the other hand, decreased to negligible levels in green turtles as swimming became faster (Davenport et al., 1984). When rotational displacements were imposed on loggerhead (*Caretta caretta*) sea turtle hatchlings, they responded to roll with coordinated corrective movements of the foreflippers and to pitch and yaw with movements of the hind flippers, showing an active response to destabilization (Arens et al., 2003). In addition, Heithaus et al. (2002) described large juvenile and adult green turtles as more maneuverable than loggerheads of similar size. These observations together suggest

that loggerheads should be more stable than green turtles because maneuverability and stability typically involve performance trade-offs (Fish, 2002; Weihs, 2002). These authors further suggested that the hydrodynamic differences between these species could explain the lower rate of shark attack injuries on green turtles compared to loggerheads (Heithaus et al., 2002).

Although some inferences regarding swimming stability have been made for sea turtles, and a capacity to actively control stability has been identified, evaluations of how differences in morphology might contribute to the stability of sea turtle species have yet to be performed. Comparisons of hydrodynamic stability between loggerhead and green turtles provide such an opportunity. The carapace of a hatchling or posthatchling green turtle is dorsoventrally flattened, without dorsal keels and elliptical in planform view, whereas that of a loggerhead is somewhat less dorsoventrally compressed, and the planform view is heart-shaped (Figure 2). Neonates have longitudinal ridges on each costal scute that persist for several months or more (Wyneken, 1994). Juvenile loggerhead turtles develop pronounced longitudinal spiny keels along the vertebral and marginal scutes. These structures persist at least until turtles reach the sizes at which they return to coastal waters. The species also differ in flipper morphology; green turtles have relatively longer, thinner (high aspect ratio) flippers, while loggerheads have relatively shorter, broader (lower aspect ratio) flippers (Wyneken, 1988, Figure 2). Of these differences, the presence of keels on loggerhead shells might be expected to have particular significance. Compared to the smooth lines that characterize green turtle form, the keels could provide additional stabilization against yaw or roll, potentially adding self-correcting vortices (Bartol et al., 2002;

2003). Alternatively, stability might be similar between these two species despite differences in shell shape if green turtles used compensatory flipper movements to improve stability.

I compared the two species to assess the functional significance of their structural differences to stability. My data showed that regardless of the differences in shell structure, both species were hydrodynamically stable, differing little in most measures. Juvenile loggerheads and green turtles effectively achieved similar stability during straight line swimming while powerstroking (simultaneous flapping of the forelimbs).

Materials and Methods

To test whether morphological differences between sea turtle species might result in differences in hydrodynamic stability, I compared the hydrodynamic performance of green turtle posthatchlings (an unkeeled species) with keeled loggerhead posthatchlings. In addition to comparing components of stability, I also evaluated anatomic and kinematic parameters that might contribute to differences in aquatic stability between species. These included the relative position of the centers of gravity and buoyancy (Marchaj, 1988; Webb, 2002) and the extent of foreflipper motion, as the dorsoventral flapping movements of sea turtle flippers, the primary propulsive structures (Davenport et al., 1984; Wyneken, 1997), could affect the position of a turtle's center of gravity and, thus, its stability.

I. Turtles

Hatchlings were collected as they emerged from natural nests in July and August, 2007. Nests were located in Boca Raton (26. 37°N, 80.11°W) and Juno Beach

(26.87°N, 80.05°W), Florida, USA (n = 20 turtles/species, 1 turtle/nest). Each hatchling was the progeny of a different female to assure sufficient genetic diversity to characterize species-specific stability and avoid pseudoreplication bias. Maternity was inferred from nest deposition interval and nest hatch dates.

Hatchlings were transported in Styrofoam[®] boxes containing a shallow layer of moist sand (to prevent dehydration) to the Florida Atlantic University (FAU) Marine Laboratory in Boca Raton. Turtles were marked for identification with non-toxic nail polish and placed in large tanks with conspecifics. Each tank received a constant flow of filtered seawater, maintained at 24-28°C. The turtles were exposed to a 12:12h light cycle. Once they began eating, they were fed once a day using an in-house manufactured diet containing gelatin, fish, turtle chow, vitamins, and minerals (Stokes et al., 2006). Straight-line carapace length (SCL) and width (SCW), body depth (BD), and mass were measured periodically, including immediately prior to filming.

A subset (n = 8/species) of the turtles was used for collection of stability data; all were as morphologically similar in age (6 ± 1 wk) and size as the filming schedule would allow, clinically healthy, and could be enticed to swim. Turtles (55-80 mm SCL, median, 67.1 mm) were of optimal size to swim at least three body lengths in the test tank. Size distributions were not normal. Upon completion of the studies, turtles were released offshore at a *Sargassum* weed line located in the Gulf Stream.

II. Collection of stability data

Each turtle was marked with small dots of children's fingernail polish to identify the body axes and flipper tips (Figure 3), then placed individually into a rectangular glass aquarium (77.5 cm x 32.4 cm x 31.75 cm) filled to a depth of 15 cm with seawater. A

submerged 100 W heater maintained water temperature between 24 and 28°C. Turtles were allowed to acclimate for three min and were then enticed to swim in a straight line by pulling a piece of food across the tank at a constant rate and depth. Turtles were filmed (200 fps) simultaneously in ventral and lateral views using two digitally synchronized high-speed video cameras (Phantom V4.1, Vision Research, Inc., Wayne, N.J., USA) each time they swam across the tank. The ventral view was captured using a mirror placed at 45° to the tank's clear bottom. A 1 cm square grid filmed in the ventral view for each trial provided a distance calibration for video analyses. A video trial was defined as when a turtle was recorded swimming a distance of no less than three body lengths and completing at least one full limb cycle (see below) in doing so. If, after several attempts at eliciting this swimming behavior a turtle did not perform a trial that met these criteria, it was returned to its holding tank and tested several h later. Between 22 and 38 videos were initially collected for each individual to ensure an adequate number met the criteria for analysis.

Lateral view videos for each trial were reviewed to ensure that turtles performed at least one limb cycle, defined as beginning when the foreflippers were at their maximum downward displacement (during a downstroke) and ending when the foreflippers returned to this same position (an upstroke occurred between the downstrokes). Trials were also evaluated to verify that the flippers did not break the surface of the water.

Any trials that did not conform to these criteria were excluded from analysis.

Acceptable trials were downloaded to a computer as CINE (.cin) files and converted to AVI format for analysis.

III. Stability and Kinematic Measures

To quantify pitch, yaw, heave, and sideslip, the positions of landmarks on the bodies of loggerhead and green turtle posthatchlings were first digitized from ventral and lateral view video files using DLTdataviewer2 software (available at <http://www.unc.edu/~thedrick/software1.html>). Because 100 fps provided sufficient temporal and spatial resolution for performance measurements at the swimming speeds of the test animals, every other video frame was digitized from each ventral and lateral movie (the lateral and ventral frame selections were identical to maintain synchrony). In the ventral view, two points describing the longitudinal body axis were digitized, the most anterior point and the most posterior point of the plastron (Figure 3a). In the lateral view, the anterior- and posterior-most points on the carapace (body axis) were digitized (Figure 3b). The tip of the foreflipper nearest the camera was also digitized (Figure 3b).

Coordinate data were input into a custom Matlab (Ver. R2007a, MathWorks, Inc.; Natick, M.A., USA) routine, and 98 equidistant points were interpolated between the two digitized points on the shell in each view, yielding 100 equidistant points along the midline (Rivera et al., 2006). The center of rotation (COR) was calculated in the Matlab routine as the point along the turtle's midline that traveled the smallest cumulative distance throughout the trial (*sensu* Walker, 2000). The COR represented a single point on each of the turtle's axes with a stable trajectory throughout the sequence. A regression was calculated for the x-y coordinates of the COR, and the regression line represented the ideal travel path of the turtle's COR. A custom Matlab[®] routine (MatSAND, developed by T. Hedrick, Univ. North Carolina) was used to fit a quintic spline function to the x and y coordinates of the digitized points and COR for each

trial. This procedure smoothed the data, clarifying the movement patterns of turtles by reducing variation resulting from minor errors in locating anatomical landmarks on video frames during digitizing (Blob et al. 2008). Through this procedure, all trials were normalized to the same duration, allowing me to identify the timing of kinematic and stability events as a percentage of total limb cycle duration, and to perform comparisons between species across runs with differences in cycle duration. A quintic spline algorithm was chosen to implement these steps because of its generally stable performance in smoothing displacement data over a wide range of video magnifications and speeds (Walker, 1998). The smoothed and normalized coordinate data were then used to calculate kinematic and stability results for each trial, from which average stability profiles and standard errors through the course of swimming cycles could be calculated for each species. Excursions represented the difference in the maximum and minimum values, or total displacement, for each stability parameter.

Pitch. The lateral view was used to evaluate pitch (the angle between the transverse body axis and path of travel). Three parameters, maximum deviation up (upward pitch), maximum deviation down (downward pitch), and excursion, described the extent to which turtles pitched relative to the path of travel (Figure 4a).

Yaw. The ventral view was used to evaluate yaw, or lateral angular deviation from the travel path. Yaw measurement followed the same procedure used to measure pitch, except that yaw angles were orthogonal to the pitch angles. Because of the synchronous and symmetric nature of this motion (each foreflipper moved along a path that mirrored that of the other simultaneously and with equal force), yaw is reported as a

single maximum deviation (to either the left or right; Figure 4b). Minimum deviations were also measured in order to calculate excursion.

Heave. The lateral view was used to evaluate heave (whole body vertical displacement from a swimming path). The maximum positive and negative deviations from the swimming path were calculated for each limb cycle, where deviations were the vertical distances between the position of the turtle's COR (x-y coordinates) and the path of travel. If the COR was positioned above the regression line, the heave value was positive, and if the COR was positioned below the regression line, the value was negative (Figure 4c). Raw heave values as well as values scaled for body length and excursion values (total vertical distance traveled) were compared between the two species.

Sideslip. The ventral view was used to evaluate sideslip, defined as whole body horizontal displacement from a swimming path. To evaluate sideslip, the maximum deviation (to either the left or the right) was calculated for each limb cycle. Minimum deviation was also calculated to evaluate excursion. Deviations were calculated as the lateral distance between the position of the turtle's COR and the path of travel. If the COR was positioned above or below the regression line, the turtle was experiencing horizontal displacement to the left or right (Figure 4d). Raw sideslip values as well as values adjusted for body length and excursion values were compared between the two species.

IV. Limb Positions

The lateral view was used to evaluate flipper position throughout each limb cycle. Two parameters were calculated to describe flipper position: maximum upward

displacement and maximum downward displacement. Maximum upward displacement defined the transition from upstroke to downstroke, and maximum downward displacement defined the transition from downstroke to upstroke and also served as the beginning point for each limb cycle. Turtles swam at approximately the same speed during each trial (mean \pm SD; loggerheads: 5.90 ± 1.42 BL/s; green turtles: 5.66 ± 1.18 BL/s). Data collection was during steady swimming and did not include the start. Trials were divided into individual limb cycles based on flipper position, and all trials were normalized to the same duration using MatSAND. The MatSAND procedure standardized each downstroke-upstroke cycle to have 100 equally spaced increments, interpolating calculations of performance variables to report values for each 1% time increment (Pace et al., 2001). Normalizing strokes to the same duration allowed examination of how the values of the stability parameters changed in relation to the flipper stroke and comparisons of stability parameters in terms of percentile of the limb cycle.

V. Centers of gravity and buoyancy

Centers of gravity (CG) were determined by suspending the turtles in air with a string. Each turtle's flippers were restrained in resting position over the carapace by lightweight rubber bands weighing less than 4% of the turtle's body weight. The turtles were then suspended head-up and head-down by a single line. A lateral view photograph was taken with the turtle parallel to the lens in each position (Figures 5a and 5b). The photographs were superimposed, and the suspension lines were extended in each so the point where the two lines crossed identified the CG (Figure 5c; Wyneken, 1988).

Centers of buoyancy (CB) were determined in a similar manner, except that individuals were submerged in a tank of seawater, and their positive buoyancy put tension on the suspension line that was anchored on the bottom of the tank. Relative positions of centers of gravity and buoyancy in terms of percentiles of SCL and BD were determined to account for the small variations among individuals. These data were compared between the species.

