

RESEARCH ARTICLE

The ontogenetic scaling of bite force and head size in loggerhead sea turtles (*Caretta caretta*): implications for durophagy in neritic, benthic habitats

Christopher D. Marshall^{1,2,*}, Alejandra Guzman², Tomoko Narazaki³, Katsufumi Sato³, Emily A. Kane⁴ and Blair D. Sterba-Boatwright⁵

¹Department of Marine Biology, Texas A&M University, Galveston, TX, USA, ²Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX, USA, ³International Coastal Research Center, Atmosphere and Ocean Research Institute, The University of Tokyo, Kashiwa, Chiba Prefecture, Japan, ⁴Department of Biology, University of California, Riverside, Riverside, CA, USA and ⁵Department of Mathematics and Statistics, Texas A&M University-Corpus Christi, Corpus Christi, TX, USA

*Author for correspondence (marshallc@tamug.edu)

SUMMARY

Ontogenetic studies of vertebrate feeding performance can help address questions relevant to foraging ecology. Feeding morphology and performance can either limit access to food resources or open up new trophic niches in both aquatic and terrestrial systems. Loggerhead sea turtles are long-lived vertebrates with complex life histories that are marked by an ontogenetic shift from an oceanic habitat to a coastal neritic habitat, and a transition from soft oceanic prey to hard, benthic prey. Although considered durophagous and strong biters, bite performance has not been measured in loggerheads, nor has the ontogeny of bite performance been characterized. In the present study, we collected measurements of bite force in loggerhead turtles from hatchlings to adults. When subadults reach the body size at which the ontogenetic shift occurs, their crushing capability is great enough for them to consume numerous species of hard benthic prey of small sizes. As loggerheads mature and bite performance increases, larger and harder benthic prey become accessible. Loggerhead bite performance eventually surpasses the crushing capability of other durophagous carnivores, thereby potentially reducing competition for hard benthic prey. The increasing bite performance and accompanying changes in morphology of the head and jaws are likely an effective mechanism for resource partitioning and decreasing trophic competition. Simultaneous measurements of body and head size and the use of non-linear reduced major axis regression show that bite force increases with significant positive allometry relative to body size (straight carapace length, straight carapace width and mass) and head size (head width, height and length). Simple correlation showed that all recorded morphometrics were good predictors of measured bite performance, but an AICc-based weighted regression showed that body size (straight carapace width followed by straight carapace length and mass, respectively) were more likely predictors of bite force than head size morphometrics (head width and head length).

Key words: biting, performance, ontogeny, durophagy, loggerhead sea turtle, competition.

Received 26 April 2012; Accepted 11 August 2012

INTRODUCTION

Vertebrate feeding morphology and performance can either restrict access to food resources or open new trophic niches through modification of the feeding apparatus (e.g. Fernandez and Motta, 1997; McCormick, 1998; Verwaijen et al., 2002). Such feeding adaptations are related to patterns of resource use in both aquatic and terrestrial systems (Osenberg and Mittelbach, 1989; Pérez-Barberia and Gordon, 1999) and can be a mechanism to avoid trophic competition (Kiltie, 1982; Dumont, 1999). Studies concerning the ontogeny of feeding performance are relatively few, but ontogenetic shifts in diet that are coupled with changes in jaw morphology and feeding performance have been observed in a variety of vertebrates, including ray-finned fish (Hernandez and Motta, 1997; Wainwright and Richard, 1995; Hjelm et al., 2000; Svanbäck and Eklöv, 2002; Hjelm et al., 2003), lizards (Ballinger et al., 1977; Capel-Williams and Pratten, 1978; DeMarco et al., 1985; Paulissen, 1987; Herrel et al., 1999; Myers et al., 2002; Herrel and O'Reilly, 2006), freshwater turtles (Herrel et al., 2002; Herrel and O'Reilly, 2006) and mammals (Binder and Van Valkenburgh, 2000; Wroe et al., 2005). The natural history of sea turtles and the development of their feeding apparatus provide a model

system for investigating the ontogeny of feeding biomechanics and performance since sea turtles undergo marked ontogenetic shifts in both habitat and diet. Several sea turtle species, such as loggerhead sea turtles, have specialized adaptations of their feeding apparatus that enable access to new trophic resources over their lifetimes.

Sea turtles are long-lived animals with complex life histories. They undergo drastic changes in body size (Owens, 1997) and exhibit ontogenetic shifts in both diet and habitat (Musick and Limpus, 1997; Reich, et al., 2007; Reich, et al., 2010) during their lifetime. The early life history of most sea turtle species is still poorly known. Currently, our best information comes from loggerhead sea turtles (*Caretta caretta*) in the North Atlantic Ocean (e.g. Carr, 1986; Carr, 1987; Bolten and Witherington, 2003). During their oceanic life history phase, juvenile loggerhead turtles raft along major oceanic gyres in association with *Sargassum* algae or 'weed lines' that provide transportation, protection and food (Carr, 1986; Carr, 1987). Loggerheads at this early stage are omnivorous, opportunistic feeders consuming soft prey items that include small invertebrates, sea grass fragments, algae, gelatinous zooplankton (i.e. jellyfish, cnidarians and small transparent organisms living in the water column of the open