VI. Lever arms

The magnitudes of rotational motions depend on the amount of torque applied in their respective planes. Torque, force acting at a distance from the rotation point, is directly proportional to lever arm length, defined as the perpendicular distance from an axis to the line of action of a force. An individual with a longer input lever arm (in-lever) relative to its output lever arm (out-lever) in a given plane will experience greater torque (rotational force) in that plane than an individual with a relatively shorter in-lever and longer out-lever. In- and out-lever arm lengths were measured as the distance from the CG to the most dorsal point on the carapace directly above the CG and the most posterior point on the carapace, respectively, for each individual tested as a possible explanation for differences in pitch between the species (Figure 6). Lever arm lengths were measured from the lateral view photographs used to determine CG, and the ratio of in-lever to out-lever length was compared between the species.

VII. Flipper length

Flipper blade length was measured from scaled photographs of turtles of each species. Flipper blade length was measured from the wrist to the flipper tip.

Comparisons of differences in flipper blade lengths were used to interpret differences in flipper displacement or stability parameters between the species.

VIII. Statistics

All statistical analyses were performed using SYSTAT 12 (Systat Software, Inc.), and in all cases, the null hypothesis of no difference between the species was rejected when $p \leq 0.05$. Stability data were transformed as needed to meet the assumptions of the statistical test used for comparison. Since moderate violations of assumptions do not generally affect analyses of variance (ANOVAs) (Sokal and Rohlf, 1995), and most stability and flipper position data met normality and homoscedacity requirements, two-level nested ANOVAs were applied to compare data for each variable between species and among individuals within a species. The following measurements of kinematics and stability performance were compared using nested ANOVAs: maximum upward flipper displacement, maximum downward flipper displacement, maximum upward pitch, maximum downward pitch, pitch excursion, maximum yaw, yaw excursion, maximum upward heave, maximum downward heave, heave excursion, maximum upward and downward heave adjusted for body length, maximum sideslip, sideslip excursion, and maximum sideslip adjusted for body length.

The percentiles of the normalized limb cycle when maximum upward and downward flipper displacements and stability components (pitch, yaw, heave, and slideslip) occurred did not meet the normality or homoscedacity requirements of parametric tests, so these values were compared between species using Mann-Whitney tests.

The positions of the CG and CB between loggerhead and green turtles were compared by Mann-Whitney tests using the positions of each variable expressed as a

percentile of SCL and BD. Metacentric height, the vertical distance between an organism's centers of gravity and buoyancy, was calculated for each individual by subtracting the BD percentile of the CG from the BD percentile of the CB. Metacentric heights also were compared between the species using a Mann-Whitney test.

The ratio of in-lever to out-lever arm lengths was compared between the species using a Mann-Whitney test. A null hypothesis of no difference between the species was rejected when $p \leq 0.05$. Flipper blade length was adjusted for body length and compared between the species using a two-sample t-test.

Results

I. Stability parameters

One hundred fifty-eight trials from 8 individual loggerheads (13-28 trials per turtle) and 91 trials from 8 individual green turtles (8-16 trials per turtle) met the criteria for analysis. Morphometric data describing these animals at time of filming are reported in Table 1. Green turtles and loggerheads overlapped in size; however loggerheads tended to be smaller than green turtles at the same age (Table 1). Loggerheads were shorter in terms of SCL and SCW, and thus had smaller carapace areas than green turtles.

The two species were similar in all measures of stability (Table 2). There were no differences between the species in any measure of pitch, yaw, heave, sideslip, or the percentiles of the limb cycle when any of the measured stability or kinematic parameters occurred (Tables 2-3, Appendix 1). Neither species averaged more than 2° of yaw or 2 mm of sideslip throughout their limb cycles (Figures 7a, 7c, and 7d).

Heave was also minimal, no more than ± 2 mm, which was less than 10% of the turtles' maximum BD (Figures 7e and 7f). In general, heave trended upwards for approximately the first and last quarters of the limb cycle (while the flipper tip was displaced below the horizontal), but shifted downwards during the middle two quarters of the limb cycle (while the flipper tip was displaced above the horizontal; Figure 7e). Thus, the transition from heaving downward to heaving upward occurred out of phase with the transition from upstroke to downstroke in both species (54th percentile of the limb cycle in green turtles, 42nd percentile of the limb cycle in loggerheads: Figure 7g), reflecting a lag between when the turtle changed the direction its flippers were moving and when its whole body changed trajectory in the vertical plane (Figures 7e-g). This lag was greater for the transition from downstroke to upstroke than for the transition from upstroke to downstroke.

In addition to similarities in stability parameters, loggerheads and green turtles showed similar upward and downward flipper displacement (Table 2). Although the difference in timing was not significant, loggerheads experienced maximum upward flipper displacement earlier in their limb cycle than green turtles, indicating that the upstroke portion of their limb cycle is shorter relative to that of greens (Table 2, Figure 7g). Loggerheads held their foreflippers at or near maximum upward displacement for almost 20% of their limb cycle (from 40-60 percentile of the limb cycle), while green turtles did not maintain this position for nearly as long (Figure 7g). In green turtles, the upstroke lasted slightly longer (about 12% of the limb cycle) than the downstroke (Figure 7g).

II. Centers of gravity and buoyancy

The CG and CB positions were described as percentiles of SCL (increasing from anterior to posterior) and dorsoventrally (increasing from plastron toward carapace) along BD for each loggerheads and green turtles whose stability was measured (Figure 8). CG position did not differ significantly between the two species when compared as either a percentile of SCL or BD (Table 4). The anterior-posterior position of the CB differed between the two species (Mann-Whitney test, $U_{0.05(2), 8, 8} = 9.00$, $X^2 = 5.835$, $p = 0.016$; Table 4), but not in dorsoventral position. The CB was located anterior to the CG in loggerheads and posterior to the CG in green turtles (Table 4).

The positions of the CG and CB varied in their dorsoventral position more than in terms of SCL (Table 4, Figure 8). Metacentric height (Table 4) was a negative value when the CG was dorsal to the CB. Four turtles (three green turtles and one loggerhead) had negative metacentric heights while the remaining animals all had positive metacentric heights. There was no significant difference in the metacentric heights of the two species (Table 4).

III. Lever arms and flipper length

Loggerheads and green turtles differed in the ratios of their in-levers to out-levers along the transverse (midsagittal) plane (Mann-Whitney test, $U_{0.05(2), 8, 8} = 55.00$, $X^2 = 5.835$, $p = 0.016$). Loggerheads had longer in-levers relative to their out-levers than green turtles. Green turtles had longer flipper blades adjusted for body length (two-sample t-test, $t_{14} = -2.374$, $p = 0.016$) than loggerheads.

Discussion

I. Factors contributing to interspecific similarities and differences in the hydrodynamic stability of sea turtles

Despite morphological differences in shape between loggerheads and green turtles as well as small size differences in the turtles tested (the green turtles were larger), they were similarly stable during swimming. Yaw and sideslip were minimal. These results are consistent with the bilaterally synchronous forelimb flapping employed by sea turtles (Davenport et al., 1984; Wyneken, 1997). Such motions should limit torquing of the body to the left or right. Reduced yaw and sideslip may be a general feature of rigid-bodied aquatic animals that produce bilaterally synchronous thrust. For example, boxfish, which also have rigid bodies, exhibit little yaw or sideslip (Gordon et al., 2000; Hove et al., 2001; Bartol et al., 2003). The fact that there were no differences in maxima, minima, or excursion values for any of the stability parameters implies that there is similar total angular, lateral, and vertical displacement between loggerheads and green turtles.

Both species also showed similar patterns of heave during swimming. The extent of heave excursion was greater than sideslip excursion, so total vertical displacement was greater than lateral displacement during each limb cycle. The differences in flipper morphology may have been expected to produce differences in heave between the species, but did not. The higher aspect ratio flippers of green turtles may produce the

same amount of vertical thrust per stroke as loggerhead flippers, resulting in similar heave. Comparisons of thrust production would require force measurements (Becking et al., 2004) or flow visualization that were beyond the scope of the current study.

In both species, there was a lag between the transition from upstroke to downstroke and the body heaving downward to heaving upward. The lag between when the turtle changed the direction its flippers were moving and when its whole body shifted position in the vertical plane was greater for the downstroke-to-upstroke transition than for the upstroke-to-downstroke transition. This temporal difference is likely because the downstroke is when sea turtles generate maximum thrust (Becking et al., 2004), producing greater vertical inertia for the body to overcome than during the upstroke. A second, lower peak in thrust (Becking et al., 2004) may contribute to the lag between downward to upward heave, causing the turtle to continue moving downward after the downstroke begins.

Both species pitched upward during the downstroke and downward during the upstroke. These patterns are consistent with the description of green turtle swimming by Davenport et al. (1984), though animals in that study pitched more than those in the present study; potentially the disparity is due to differences in the sizes of animals or test arenas. In addition, both loggerheads and greens experienced their maximum downward pitch when they transitioned from upstroke to downstroke (Table 2, Figures 7b and 7g), the same timing of this event identified for juvenile loggerheads by Becking et al. (2004). Although overall pitch profiles did not differ significantly between the species, the details differed so that loggerheads experienced greater downward pitch for a larger percentage of their limb cycle than green turtles.

Given the differences in shell morphology between the species, it may be surprising that differences in pitch were not detected. Bartol et al. (2002, 2003) found that the ventral keels of boxfishes, as well as the dorsal keels found in some species, generate self-correcting forces that reduce pitch in these animals compared to many other fishes (Webb, 2004). The presence of longitudinal keels on both the carapace and plastron of loggerhead shells might have been expected to reduce overall pitch in this species relative to that in green turtles, but they did not. Potential explanations for the difference in the effect of keels on pitch in loggerheads compared to boxfish include that the ventral keels of boxfish project laterally more than those of loggerheads. Similarly, the boxfish keels are finer and more isolated from other surface structures than the vertebral and costal scute keels of loggerheads.

Measurements of the lever arms contributing to pitch indicated that in-levers were longer relative to out-levers in loggerheads than in green turtles. This functional difference is a consequence of the morphological difference between the species. While one might expect the longer loggerhead in-lever to generate greater pitch than in green turtles (Figure 6), loggerheads simply show a different range of pitch angles than green turtles, rather than a larger magnitude. This result suggests the possibility that any increase in pitch related to the lever arm length in loggerheads might be countered by carapace width or area, the smaller effects of shell keels, or subtle compensatory limb movements.

The difference in the relative positions of CB and CG between the species also does not result in differences in pitch. Thus, the difference in the relative positions of CB and CG between the species may not be great enough to affect pitch.

No differences were observed between the species in maximum upward or downward flipper displacement (Table 2). This result is unexpected based on the morphological differences between the species, as green turtles have longer flipper blades in proportion to body length than loggerheads and so should have greater displacement in both vertical directions. The similarities in maximum upward and downward flipper displacement (despite differences in flipper length) may be a function of species-specific swimming kinematics, including patterns of angular limb motion. While differences in flipper kinematics may be found between these species, their functional implications for stability are not clear from this study. Previous studies of swimming kinematics (loggerheads: Becking et al., 2004; green turtles: Davenport et al., 1984) found that loggerheads held their flippers at or near maximum upward displacement for 15% of the limb cycle, while green turtles moved their flipper past this position (Figure 7g) quickly, suggesting that loggerheads may rely on the forward thrust generated during the upstroke to coast as part of their routine swimming. Observations of video collected for this study suggest that loggerheads rotate their flippers while maintaining them at or near maximum upward displacement while green turtles do not. This rotation of the flippers in loggerheads may assist them as they transition to the downstroke. Determination of how kinematic differences between the species reflect the production of stabilizing forces requires additional experimental approaches, such as modeling and flow visualization.

II. Sea turtle hydrodynamic stability: comparisons to other taxa and ecological implications

A broad conclusion from the analyses of this study is that despite their morphological differences, loggerhead and green posthatchlings are remarkably stable swimmers. For example, both species yawed around just 2° throughout their limb cycle, a value comparable to that of boxfish, which are particularly stable swimmers (Gordon et al., 2000). The Hawaiian spotted boxfish, *Ostracion meleagris camurum*, for instance, showed a $1.5\text{-}7.0^\circ$ range of yaw while swimming at various speeds (Hove et al., 2001). Pitch was also lower in the sea turtle posthatchlings tested than in a range of fish species, including flatter, presumably pitch-resistant taxa such as sturgeons and some bottom-dwelling sharks, in which pitch can measure $8^\circ\text{-}11^\circ$ when swimming (Wilga & Lauder, 1999, 2000, 2001; Webb, 2004).

The bilateral production of thrust by synchronized forelimb flapping likely contributes to the stability of sea turtles, as this should limit lateral torquing of the body. Another anatomical feature that may contribute to hydrodynamic stability in sea turtles is the similar positions of their centers of gravity and buoyancy. Although the CB is found slightly more anteriorly in loggerheads, the CB and CG of both species are, on average, in very similar locations (Table 4). The anterior positioning of the CG found in both loggerheads and green turtles might enhance stability for both species (Fish, 2002).

Performance during steady swimming is behaviorally and ecologically important for aquatic animals. Fish (2002) found that features that affect stability of cetaceans are related to their prey type and habitats. He suggested that the stable design of fast swimming cetaceans may limit these animals to moving and foraging in pelagic habitats since rivers, lakes, and coastal waters are more structurally complex, requiring

maneuverability rather than stability (Fish, 2002). Stability and the mechanics of locomotion are also linked. Webb (2002) categorized several control problems related to locomotion. These include control of body orientation (posture), depth in the water column, and trajectory. Minimizing energy costs is important for sea turtles because of their migratory habits. The stabilization of posture and swimming trajectories provides a stable base for sensory systems and minimizes energy costs by orienting the body to minimize drag (Weihs, 1993; Webb, 2002).

Stabilizing the “platform” housing sensory systems is important for sea turtles. Marine turtles have visual areas or visual streaks which function in detecting predators and prey along open horizons. Both species possess visual streaks (areas of densely packed ganglion cells running along the antero-posterior retinal axis), which they attempt to keep horizontal (Oliver et al., 2000) using compensatory eye reflexes and movements of the head (Oliver et al., 2000). Body stability may also aid the turtles in reducing how much the eye must compensate. Both loggerheads (Carr, 1986; Richardson & McGilivray, 1991; Witherington, 2002) and green turtles (Carr, 1987; Smith, 2007) are visual hunters (Dalton, 1979) that associate with floating *Sargassum* mats. The mats provide both feeding opportunities and protection; they appear as linear structures when viewed from near the water’s surface.

Based on the demands of the similar early natural history of loggerheads and green turtles and the close evolutionary relationship (both taxa are within the Cheloniidae), it may not be surprising that these species exhibit similarly high levels of stability. It is possible that some of the morphological differences between these species arose in relation to non-hydrodynamic functions, and that any hydrodynamic implications of

these features are incidental (Gould & Lewontin, 1979). For example, the keels of loggerheads may have initially evolved as structures associated with protection, rather than stabilization. It is also possible that loggerhead and green turtles may employ different behavioral mechanisms such as subtle compensatory motions of the head and flippers to achieve comparable levels of high stability. Thus, despite morphological differences, both loggerhead and green turtles show a capacity to meet even very high demands for stability that may be required by their habitat and behavioral habits.

Finally, understanding stability in sea turtles has practical value. To understand habitat use and movement patterns of sea turtles, it is common for researchers to attach tracking devices such as satellite or GPS transmitters to the shell. The decisions for device placement are usually based on maximizing antenna exposure and largely ignore the consequences to swimming efficiency. Guidelines limit transmitter size to no more than 15% of bodyweight in air. How this guideline relates to turtle stability will vary with attachment location and shape (Watson & Granger, 1998). The data from this study provide baselines for comparing the consequences of transmitter placement and evaluating costs or benefits to stability and minimizing deleterious effects of transmitter use (Godley et al., 2008).

Table 1. Measurements taken at time of filming of turtles used in stability study (n = 8/species).
C. caretta = loggerhead; *C. mydas* = green; SCL = straight carapace length; SCW = straight carapace width;
 BD = body depth

| Species | Min SCL (mm) | Max SCL (mm) | Median SCL (mm) | Min SCW (mm) | Max SCW (mm) | Median SCW (mm) | Min BD (mm) | Max BD (mm) | Median BD (mm) | Min Mass (g) | Max Mass (g) | Median Mass (g) |
|-------------------|--------------------|--------------------|------------------------|--------------------|--------------------|-----------------------|-------------------|-------------------|----------------------|--------------------|--------------------|-----------------------|
| <i>C. caretta</i> | 55.50 | 68.30 | 57.20 | 46.20 | 56.75 | 48.03 | 23.05 | 29.60 | 24.15 | 31.65 | 53.54 | 34.56 |
| <i>C. mydas</i> | 65.80 | 80.00 | 73.70 | 53.70 | 64.50 | 59.43 | 22.60 | 28.90 | 27.00 | 42.19 | 75.89 | 59.98 |

Table 2. Kinematic and stability variables evaluated for *C. caretta* and *C. mydas*. Values are means \pm standard errors; *C. caretta* (8 turtles, n=159 trials) and *C. mydas* (8 turtles, n=91 trials).

| Kinematic or stability parameter | <i>C. caretta</i> | <i>C. mydas</i> | p-value |
|---|--------------------|--------------------|---------|
| Max. upward flipper displacement (cm) | 3.10 \pm 0.07 | 3.44 \pm 0.10 | 0.321 |
| Max. downward flipper displacement (cm) | -2.55 \pm 0.05 | -3.06 \pm 0.10 | 0.094 |
| Max. upward pitch (degrees) | 4.10 \pm 0.37 | 5.80 \pm 0.59 | 0.423 |
| Max. downward pitch (degrees) | -3.89 \pm 0.41 | -2.15 \pm 0.57 | 0.332 |
| Pitch excursion (degrees) | 7.99 \pm 0.31 | 7.95 \pm 0.39 | 0.756 |
| Max. yaw (degrees) | 10.18 \pm 0.38 | 7.53 \pm 0.38 | 0.065 |
| Yaw excursion (degrees) | 7.72 \pm 0.35 | 6.95 \pm 0.38 | 0.360 |
| Max. upward heave (mm) | 2.41 \pm 0.16 | 2.66 \pm 0.19 | 0.430 |
| Max. downward heave (mm) | -2.39 \pm 0.15 | -2.77 \pm 0.17 | 0.150 |
| Heave excursion (mm) | 4.81 \pm 0.19 | 5.43 \pm 0.24 | 0.144 |
| Max. upward heave/BL | 0.041 \pm 0.003 | 0.036 \pm 0.003 | 0.527 |
| Max. downward heave/BL | -0.041 \pm 0.003 | -0.038 \pm 0.002 | 0.994 |
| Heave/BL excursion | 0.082 \pm 0.003 | 0.074 \pm 0.003 | 0.728 |
| Max. sideslip (mm) | 3.23 \pm 0.14 | 3.03 \pm 0.14 | 0.763 |
| Sideslip excursion (mm) | 4.16 \pm 0.20 | 4.27 \pm 0.22 | 0.905 |
| Max. sideslip/BL | 0.055 \pm 0.002 | 0.041 \pm 0.002 | 0.075 |
| Sideslip/BL excursion | 0.071 \pm 0.003 | 0.058 \pm 0.003 | 0.113 |

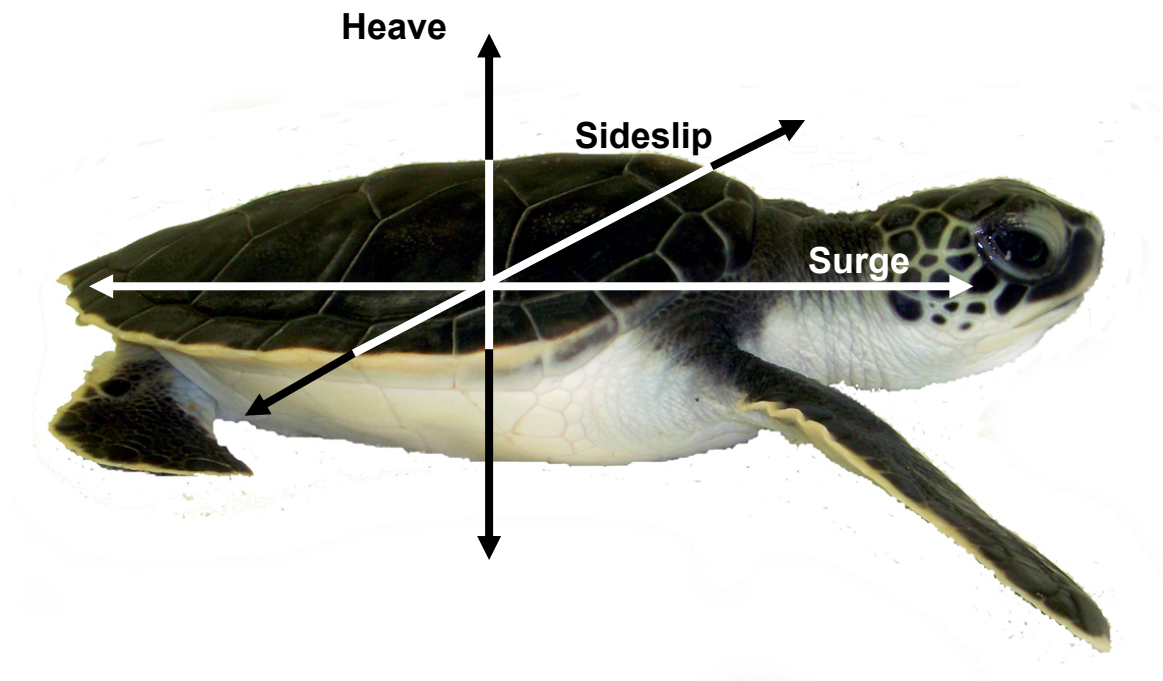
Table 3. Timing of kinematic and stability parameters. The average percentile of the limb cycle when each parameter occurred in *C. caretta* and *C. mydas* was compared using a Mann-Whitney test, Df = 1 for all comparisons. Comparisons were made using averages of all trials for each individual.

| Kinematic or stability parameter | U _{0.05(2), 8, 8} | p-value |
|------------------------------------|----------------------------|---------|
| Max. upward flipper displacement | 17.00 | 0.115 |
| Max. downward flipper displacement | 28.00 | 0.674 |
| Max. upward pitch | 43.00 | 0.248 |
| Max. downward pitch | 42.00 | 0.294 |
| Max. yaw | 25.00 | 0.462 |
| Max. upward heave | 27.00 | 0.600 |
| Max. downward heave | 39.00 | 0.462 |
| Max. sideslip | 42.00 | 0.294 |

Table 4. Centers of gravity and buoyancy relationships for *C. caretta* and *C. mydas*. Values are medians with ranges in parentheses. Df = 1 for all comparisons.
*Significant difference between species based on Mann-Whitney tests. Sample sizes of *C. caretta* and *C. mydas* were 8 individuals of each species.

| Center of gravity or buoyancy parameter | <i>C. caretta</i> | <i>C. mydas</i> | U _{0.05(2), 8, 8} | p-value |
|---|-------------------------|------------------------|----------------------------|---------|
| Position of center of gravity (percentile of SCL) | 33.86 (31.68-36.48) | 33.86 (28.96-37.52) | 34.00 | 0.834 |
| Position of center of gravity (percentile of body depth) | 46.34 (37.08-59.31) | 42.55 (38.66-61.34) | 32.00 | 1.000 |
| Position of center of buoyancy (percentile of SCL) | 30.64 (23.01-35.35) | 34.84 (31.70-41.42) | 9.00 | 0.016* |
| Position of center of buoyancy (percentile of body depth) | 59.95 (34.69-76.82) | 61.10 (34.15-77.45) | 29.00 | 0.753 |
| Metacentric height (difference in percentiles) | 10.33 (-21.70-36.22) | 15.57 (-8.76-36.10) | 32.00 | 1.000 |

a.



b.