ocean) and decapod larvae (Bjorndal and Zug, 1995; Parker et al., 2005). The time spent in this oceanic stage is species dependent, but is followed by an ontogenetic shift from oceanic to coastal, neritic developmental habitats, where turtles continue to grow and complete their sexual maturation. For loggerheads in the North Atlantic Ocean, this shift occurs at a standard carapace length (SCL) of ~40–60 cm (Carr, 1986; Carr, 1987; Bolten and Balazs, 1995; Bjorndal et al., 2000; Bjorndal et al., 2003). Loggerheads in the Pacific ocean, including Japan in the North Pacific and also Australia in the South Pacific, recruit to neritic habitats at SCLs of up to 75 cm (Nichols et al., 2000; Limpus and Limpus, 2003; Snover, 2008; Ishihara et al., 2011). Regardless, the optimal size at which they shift to neritic habitats is variable (Snover, 2008). This ontogenetic shift in habitat is associated with an ontogenetic shift from a pelagic to a benthic diet. During this shift, loggerheads increasingly consume hard-shelled prey (Bjorndal, 1997; Seney and Musick, 2007) such as crabs, gastropods, bivalves and barnacles but also gelatinous zooplankton, squid and occasionally fish.

Ontogenetic shifts in habitat are ultimately tied to fitness (Werner and Gilliam, 1984; Snover, 2008). One strategy to increase fitness is to maximize growth rates and minimize time to reproductive maturity. There is substantial evidence that aquatic organisms remain in habitats that increase the ratio of growth rate to mortality risk (Werner and Gilliam, 1984; Werner and Hall, 1988; Dahlgren and Eggleston, 2000). Although fast growth is advantageous in that it reduces the risk of predation, it is also energetically costly. Such ecological trade-offs manifest themselves in interesting and varied responses by organisms.

The morphology and performance of the feeding apparatus of juvenile loggerhead sea turtles likely constrains access to hard-shelled prey until it matures to the durophagous phenotype. Prior to their ontogenetic shift, juvenile loggerheads consume only soft prey (Bjorndal and Zug, 1995; Parker et al., 2005). High bite forces at this life stage are not needed and the extra energy expended to maintain hypertrophic adductor mandibulae could be better spent on growth. Therefore, it would be advantageous for loggerheads to significantly increase the development of bite force relative to body size by the time of their ontogenetic shift to neritic, benthic habitats. After their ontogenetic shift to coastal and benthic habitats where they encounter hard prey, increasing bite force and durophagy over their ontogeny would allow loggerheads access to either higher calorie prey, or an abundance of lower calorie but previously unattainable prey, ultimately giving them a trophic advantage that maximizes growth.

Recently, it has been demonstrated that the ontogenetic shift of some individual loggerheads in the North Atlantic Ocean may be more complex than once thought. After the initial ontogenetic shift to neritic habitats, some individuals oscillate between neritic and more pelagic environments (Bolten, 2003; McClellan and Read, 2007; McClellan et al., 2010). While back in the oceanic habitat, these individuals often feed on soft prey (e.g. Dodd, 1988; Plotkin et al., 1993; Limpus et al., 1994; Bjorndal, 1997; Tomás et al., 2001; Bjorndal et al., 2003; Spotila, 2004; Seney and Musick, 2007). The reasons for this 'complex' and often 'reversible' ontogenetic habitat shift are not completely understood (McClellan and Read, 2007; McClellan et al., 2010). Juvenile loggerheads recently recruited to neritic habitats may be at a competitive trophic disadvantage because of their smaller size if competition is high. Functionally, movement between neritic habitats and more pelagic habitats may provide additional time for the feeding apparatus to develop into its crushing, durophagous phenotype.

For juvenile loggerhead sea turtles, it appears that access to hard prey is constrained by an interaction of body size, feeding morphology

and performance. Major changes in head and jaw phenotype may contribute to the timing of the ontogenetic shift in habitat and diet. As their name suggests, adult coastal loggerhead sea turtles possess larger and wider heads than green (*Chelonia mydas*) and hawksbill turtles (*Eretmochelys imbricata*) (Kamezaki, 2003). The morphology of the head and jaws is thought to be an adaptation for a durophagous niche (Kamezaki and Matsui, 1997; Kamezaki, 2003) and the head and jaw morphology of adults results in a strong bite capability (Guzman, 2008). The short jaws (Kamezaki and Matsui, 1997; Kamezaki, 2003) are thought to decrease the jaw out-lever and increase mechanical advantage. Any increase in physiological cross-sectional area of the mandibular adductors (the main input of force for jaw closing) should also increase bite force by simply increasing the force-in component of this lever system. Further increases of bite force could also be achieved by changes in mandibular adductor muscle architecture and muscle fiber type. Since there are numerous variables that contribute to a strong bite force, measuring bite performance directly is desirable. This has only recently been done in loggerhead sea turtles (Guzman, 2008). Therefore, the objectives of this study were to (1) measure bite performance in loggerheads throughout their ontogeny, (2) characterize how bite performance scales to body and head morphometrics, and (3) determine which body or head morphometric best predicts bite force over their natural history. We hypothesized that the ontogenetic change in habitat and diet from juvenile to sub-adult and adult age classes is accompanied by a increase in head size and a biomechanical shift resulting in increased bite force performance. We also hypothesized that bite force should increase dramatically in these age classes after the transition to their coastal habitats when they begin to consume hard prey, and that head width and height would be the best predictors of bite force in loggerhead turtles.