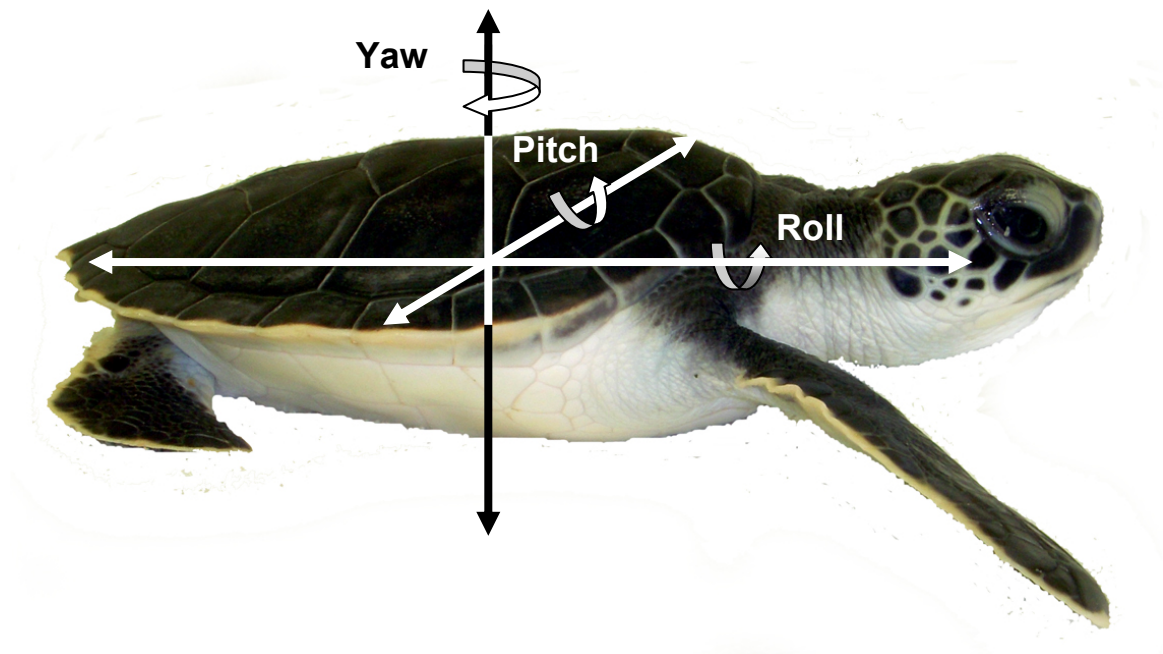


Figure 1. Images of green turtle posthatchling illustrating potential motions resulting from destabilizing forces. **(a)** Translational movements. **(b)** Rotational movements.

a.

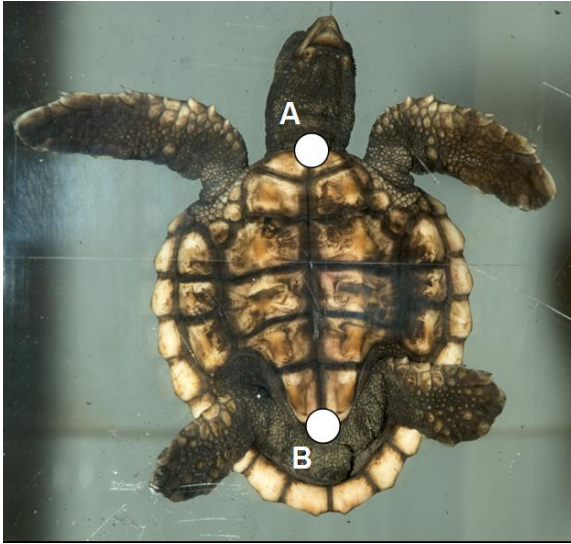


b.



Figure 2. A comparison of posthatchling loggerhead (*Caretta caretta*) (left) and green turtle (*Chelonia mydas*) (right) morphology showing features potentially related to stability (see text). **(a)** Loggerheads have a somewhat heart-shaped carapace on dorsal view, whereas green turtles appear more elliptical. **(b)** Loggerheads possess longitudinal keels while green turtles lack keels at all life stages and have a dorsoventrally flattened carapace. Green turtles have high aspect ratio flippers while those of loggerheads are lower in aspect ratio.

a.



b.

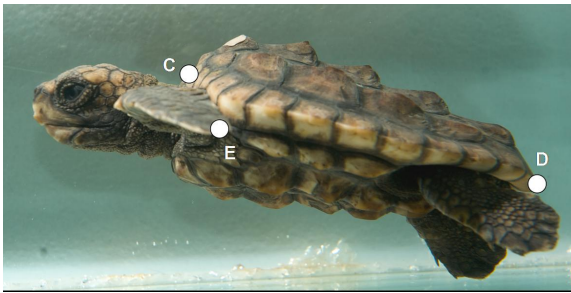
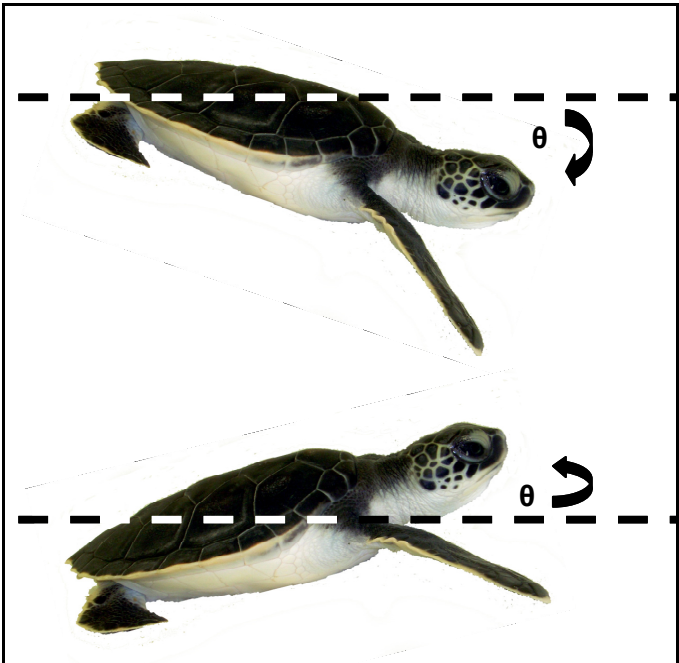
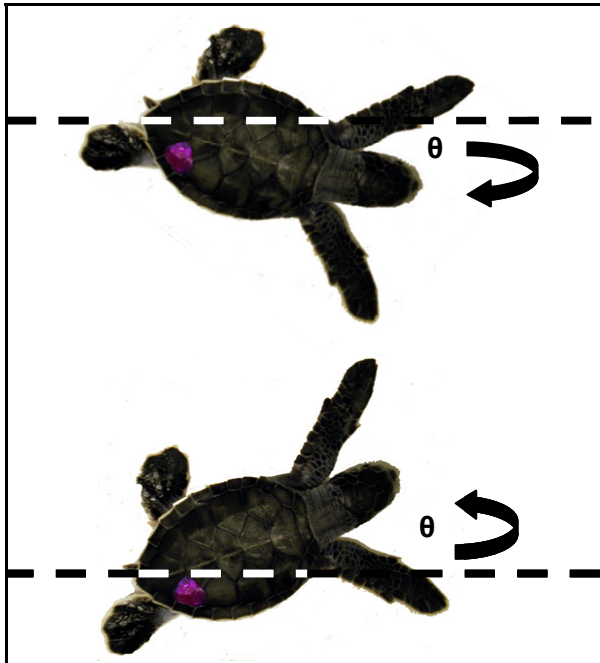


Figure 3. Images of loggerhead posthatchling illustrating landmarks digitized for analysis of swimming stability and kinematics. **(a)** Ventral view. Points A (anterior plastron) and B (posterior plastron) were digitized. **(b)** Lateral view. Points C (anterior carapace), D (posterior carapace), and E (foreflipper tip) were digitized.

a.



b.



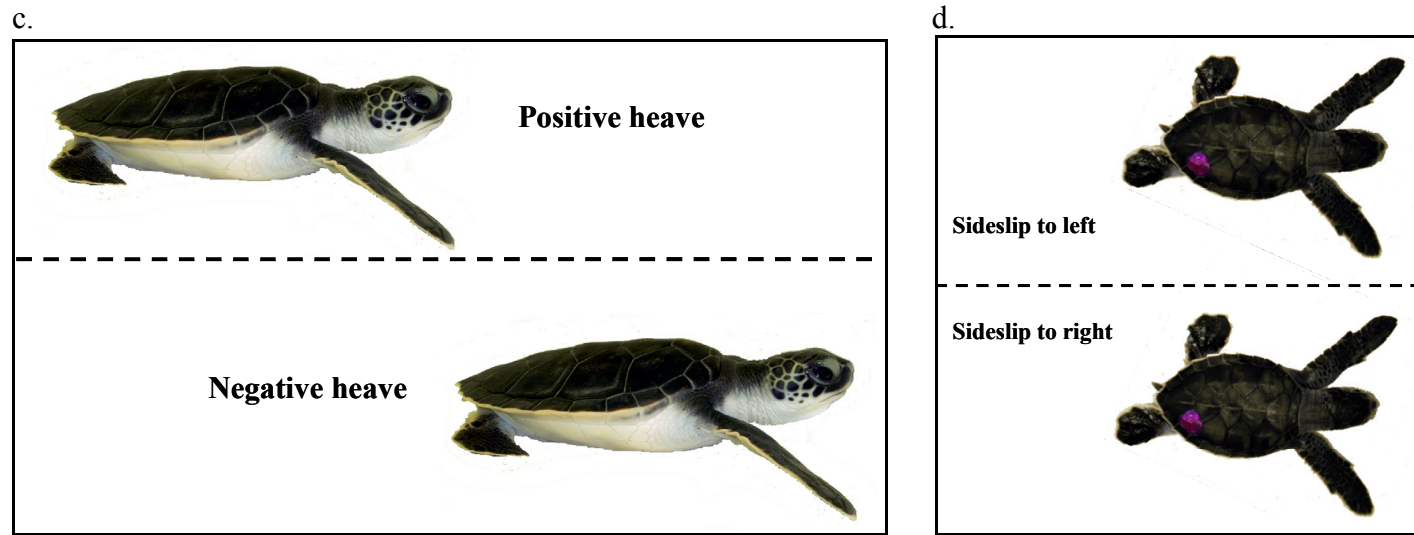


Figure 4. Illustration of stability variables and designations as used in this study. The dashed line in each panel represents the turtle's travel path. **(a)** Pitch angle was measured relative to the travel path; θ represents pitch angle in degrees. **(b)** Yaw angle (θ) represents the lateral deviation of the body axis from the path of travel. Yaw to the right is shown by the upper turtle while yaw to the left is shown by the lower turtle. **(c)** Heave is whole body vertical displacement (measured at the COR) from the swimming path. Displacement of the body axis at the COR above the travel path is positive while displacement of the COR below the path is negative. **(d)** Sideslip is horizontal displacement of the whole body in which the body axis is displaced to the right or left of the travel path.

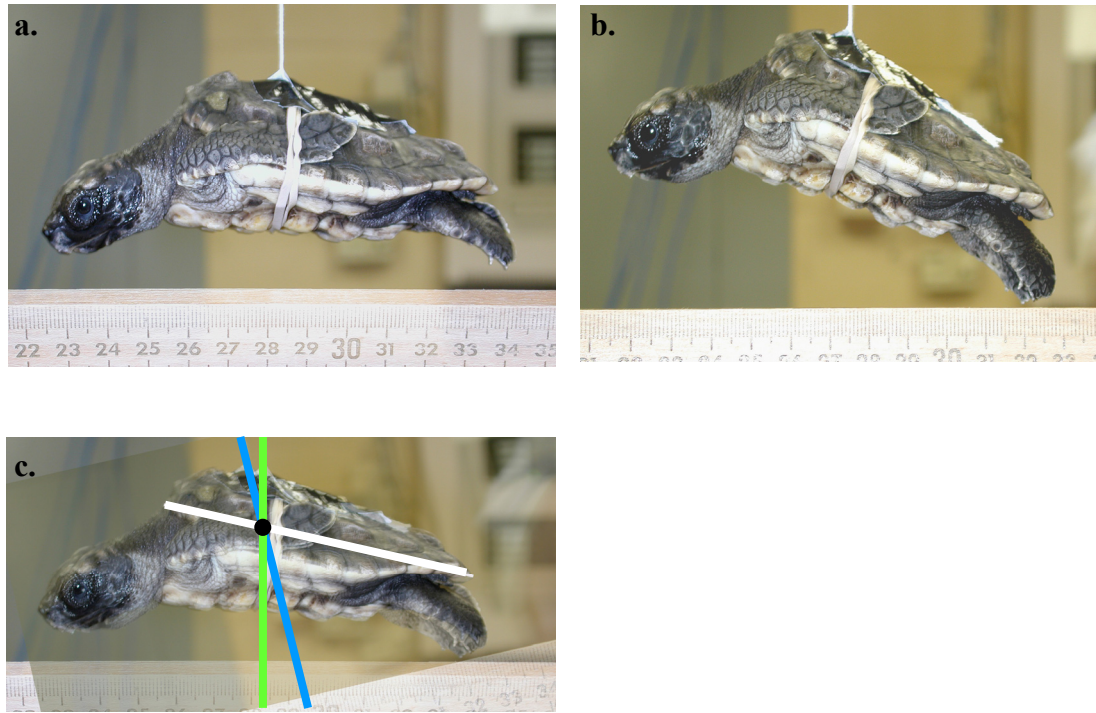
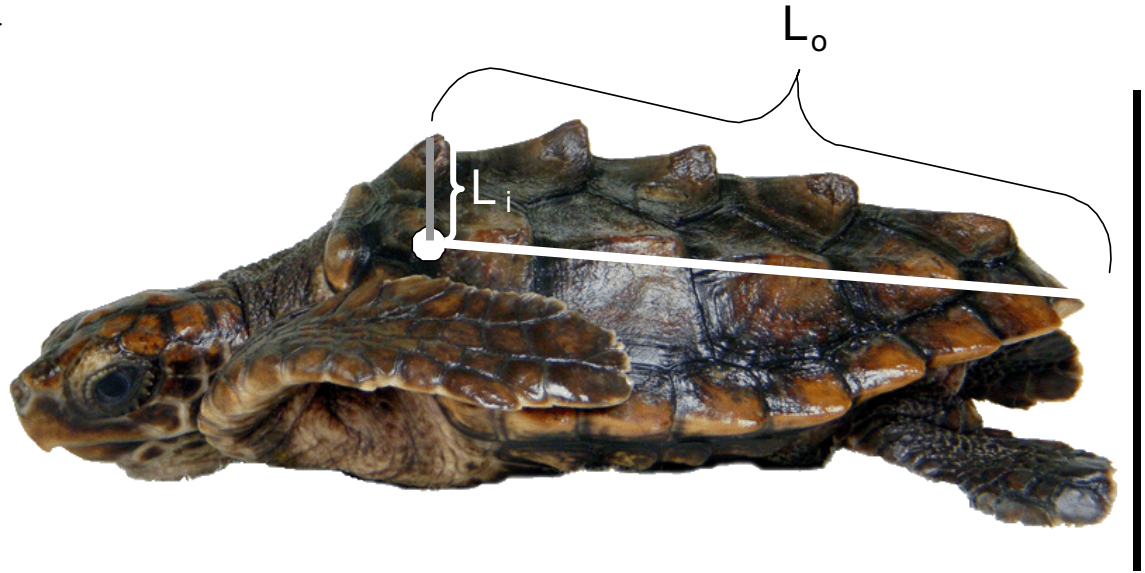


Figure 5. Method used to determine centers of gravity in turtles. **(a, b)** Turtle suspended at two different angles and photographed. **(c)** Photographs superimposed with suspension lines (blue and green) extended. White line from anterior to posterior carapace indicates the line along which images were superimposed. Point where suspension lines cross (indicated by the black dot) represents the center of gravity.

a.



b.

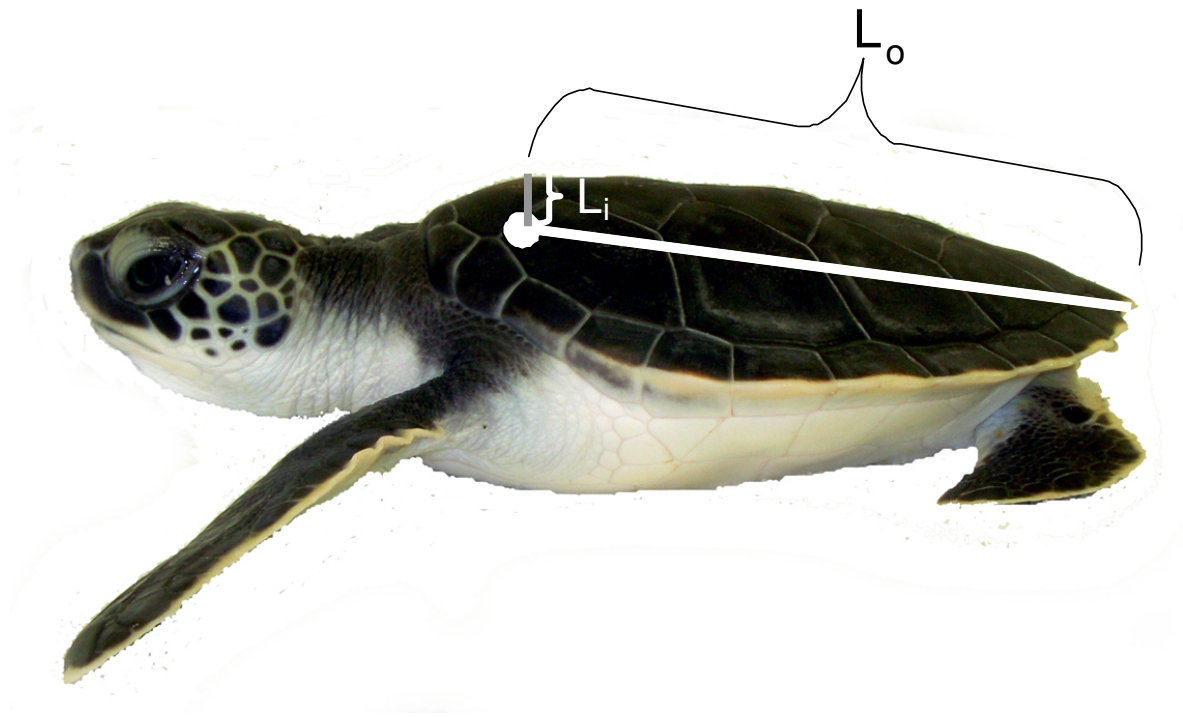
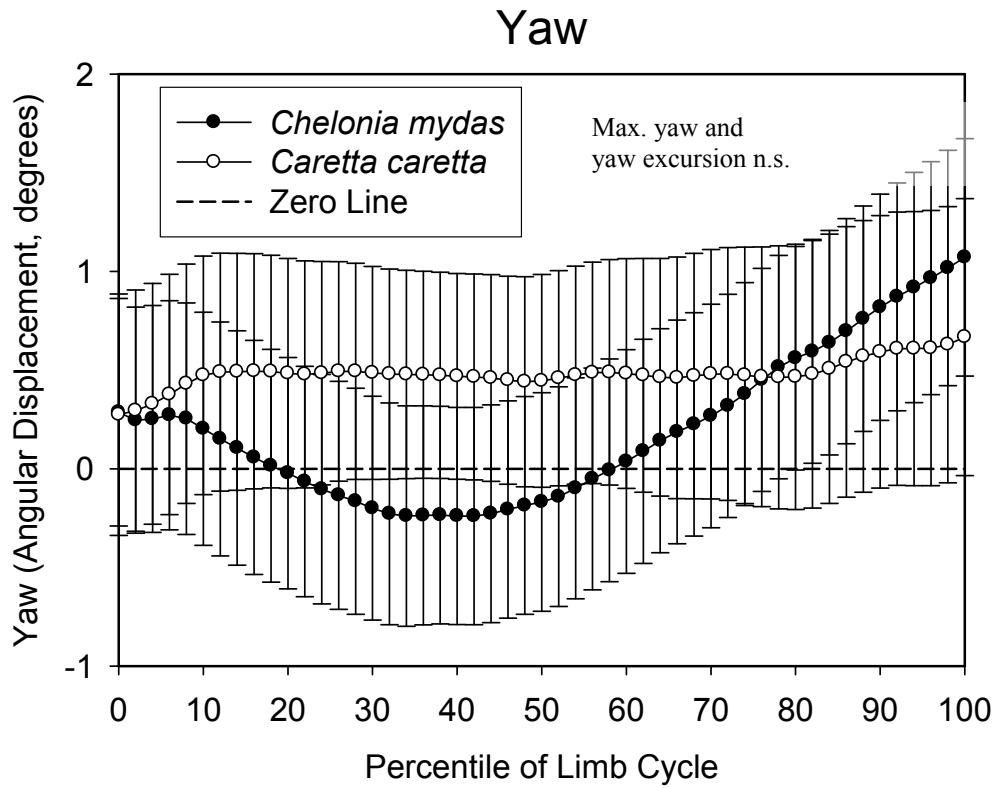
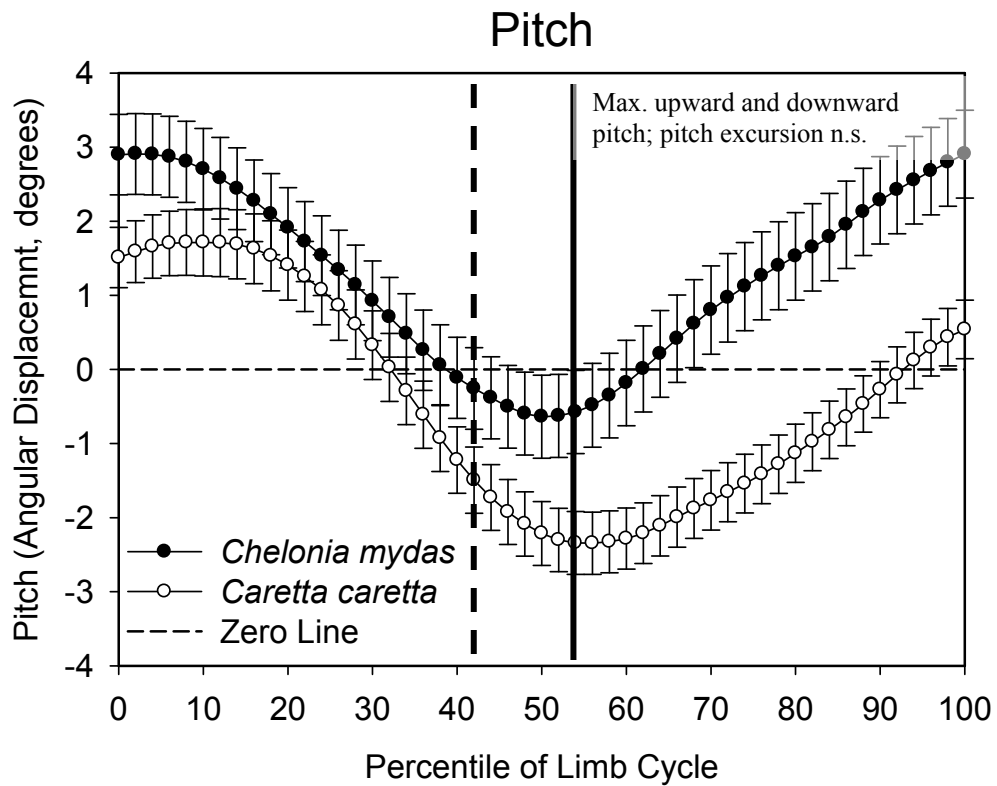


Figure 6. Illustrations of lever-arms associated with pitching of the shell in swimming loggerheads **(a)** and green turtles **(b)**. L_i = in-lever; L_o = out-lever. Pitch is defined as rotation about the transverse axis, which runs through the turtle's center of rotation (indicated by the white circle).