MATERIALS AND METHODS

Subjects

Loggerhead sea turtles, *C. caretta* (Linnaeus 1758), used in this study were held at numerous facilities. Hatchling and juvenile loggerheads were held at the National Oceanic and Atmospheric Administration (NOAA) Fisheries sea turtle facility in Galveston (TX, USA). Bite force and morphometric measurements at this facility were collected from four age classes: hatchlings (3–6 months, 2006 year class), 9 month old hatchlings (2005 year class), 20 month old juveniles (2004 year class) and 34 month old juveniles (2003 and 2004 year classes). Bite force and morphometric measurements were also collected from subadult and adult loggerhead turtles at the International Coastal Research Center, Atmosphere and Ocean Research Institute, the University of Tokyo (Otsuchi, Iwate Prefecture, Japan). These turtles were part of a tag and release program in which loggerhead turtles caught as set net by-catch in the Iwate Prefecture region were turned over by fishermen to university researchers. Turtles were retained in an outdoor flow-through saltwater holding facility from 1 week to 2 months to collect fecal samples. These turtles participated in a variety of studies before being released offshore away from fishery gear in the many bays of Iwate prefecture. Some adults were sampled from a variety of locations in the USA and Japan: Sea Turtle Inc. (S. Padre Island, TX, USA), Moody Gardens Aquarium (Galveston, TX, USA), Enoshima Aquarium (Fujisawa, Kanagawa Prefecture, Japan) and the St Lucie power plant (Port St Lucie, FL, USA). In addition, several turtles were measured after recovery from hook and line captures, incidental captures, oil platform removals and live strandings along the Texas Gulf Coast.

Permits on all captive loggerheads at the Galveston NOAA Sea Turtle facility were held under Florida Wildlife Conservation

Commission permit TP#015. All wild turtles encountered in Texas waters were temporarily housed at the NOAA sea turtle facility. All wild turtles were later released. All procedures were approved by the Texas A&M University Institution Animal Care and Use Committee (AUP no. 2005-204). All measurements in Iwate Prefecture were conducted under permission from the Ethics Committee of the University of Tokyo.

Morphometrics

For all turtles, prior to bite performance trials, mass (kg), SCL and straight carapace width (SCW) were collected (see Wyneken, 2001) using a spring scale and net and large calipers for standard morphometrics (cm). Digital calipers were used for the following head morphometrics (all measurements in cm). Greatest head width (HW) was measured at the widest part of the skull, which also coincided with the location of the adductor mandibulae. Greatest head height (HH) was measured from the dorsal-most parietal to the ventral-most dentary near the jaw joint. Greatest head length (HL) was measured from the anterior-most tip of the snout to the posterior-most part of the supraoccipital.

Bite force

Bite performance was measured *in vivo* using a force transducer fitted into bite force apparatus (see Herrel et al., 1999; Herrel et al., 2001a; Herrel et al., 2001b; Aguirre et al., 2002) (Fig. 1) with customized bite force plates fitted for a loggerhead mouth. Bite force was measured using a low level force transducer (± 500 N Kistler FSH 9203, Amherst, NY, USA) for turtles younger than 2.5 years. All other turtle bite force measurements were collected using a larger force transducer (± 5000 N Kistler FSH 9312A). The responses of these force transducers are linear across their entire range and at a wide range of temperatures. Once bitten upon, the upper bite plate transferred the force to a piezo-electric force transducer. Signals from the transducer were amplified by a handheld charge amplifier (Kistler FSH 5995) and recorded. The resolution of force detection for both transducers depends on the set range and sensitivity of the amplifier and varies from 0.01 to 0.5 N. The sensitivity of each transducer is a function of linearity based on the input against output and deviates by less than 1%. The accuracy of the bite force meter output was calibrated by hanging a series of weights from the end of the bite force plates, and output



Fig. 1. An adult loggerhead sea turtle biting on the bite force apparatus at the bite stops on the bite plates.

was plotted to ensure linearity. Bite placement was always at the anterior tip of the jaws (Fig. 1) and was rigorously controlled with stops on the bite plates. Raw bite force values were adjusted for mechanical advantage depending on the length of the bite force plates used and calibration as needed. Bite force measurements in all turtles were taken prior to daily feeding so that the motivation to bite would be high. Since gape angle can affect bite force (Dumont and Herrel, 2003), gape angle at the time of bite measurement was determined using digital photographs and analyzed using Image J software (Bethesda, MD, USA) to standardize the percentage biting gape angle (~ 10 deg) throughout the ontogeny study by adjusting the distance between the bite force plates. A trial consisted of three bite force measurements with at least 15 min between bites. A total of five bite force measurements were collected from each hatchling and juvenile loggerhead in Texas. Three bite force measurements were collected from each adult wild or captive individual in Texas. At least five bite force measurements were collected from each subadult and adult loggerhead in Japan. A total of 2732 bite force measurements were collected during 1380 trials. The maximum value for each individual was considered to be the maximum bite force for that turtle. All subjects had to meet the criteria of motivated biting to be included in the analyses.

Statistics

Statistical tests were performed using R 2.15.1 (R Core Team, 2012) and JMP 9.0 (SAS Institute, Cary, NC, USA). Normality of data was tested using a Kolmogorov–Smirnov test. Levene's test was used to test the assumption of homogeneity of variance. For a regression model relating morphological measurements to maximum bite force, all data were \log_{10} transformed to normalize variance. Following the approach of Burnham and Anderson (Burnham and Anderson, 2002), we used AICc (corrected Akaike information criterion)-weighted regression to assign a weight to every possible linear model involving the given variables. Weights are normalized so that their sum was 1. For each variable, the sum of the model weights for those models containing that variable was calculated. A result of 1 means that that variable is in essentially every top-ranked model, while a result of 0 means that that variable is in essentially none of the top-ranked models. Weighted regression was performed using MuMIn library in R (Barton, 2012).

Scaling terminology follows Schmidt-Nielsen (Schmidt-Nielsen, 1984). Since isometry refers to the slope of two variables (x and y), predicted isometry depends on the dimensionality of these variables. That is, bite force scales to length to the second power because of the cross-sectional area of the adductor mandibulae (Hill, 1950), and mass scales to length to the third power. A thorough exploration of the general properties of the arithmetic distribution, and the observed non-linear behavior of \log_{10} -transformed data strongly suggested that a power function fitted to the original data using a non-linear regression approach to allometry as recommended by Packard (Packard, 2012) was the most appropriate analysis. Therefore, models with algebraic form $y=ax^b$ were directly fitted to untransformed data in the measurement space using non-linear regression. Since error could occur in either x or y variables, model fitting was performed by minimizing a non-linear version of the standard reduced major axis (RMA) criterion (Ebert and Russel, 1994). R^2 was computed using Eqn 1:

$$R^2 = 1 - \frac{SS_{\text{Residual}}}{SS_{\text{Total}}}, \quad (1)$$

for the non-linear RMA model, where SS is sum of squares. R^2 as calculated for RMA regression will always be less than R^2 for ordinary

non-linear least squares regression, but similar values for the two confirm the fit of the RMA model. In all cases except bite force *versus* HL, the difference in R^2 between the two methods was less than 0.015; for bite force *versus* HL, the difference was 0.08. Significant allometry was confirmed by inspection of the 95% confidence intervals relative to isometry. To estimate confidence intervals for the exponents, and one-tailed P -values to test the hypothesis that the isometric (predicted) exponent is the same as the regression exponent, an ordinary bootstrap (Davison and Hinkley, 1997) was used; 95% confidence intervals for the exponent b used 4999 bootstrap replicates. A value of $P < 0.001$ in the results below indicates that the predicted exponent b was not in a 99.8% confidence interval computed using 49,999 bootstrap replicates. A value of $P < 0.01$ indicates the predicted exponent b was not in a 98% confidence interval. All intervals were estimated using the adjusted bootstrap percentile (BCa) method (Davison and Hinkley, 1997). Calculations were performed using R code written by the authors in R version 2.15.1. Bootstrap calculations used R boot package version 1.3-5 (Canty and Ripley, 2012). All R code is available on request.

RESULTS

Bite force and morphometric data from a total of 519 loggerhead turtles were collected. Only 450 loggerhead turtles met the performance criteria (motivated aggressive biting) to be included in the study. Because of the ontogenetic nature of the study, mass and morphometric data covered a wide range of values. Mass ranged from 0.04 to 95.5 kg (mean mass = 9.81 ± 16.20 kg). SCL ranged from 5.8 to 99 cm (mean SCL = 29.4 ± 20.43 cm). SCW ranged from 4.8 to 71 cm (mean SCW = 25.3 ± 16.10 cm). HW ranged from 1.7 to 16.9 cm (mean HW = 6.25 ± 3.60 cm). HH ranged from 1.4 to 15.4 cm (mean HH = 5.42 ± 3.2 cm). HL ranged from 2.6 to 20.6 cm (mean HL = 8.9 ± 4.50 cm). Maximum bite force for each individual ranged from 0.9 to 1766 N.

Non-linear RMA regressions (Table 1, Fig. 2) of maximum bite force *versus* mass, SCL, SCW, HW, HL and HH were all significant ($P < 0.001$) with R^2 values of 0.87, 0.85, 0.84, 0.90, 0.58 and 0.91, respectively. Under geometric similarity, the maximum bite force is predicted to scale with (mass)^{2/3} since bite force represents an area (physiological cross-sectional area of muscle) and mass represents a volume (Hill, 1950). Likewise, maximum bite force is predicted to scale with (SCL)², (SCW)², (HW)², (HL)² and (HH)². However, maximum bite force scaled with significant positive allometry relative to all body and head morphometrics.

The AICc was used to weigh all linear regression models with log(maximum bite force) as the dependent variable and different combinations of log(mass), log(SCL), log(SCW), log(HW), log(HL) and log(HH) as the independent variables. The sums of the resulting weights demonstrated that SCW and SCL were the most important variables in predicting maximum bite force, followed by mass (importance weightings of 1.00, 0.90 and 0.71, respectively). A

subsequent AIC-based stepwise regression with SCL, SCW and mass removed demonstrated that HW and HL best predicted maximum bite force (importance ratings of both were 1.00). Although all logged variables explained log(maximum bite force) well (correlation $r > 0.975$ in all cases), body morphometrics were slightly better than head morphometrics alone.

As head morphometrics were also good predictors of maximum bite performance in loggerhead sea turtles, we asked whether HW, HL and HH also scaled with significant positive allometry relative to SCL. Non-linear RMA regressions of HW, HL and HH *versus* SCL showed a significant correlation among all relationships (HW and HL: $P < 0.001$; HH: $P < 0.01$) with R^2 values of 0.98, 0.97 and 0.97, respectively (Table 2). However, all head morphometrics scaled with significant negative allometry (Table 2, Fig. 3) relative to SCL.