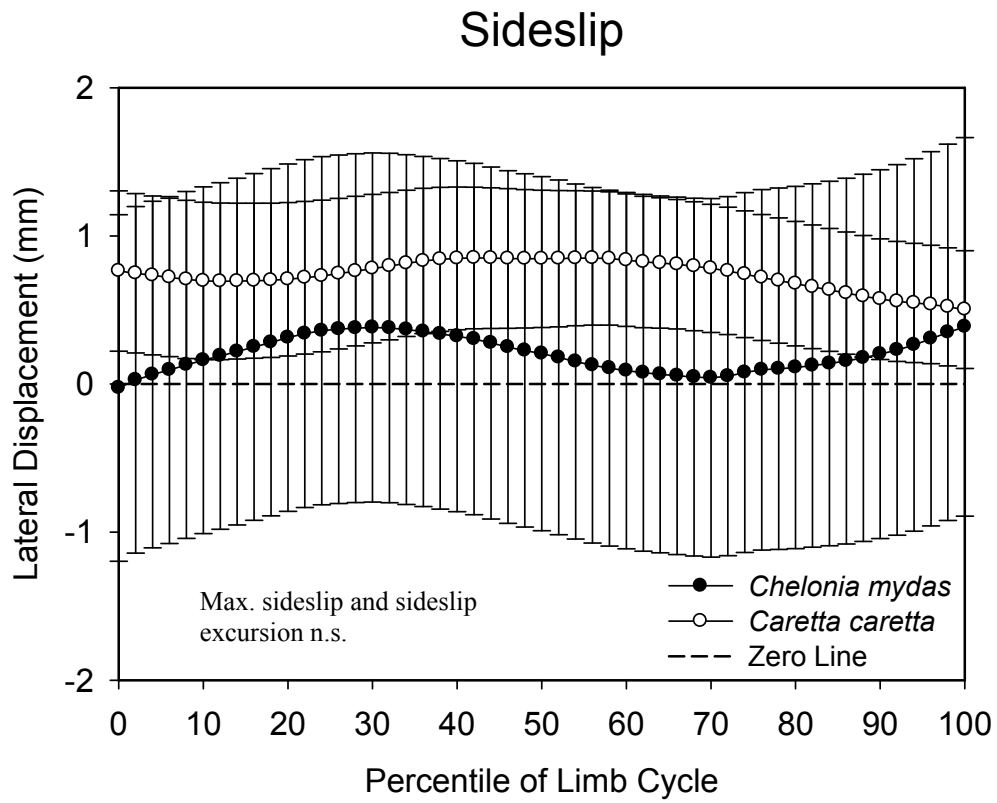
a.



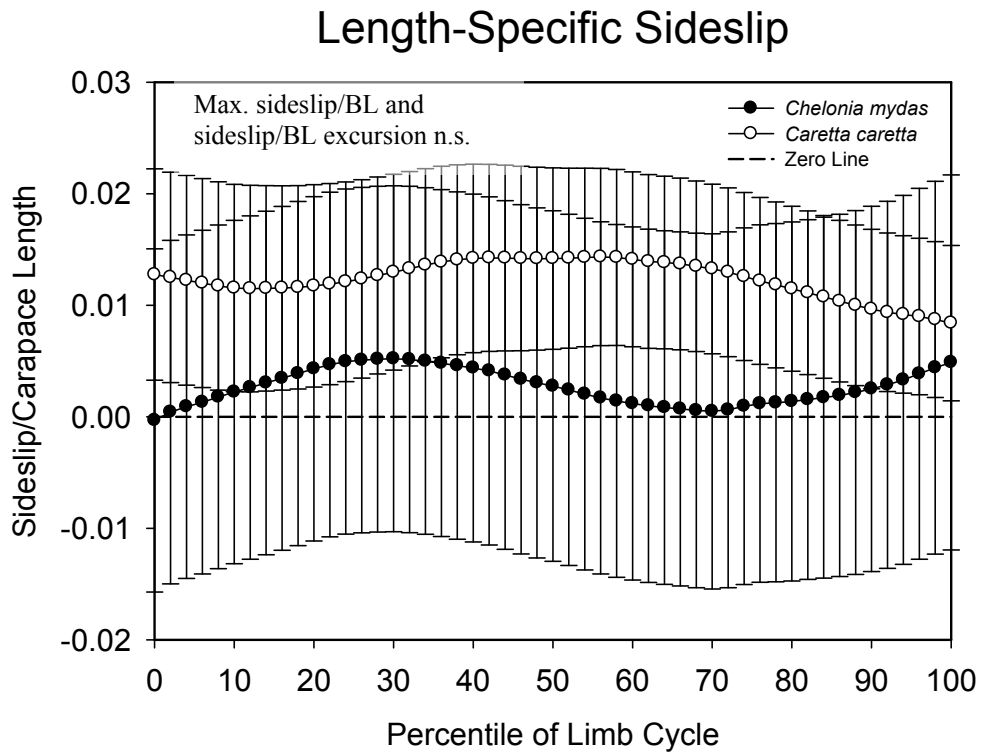
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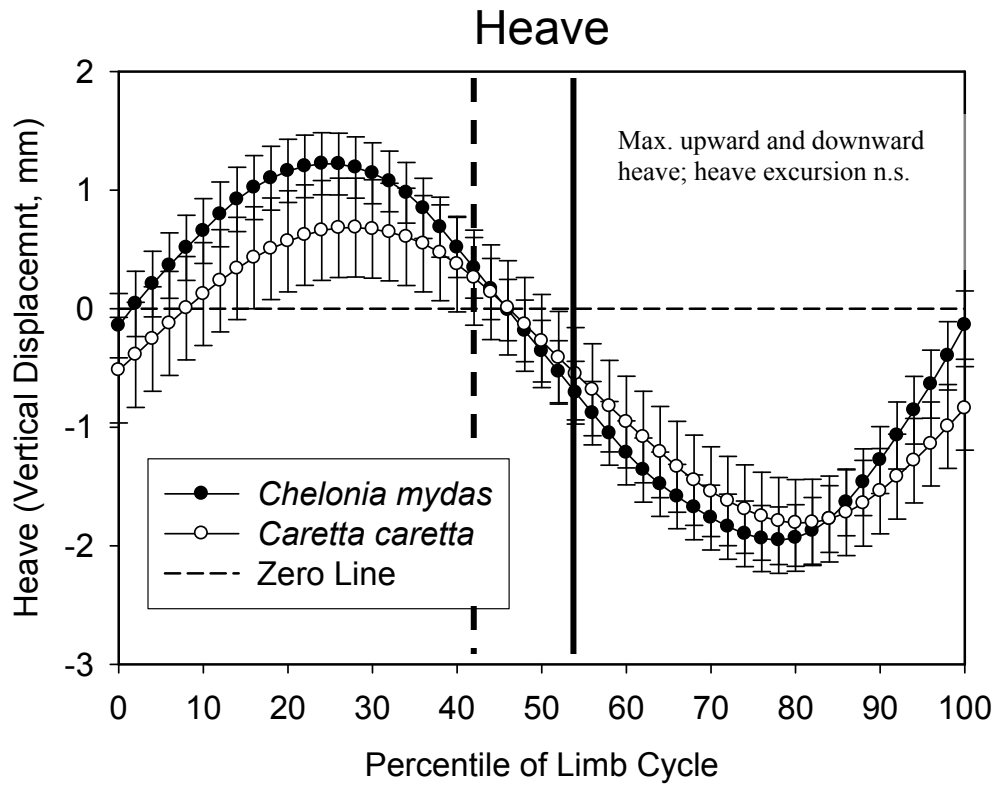
c.



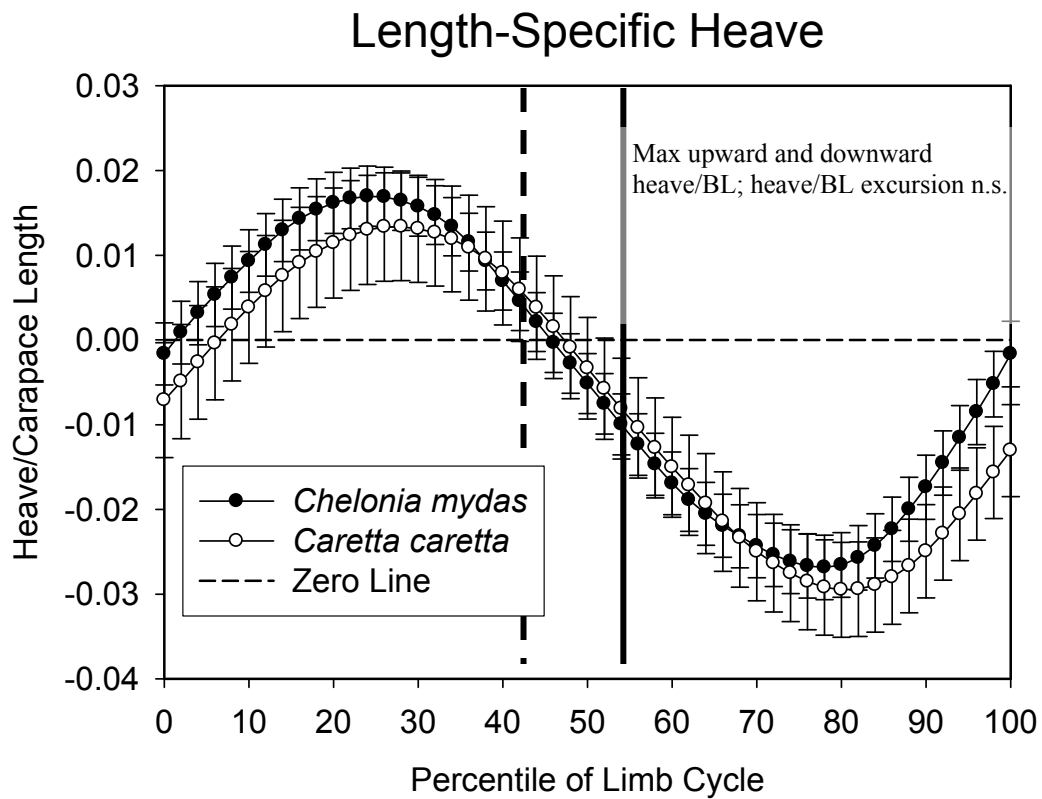
d.



e.



f.



g.

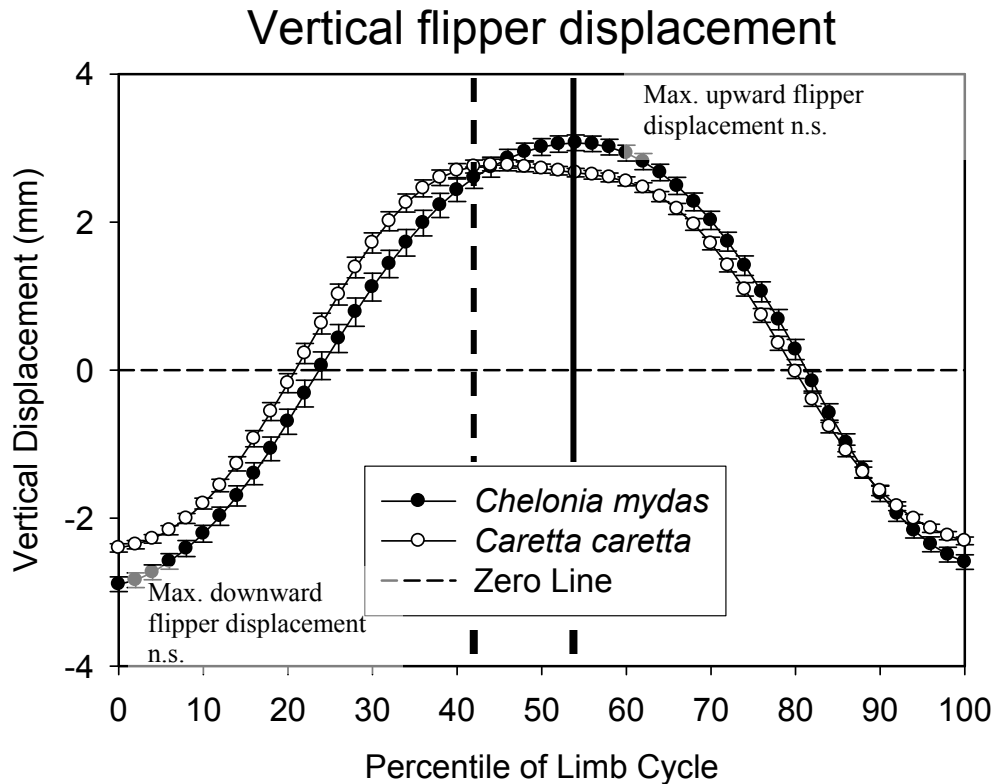


Figure 7. Graphs of changes in stability variables through the course of limb cycles in swimming sea turtle posthatchlings. Points are the means of the parameter represented at each percentile of the limb cycle; error bars are the SE of the means. Data from the two species were compared using a nested ANOVA with 233 df (Appendix 2). In all graphs, the dashed vertical line represents the transition from upstroke to downstroke in loggerheads, and solid vertical line represents this transition in green turtles. **(a)** Yaw. Neither species averaged more than 2° of yaw throughout its limb cycle. **(b)** Pitch. Loggerheads experienced greater downward pitch for a greater proportion of the limb cycle than green turtles. **(c)** Sideslip. Neither species averaged more than 2 mm of sideslip throughout its limb cycle. **(d)** Sideslip normalized by carapace length. Neither species averaged more than 2% carapace length of sideslip. **(e)** Heave. Neither species heaved more than ± 2 mm. Turtles heaved upward during the downstroke and downward during the upstroke portion of the limb cycle. **(f)** Heave normalized by carapace length. Neither species heaved more than 2% carapace length. **(g)** Vertical displacement of the foreflipper.