DISCUSSION

Understanding the timing of ontogenetic shifts is critical to the conservation and management of endangered species (Snover et al., 2008). We hypothesized that the ontogeny of bite force in loggerheads would show a substantial increase, indicated by an abrupt increase in magnitude, after their ontogenetic shift from oceanic to neritic habitats. However, bite performance values did not show an abrupt change in magnitude at the size range when the ontogenetic shift occurs, or at any other time during development. Instead, the data show that bite force increased smoothly during ontogeny with significant positive allometry relative to all size measurements (SCW, SCL and mass), and all head morphometrics (HW, HL and HH). Although all morphometrics were good predictors of bite force, body morphometrics were slightly better predictors than head morphometrics alone.

Our data support the premise that a SCL of 40–60 cm is the minimum size that correlates with the development of the feeding apparatus that allows juvenile loggerheads to begin to consume harder prey. Although more variable after 60 cm SCL, bite forces of juvenile loggerheads in this dataset ranged from ~330 to 575 N. This performance level is adequate for consuming numerous species of hard prey from small size classes initially (Fig. 4). For example, crabs are common prey of loggerheads. The breaking force of small blue crabs (*Callinectes sapidus*) ranges from 30 to 490 N (carapace length 23.3–68.4 mm) (Mara et al., 2010), well within the capability of loggerheads newly recruited to neritic habitats. Furthermore, there is evidence that loggerheads begin to feed upon bivalves in the range 10–30 mm in length (Godley et al., 1997). If we assume that loggerheads first begin to consume bivalves that are 25 mm in length, then loggerhead bite performance at a SCL of 40–60 cm is great enough to crush many species of mollusk bivalves. A survey of the literature on marine bivalve breaking force at a length of 25 mm reveals the following data: common mussel (*Geukensia demissa*), 280 N (Hernandez and Motta, 1997); quahog (*Mercenaria mercenaria*), 500–600 N (Fisher et al., 2011); and venus or smooth clam (*Callista*

Table 1. Maximum BF *versus* mass, SCL, SCW, HW, HL and HH

Variables	R^2	Constant a	Exponent b	Lower 95% CI	Upper 95% CI	Predicted exponent	P
BF <i>versus</i> mass	0.874	38.162	0.800	0.749	0.862	0.667	<0.001
BF <i>versus</i> SCL	0.850	0.050	2.301	2.198	2.446	2	<0.001
BF <i>versus</i> SCW	0.843	0.086	2.276	2.115	2.435	2	<0.001
BF <i>versus</i> HW	0.900	2.118	2.295	2.196	2.420	2	<0.001
BF <i>versus</i> HL	0.578	0.118	3.144	2.882	3.410	2	<0.001
BF <i>versus</i> HH	0.914	3.463	2.204	2.111	2.299	2	<0.001

Bite force, BF; SCL, standard carapace length; SCW, straight carapace width; HW, head width; HL, head length; HH, head height. R^2 calculated from non-linear reduced major axis (RMA) regression models. CI, confidence interval.

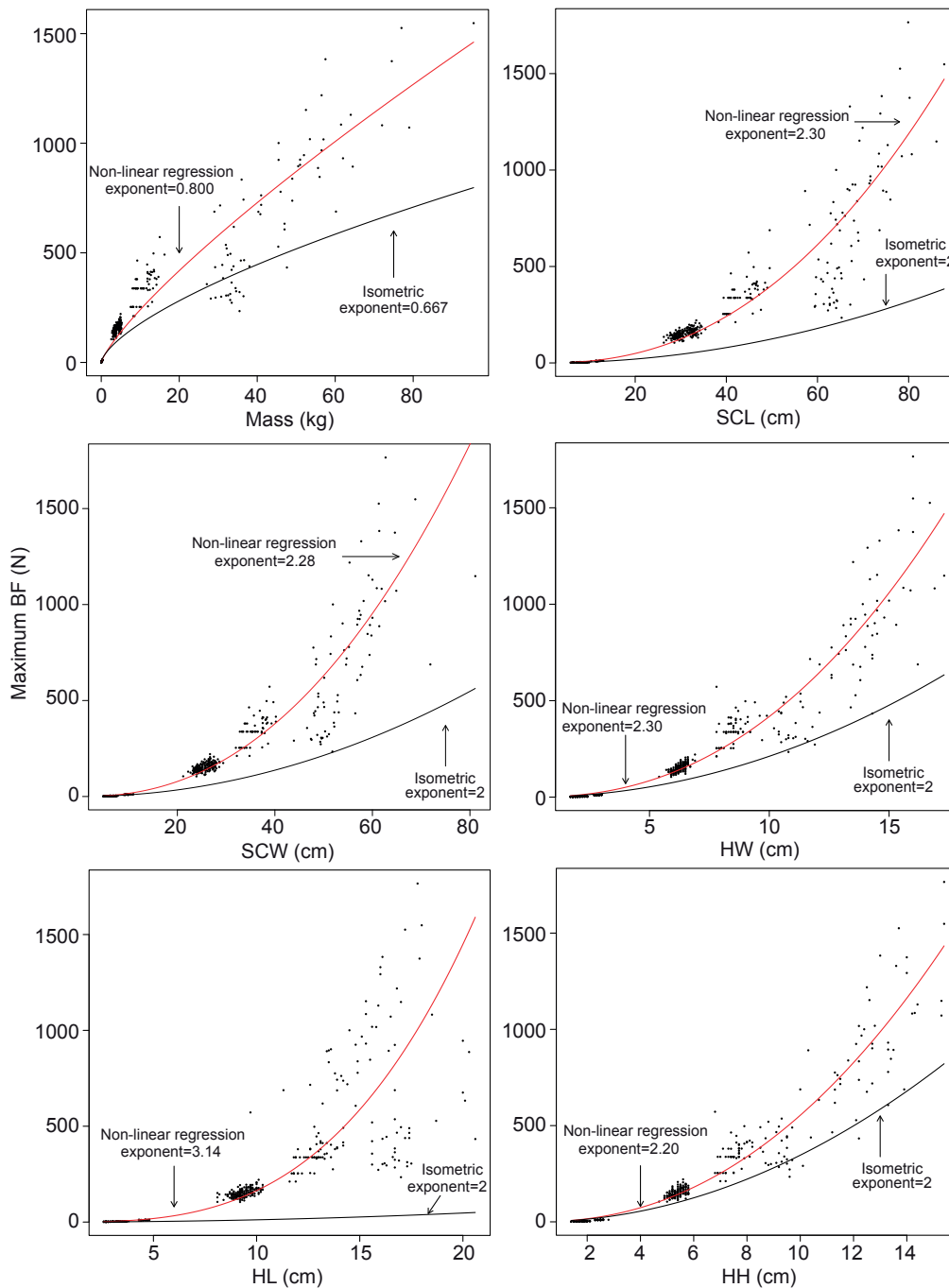


Fig. 2. Non-linear reduced major axis (RMA) regressions of maximum bite force (BF) versus mass, straight carapace length (SCL), straight carapace width (SCW), head width (HW), head length (HL) and head height (HH). Red line, fitted line; black line, line of isometry. Lines of isometry were plotted using the same constant a as the fitted line.

chione), 300 N (Vasconcelos et al., 2011). However, some bivalves of 25 mm length require a breaking force greater than the capability of loggerhead turtles newly recruited to neritic habitats. These bivalves include: eastern oysters (*Crassostrea virginica*), 800 N (Fisher et al., 2011), and Florida carditas (*Cardita floridana*), 830 N (Hernandez and Motta, 1997). Larger and deeper bivalves have greater breaking forces: *C. chione* at a shell length of 100 mm breaks at ~1730 N (Vasconcelos et al., 2011). Fecal samples collected from subadult and adult loggerhead turtles that migrated to the study sites in Iwate Prefecture, Japan, contained broken shells of Oregon hairy tritons (*Fusitriton oregonensis*), a sea snail. Broken shells from this gastropod tended to appear in fecal samples from larger turtles more than those of smaller turtles. The force required to crush *F. oregonensis* was 524.0 ± 129.4 N ($N=21$) (Takuma, 2010).

The highest loggerhead bite force recorded in this study was 1766 N from an individual at ~90 cm SCL. Although this carapace length is above the minimum for adult loggerhead turtles, loggerheads are long lived and continue to grow their entire lives; they can reach SCLs of 110 cm in Florida (Kamezaki, 2003). Based on our dataset, such an individual is estimated to produce a bite force in excess of 2105 N. Large loggerheads have been observed to consume queen conch (*Strombus gigas*) (Babcock, 1937) and giant clams in excess of 19 cm (*Tridacna maxima*) (Limpus, 1973). Because of the high breaking forces of the largest size classes of these molluscan prey (e.g. *S. gigas*) (Jory and Iversen, 1988), it likely that only the largest loggerheads can crush and consume them.

Molluscivores that potentially compete with loggerheads include numerous species of durophagous crabs and fishes, including sharks

Table 2. HW, HL and HH versus SCL

Variables	R^2	Constant a	Exponent b	Lower 95% CI	Upper 95% CI	Predicted exponent	P
HW versus SCL	0.977	0.250	0.940	0.921	0.959	1	<0.001
HL versus SCL	0.967	0.744	0.738	0.714	0.764	1	<0.001
HH versus SCL	0.970	0.194	0.972	0.949	0.995	1	<0.01

SCL, standard carapace length; HW, head width; HL, head length; HH, head height.

and rays. However, it is evident that as loggerhead sea turtles increase in size, their bite performance allows them to crush larger prey, eventually reducing competition. For example, durophagous crabs breaking four species of gastropod mollusk (*Littorina littorea*, *Osilinus lineata*, *Gibbula ceneraria* and *G. umbilicalis*) could only generate forces from 250 to 300 N in the transverse plane (Cotton et al., 2004), which was also near the breaking limit of their claws. Cownose rays (*Rhinoptera bonasus*) are limited to preying upon oysters with a shell depth of 22–24 mm or less; larger oysters are beyond their crushing capability (1400 N) (Fisher et al., 2011), but well within the capability of loggerhead turtles. Similarly, bonnethead sharks (*Sphyrna tiburo*), which are durophagous crab specialists, demonstrate a maximum bite force of ~108 N posteriorly and ~26 N at the jaw tips (Mara et al., 2010). More impressive are horn sharks (*Heterodontus francisci*) and black tip sharks, for which the maximum theoretical bite force is reported as 128 and 423 N, respectively, at the anterior teeth (Huber et al., 2005; Huber et al., 2006). These data suggest that loggerhead turtles newly recruited to neritic habitats have a bite capability great enough to allow them to consume a variety of smaller hard prey, and as individuals grow, larger and harder items become available, reducing competition.