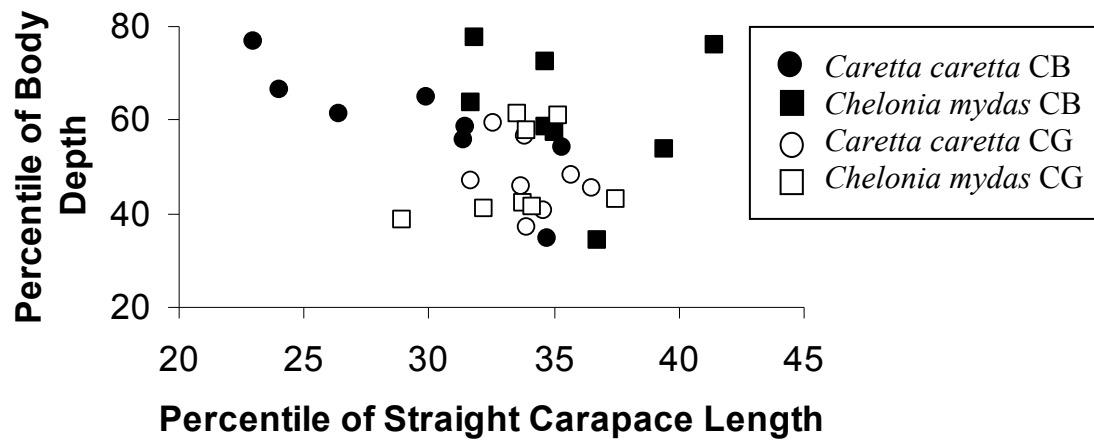
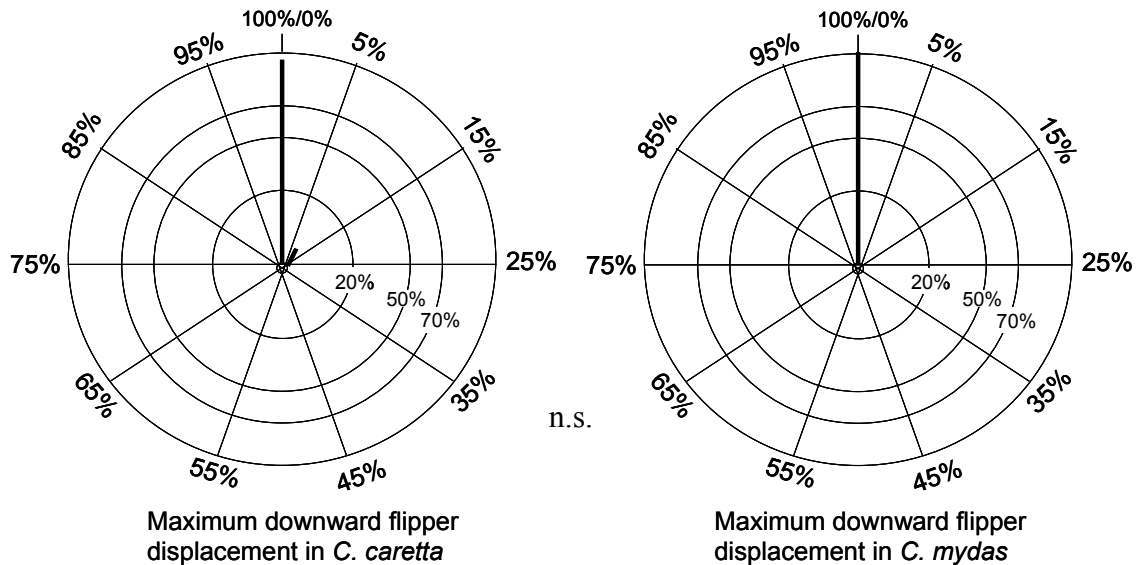


Figure 8. Positions of centers of gravity and buoyancy in loggerhead and green posthatchlings in terms of percentiles of body depth and straight carapace length. CB: Center of Buoyancy; CG: Center of Gravity. The CB tended to more anterior in loggerheads than in green turtles. The CG position was similar along the body's length in both species. Dorsoventral position of the CB relative to the CG varied.

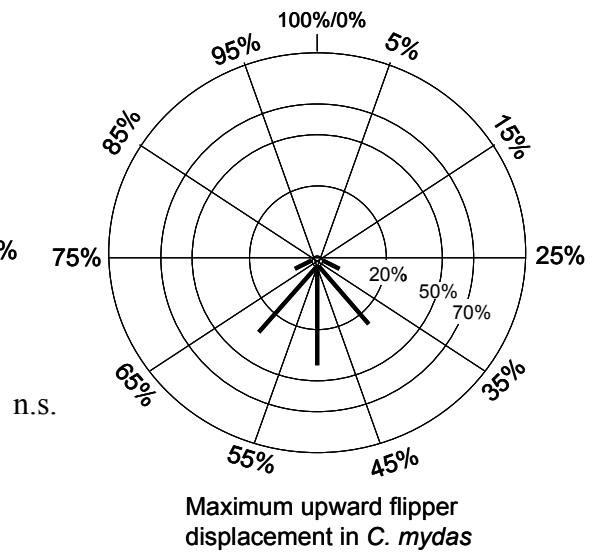
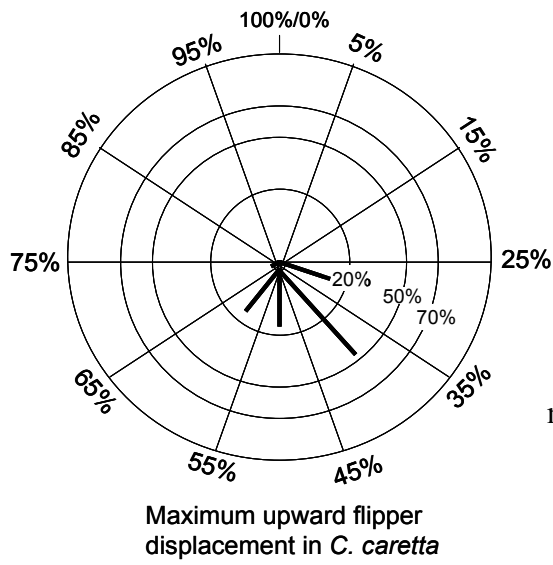
Appendices

Appendix 1. Distributions of the part of the limb cycle when maximum and minimum kinematic or stability parameters occurred in loggerheads (*C. caretta*) left columns, and green turtles (*C. mydas*), right columns. Limb cycles, defined as the movement of the flipper tip from a starting position downward then up and back to the same starting position, were divided into the 100 parts of equal duration shown as percentiles along the perimeters of each graph. The % of maximum destabilizing events that occurred during each percentile of the limb stroke are shown by the thick lines radiating from the center. The concentric circles provide reference to track the distributions of maximum destabilizing events as percentages. Comparisons are made between when in the stroke (A.) the flipper shows the maximum downward displacement, (B.) the flipper shows maximum upward displacement, (C.) maximum upward pitch occurs, (D.) maximum downward pitch occurs, (E.) maximum yaw occurs, (F.) maximum upward heave occurs, (G.) maximum downward heave occurs, and (H.) maximum sideslip occurs.

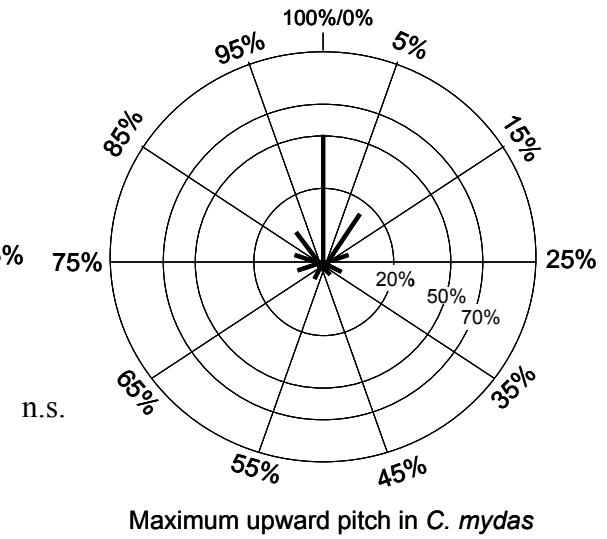
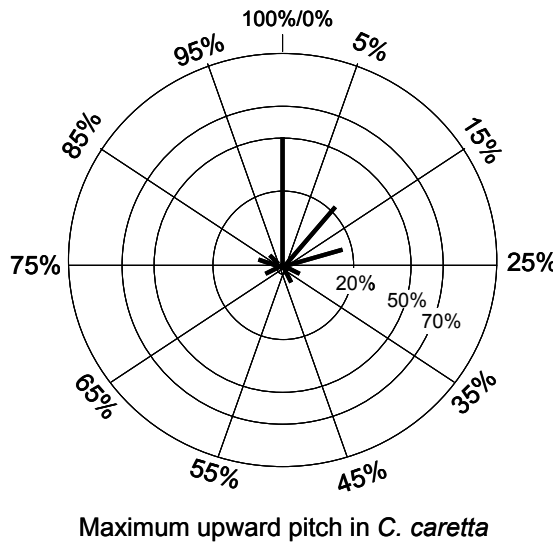
A.



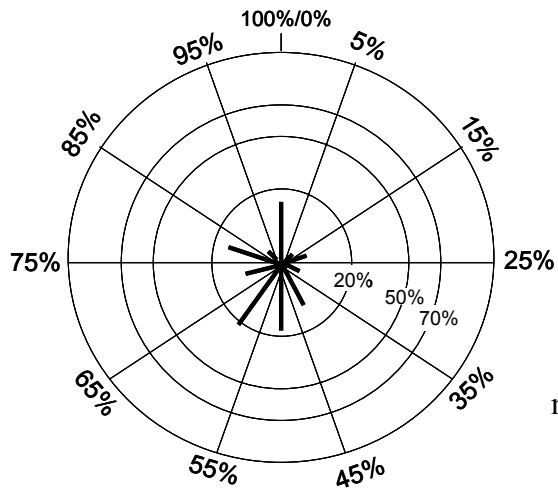
B.



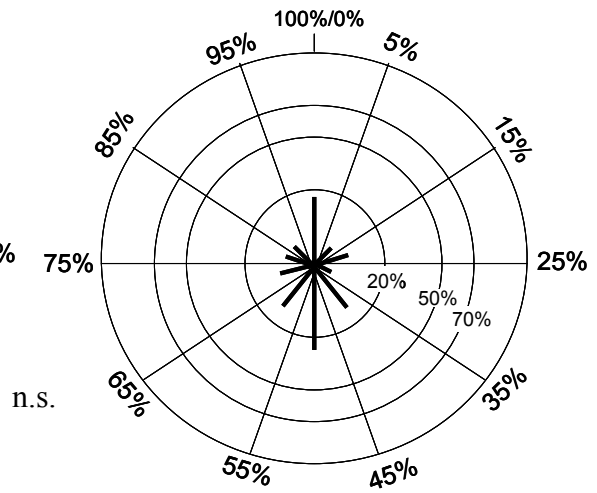
C.



D.