The finding that juvenile loggerhead turtles did not exhibit performance levels near those of adults is in agreement with similar ontogenetic studies of performance in squamates and archosaurs (Irschick, 2000; Myers et al., 2002). Furthermore, the lack of an abrupt change in magnitude in bite performance in association with an ontogenetic shift in diet was also similar to the results of an ontogenetic study of bite force in American alligators (*Alligator mississippiensis*) (Erickson et al., 2003). The scaling pattern of performance over the ontogeny of loggerheads is similar to that in studies of mammals, lizards, freshwater and terrestrial turtles, birds and fish, where bite performance scales with significant positive allometry to head dimensions, despite the differing growth trajectories among these various vertebrates (reviewed by Herrel

and Gibb, 2006). Feeding performance studies in reptiles have shown that simple head morphometrics such as maximum head width, height and length are good indicators of bite performance (Herrel et al., 1999; Herrel et al., 2001a; Herrel et al., 2001b; Herrel and O'Reilly, 2006; Herrel et al., 2006). Although head width in freshwater turtles has been shown to increase bite force as a result of a greater physiological cross-sectional area of the adductor mandibulae, an increase in head height has also been reported to increase bite force. Presumably, increased head height reduces the angle of the adductor mandibulae tendon line of action as it curves around the otic chamber of the skull (Gaffney, 1979; Herrel et al., 2002). This simple change would increase the mechanical advantage of the jaw lever system. In some species of freshwater turtles, a higher than predicted bite force was explained by increased head height (Herrel et al., 2002; Herrel and O'Reilly, 2006). In other species, other head morphometrics were better predictors. For example, head width was the only significant predictor of bite force in *Trachemys* (Herrel and O'Reilly, 2006). However, when body dimensions were included in this model, head length was the best predictor of bite followed by head height and carapace length for all three species. Similar findings were reported in a broader comparative study of bite force in turtles (Herrel et al., 2002). Our data demonstrate that body size (SCW, followed by SCL and mass) was only slightly better at predicting bite performance than head morphometrics (HW and HL). Body size explained 98% of the variance in our dataset. Excluding measurements of overall size, HW and HL were good predictors of bite force (96.6% of the variance explained). For the whole model, all morphometric measurements were good predictors of bite force. It seems clear that among all turtles, including loggerheads, there are several mechanisms that increase bite performance. In loggerhead turtles, bite performance increases with size, as with most vertebrates, and increasing HW and HL appears to be the important mechanism to produce larger than predicted bite performance based on size alone.

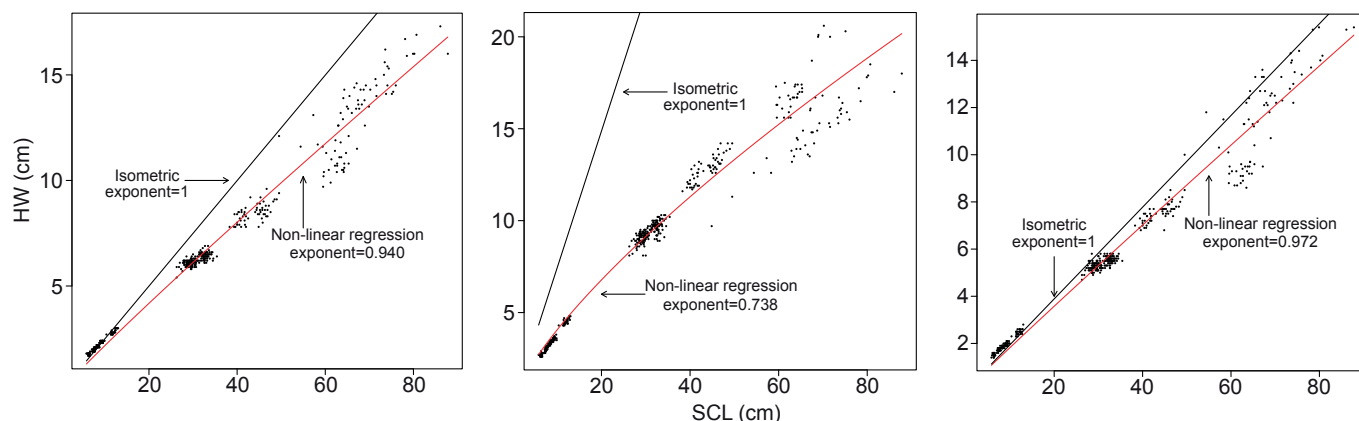


Fig. 3. Non-linear RMA of HW, HL and HH versus SCL. Red line, fitted line; black line, line of isometry. Lines of isometry were plotted using the same constant a as the fitted line.

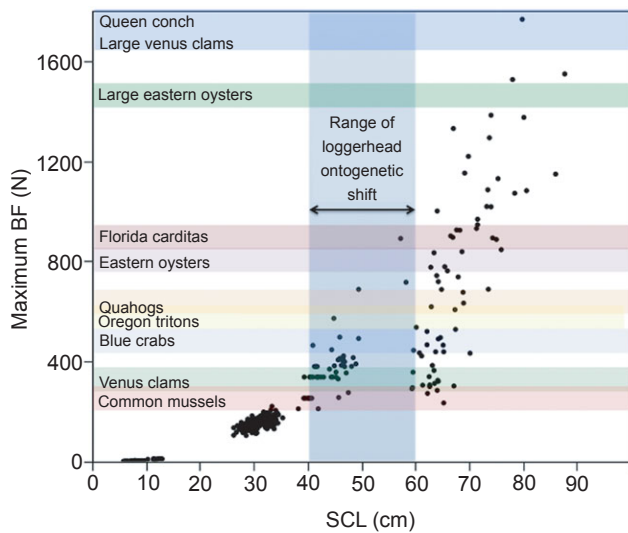


Fig. 4. Maximum bite force *versus* straight carapace length (SCL) plot for loggerhead turtles overlaid with labels of prey at their approximate breaking forces during and after the ontogenetic shift from oceanic to neritic habitats by loggerhead sea turtles.