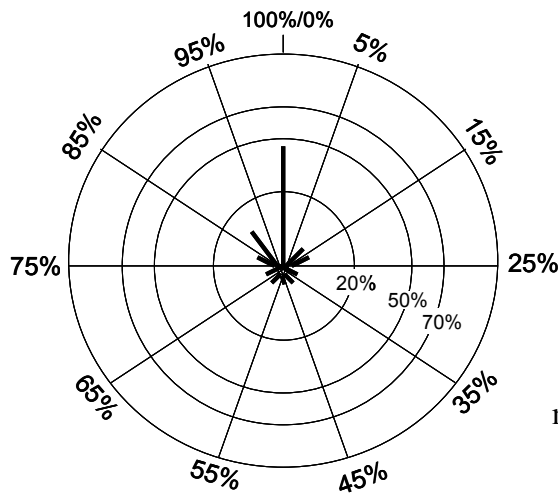


Maximum downward pitch in *C. caretta*

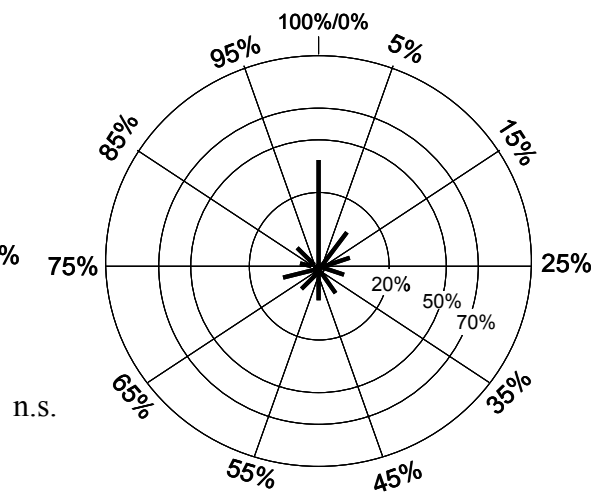


Maximum downward pitch in *C. mydas*

E.

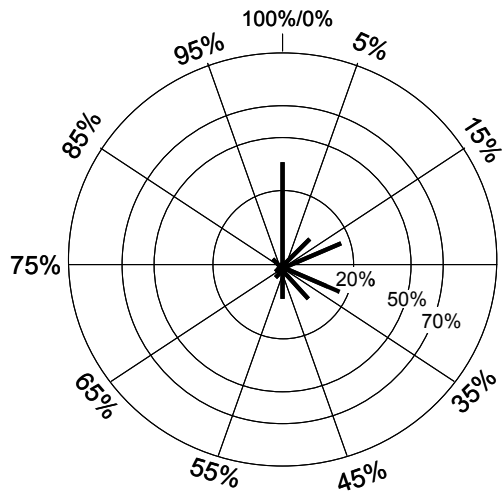


Maximum yaw in *C. caretta*

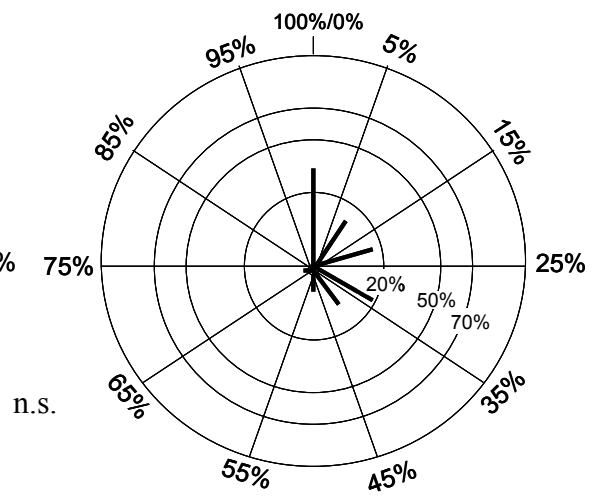


Maximum yaw in *C. mydas*

F.

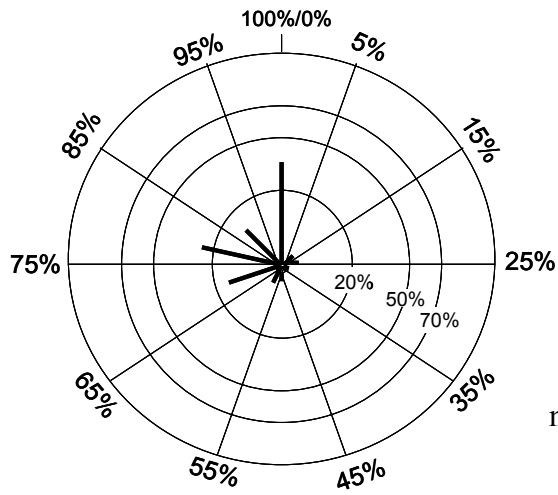


Maximum upward heave in *C. caretta*

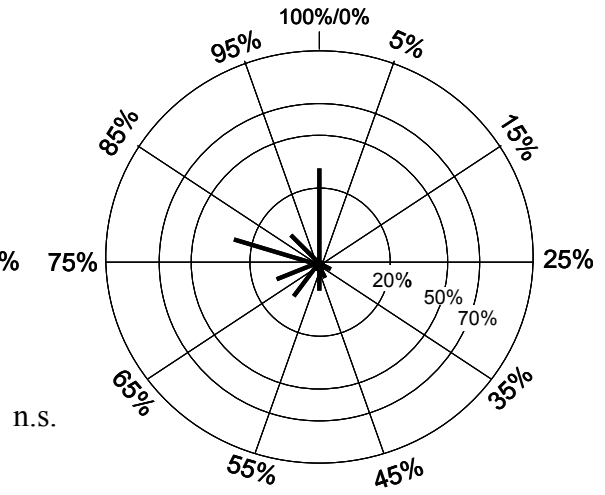


Maximum upward heave in *C. mydas*

G.

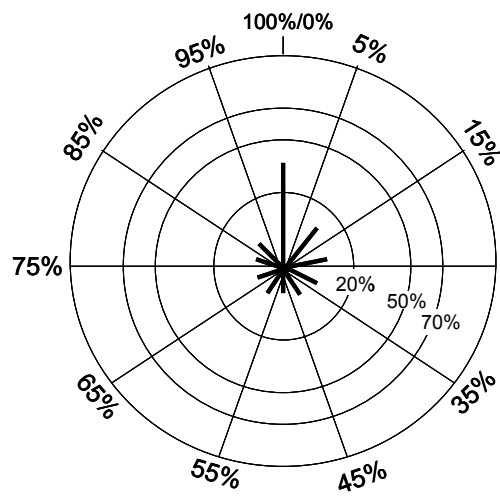


Maximum downward heave in *C. caretta*



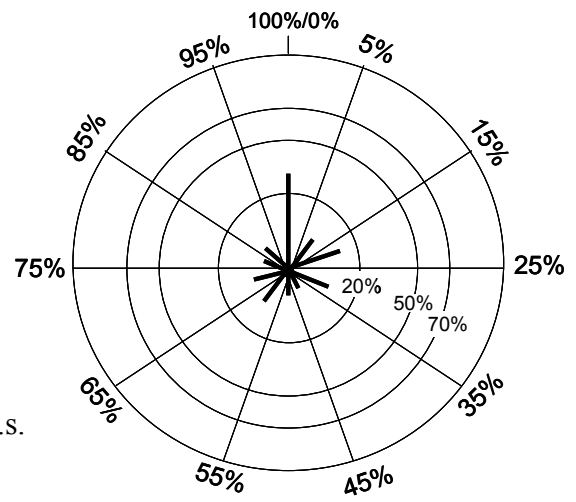
Maximum downward heave in *C. mydas*

H.



Maximum sideslip in *C. caretta*

n.s.



Maximum sideslip in *C. mydas*

Appendix 2. Nested ANOVA comparisons between species.

A. Comparison of maximum upward flipper displacement between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.000 | 1 | 0.000 | 1.041 | 0.321 |
| Indiv(Species) | 0.001 | 15 | 0.000 | 9.040 | 0.000 |
| Error | 0.002 | 233 | 0.000 | | |

B. Comparison of maximum downward flipper displacement between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.001 | 1 | 0.001 | 3.124 | 0.094 |
| Indiv(Species) | 0.005 | 15 | 0.000 | 7.870 | 0.000 |
| Error | 0.010 | 233 | 0.000 | | |

C. Comparison of maximum upward pitch between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.696 | 1 | 0.696 | 0.667 | 0.423 |
| Indiv(Species) | 23.090 | 15 | 1.539 | 3.671 | 0.000 |
| Error | 97.715 | 233 | 0.419 | | |

D. Comparison of maximum downward pitch between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 76.083 | 1 | 76.083 | 0.990 | 0.332 |
| Indiv(Species) | 1,812.503 | 15 | 120.834 | 5.604 | 0.000 |
| Error | 5,024.078 | 233 | 21.563 | | |

E. Comparison of pitch excursion between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.012 | 1 | 0.012 | 0.099 | 0.756 |
| Indiv(Species) | 2.646 | 15 | 0.176 | 4.354 | 0.000 |
| Error | 9.441 | 233 | 0.041 | | |

F. Comparison of maximum yaw between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 4.204 | 1 | 4.204 | 3.751 | 0.065 |
| Indiv(Species) | 24.482 | 15 | 1.632 | 3.417 | 0.000 |
| Error | 111.305 | 233 | 0.478 | | |

G. Comparison of yaw excursion between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.085 | 1 | 0.085 | 0.871 | 0.360 |
| Indiv(Species) | 2.032 | 15 | 0.135 | 2.715 | 0.001 |
| Error | 11.622 | 233 | 0.050 | | |

H. Comparison of maximum upward heave between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.000 | 1 | 0.000 | 0.635 | 0.430 |
| Indiv(Species) | 0.000 | 15 | 0.000 | 0.990 | 0.466 |
| Error | 0.001 | 233 | 0.000 | | |

I. Comparison of maximum downward heave between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.000 | 1 | 0.000 | 2.178 | 0.150 |
| Indiv(Species) | 0.000 | 15 | 0.000 | 1.668 | 0.058 |
| Error | 0.001 | 233 | 0.000 | | |

J. Comparison of heave excursion between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.001 | 1 | 0.001 | 2.278 | 0.144 |
| Indiv(Species) | 0.010 | 15 | 0.001 | 2.798 | 0.001 |
| Error | 0.053 | 233 | 0.000 | | |

K. Comparison of maximum upward heave/BL between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.000 | 1 | 0.000 | 0.407 | 0.527 |
| Indiv(Species) | 0.017 | 15 | 0.001 | 1.109 | 0.349 |
| Error | 0.237 | 233 | 0.001 | | |

L. Comparison of maximum downward heave/BL between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.000 | 1 | 0.000 | 0.000 | 0.994 |
| Indiv(Species) | 0.022 | 15 | 0.001 | 1.740 | 0.045 |
| Error | 0.198 | 233 | 0.001 | | |

M. Comparison of heave/BL excursion between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.011 | 1 | 0.011 | 0.124 | 0.728 |
| Indiv(Species) | 1.891 | 15 | 0.126 | 3.432 | 0.000 |
| Error | 8.556 | 233 | 0.037 | | |

N. Comparison of maximum sideslip between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.008 | 1 | 0.008 | 0.092 | 0.763 |
| Indiv(Species) | 1.634 | 15 | 0.109 | 2.125 | 0.010 |
| Error | 11.943 | 233 | 0.051 | | |

O. Comparison of sideslip excursion between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.001 | 1 | 0.001 | 0.014 | 0.905 |
| Indiv(Species) | 1.219 | 15 | 0.081 | 1.307 | 0.199 |
| Error | 14.488 | 233 | 0.062 | | |

P. Comparison of maximum sideslip/BL between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.339 | 1 | 0.339 | 3.457 | 0.075 |
| Indiv(Species) | 2.028 | 15 | 0.135 | 2.638 | 0.001 |
| Error | 11.943 | 233 | 0.051 | | |

Q. Comparison of maximum sideslip/BL excursion between species.

| Source | Type III SS | Df | Mean Squares | F-ratio | p-value |
|----------------|-------------|-----|--------------|---------|---------|
| Species | 0.213 | 1 | 0.213 | 2.652 | 0.113 |
| Indiv(Species) | 1.425 | 15 | 0.095 | 1.528 | 0.096 |
| Error | 14.488 | 233 | 0.062 | | |

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