HH contributed the least to increased bite force and this may be due to hydrodynamic constraints in the marine environment.

Loggerhead bite performance in this study scaled with significant positive allometry relative to all size and head morphometrics (Table 1, Fig. 2). However, all head morphometrics of loggerheads scaled with significant negative allometry relative to SCL (Table 2, Fig. 3). An earlier morphometric study of loggerheads also reported that head size scales with significant negative allometry relative to SCL (Kamezaki and Matsui, 1997). Similarly, Herrel and O'Reilly (Herrel and O'Reilly, 2006) found that head morphometrics scaled with significant negative allometry relative to carapace length in freshwater turtles. This result was somewhat surprising given head morphometrics in lizards generally scale isometrically relative to body size (Herrel and O'Reilly, 2006).

For turtles, increasing head size for increased bite force over their ontogeny comes with several trade-offs. For some species, a larger head results in the inability to retract the head into the shell for defensive purposes (Herrel et al., 2002). However, loggerhead sea turtles (and all cheloniids) have lost this ability (Pritchard, 1997). Compared with terrestrial and aquatic turtles, marine turtles face very different threats from large marine predators. In a marine environment, large size and increased escape behaviors (maneuverability) are likely the best protection against most predators. Furthermore, large size is likely favorable for completing the long migrations known to occur in several sea turtle species (e.g. Nichols et al., 2000; Boyle et al., 2009), and maneuverability is likely important for negotiating oceanic environmental features that concentrate prey resources (Cardona et al., 2005; Eckert et al., 2008). We suggest that the differential scaling of head morphometrics to body size between turtles (freshwater and marine) and lizards is related to the strong selection pressures of the aquatic environment, and that marine turtles likely face greater selection pressures for large body size that further influence the scaling relationships of their feeding apparatus relative to body size and mass, compared with freshwater turtles.

A second trade-off of improved bite performance is a decrease in jaw closing velocity. Force and velocity mechanically trade off in musculoskeletal systems (Vogel, 2003), including jaw lever

systems (Westneat, 1994; Case et al., 2008; Herrel et al., 2009). In general, parallel fiber 'strap' muscles increase the speed of muscle contraction, but increased muscle contraction force is attained through increased muscle pennation and short muscle fibers (Gans et al., 1985; Gans and de Vree, 1987). In addition, lever mechanics and linkages maximize either force or velocity, but not both simultaneously (Westneat, 1994; Levinton and Allen, 2005; Herrel et al., 2009). Consequently, forceful jaws are expected to perform with reduced velocity. Although more detailed work on the underlying biomechanics of biting in loggerheads remains to be conducted, current evidence indicates that their short jaws and highly pennate adductor mandibulae result in increased force production potentially at the expense of jaw closing velocity. This likely contributes to the adult loggerhead turtle diet, which is primarily composed of large hard prey that are also slow moving or sessile.

In summary, the morphology of the feeding apparatus of loggerhead sea turtles likely constrains their biting performance, which, in turn, constrains their trophic ecology (Arnold, 1983; Wainwright and Reilly, 1994) during early ontogeny, but facilitates niche expansion as a result of an increase in performance later in their ontogeny. Loggerhead sea turtles increase their bite capability through significant positive allometric growth of the body (SCW, SCL and mass) and head size (HW, HL and HH) and hypertrophied adductor mandibulae. Over the long lives of loggerheads, increased bite force allows larger and harder prey to be crushed and consumed. The widespread availability of such prey, the size of the prey and the potential decrease in competition likely makes such a foraging niche more profitable.

ACKNOWLEDGEMENTS

We thank Anthony Herrel for conversations regarding construction of a bite force meter and for details on collecting bite force measurements and their analyses. Many thanks are due to the Galveston NOAA sea turtle facility staff: Ben Higgins, Cain Bustinza, Erin Seney, Shanna Kethan and Mauricio Rodriguez. Assistance in data collection by Laura McCalla, Shannon Keenon, Katie Madden, Renae DiGuardi, Robin Culp, Gabriel Guzman, Baltazar Salazar and Daniella Salazar is greatly appreciated. We thank Moody Gardens Aquarium curators Greg Whittaker and Roy Drinnen. We are grateful to the staff at Enoshima Aquarium for assistance with additional measurements of their animals. We also thank S. Takuma for assistance in data collection while in Otsuchi, Japan. Fishermen, who supported the field study in Iwate Prefecture, Japan, suffered greatly from a large Tsunami on 11 March 2011. We sincerely hope they will be able to reconstruct their ports and set nets, and then resume their fishing activities.

FUNDING

Funding for this work was provided through the National Oceanic and Atmospheric Administration (NOAA) contract no. AB133F05SE4495/NFFR7400-5-00145 to C.D.M., a University of Tokyo Visiting Professorship to C.D.M. and the program Bio-Logging Science of the University of Tokyo (UTBLS). A.G. was supported by a Texas A&M University Diversity Fellowship and the Department of Marine Biology at Texas A&M University at Galveston.

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