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Scaling of bite performance with head and carapace morphometrics in green turtles (*Chelonia mydas*)

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ABSTRACT

Adult green turtles (*Chelonia mydas*) are unusual relative to other sea turtles in that they are predominately herbivorous. This herbivorous diet is reflected in the serrated morphology of their beak, bite performance and the relative morphometrics of their heads. Recent bite performance data in loggerhead turtles (*Caretta caretta*), which are known for their durophagous capability, have demonstrated that bite force is correlated with head morphometrics. The objective of this study was to characterize bite force in green turtles and correlate bite performance with head and carapace morphometrics. We predicted that maximum bite force in green turtles would be less in magnitude relative to loggerheads, but would be positively correlated with head morphometrics. Therefore, mass, straight carapace length, straight carapace width, greatest head width, height, and length were collected with bite force from free-ranging green turtles from Punta Abreojos, Baja California Sur, Mexico and Otsuchi, Japan. Subjects ranged from 10.9 to 48 kg, with straight carapace length and width ranged from 40.6 cm to 71.9 cm (mean = 56.3 ± 8.5 cm) and from 33.5 cm to 55.9 cm (mean = 44.8 ± 5.7 cm), respectively. A bite force apparatus was used to collect bite performance from subjects. The maximum bite force was 303 N. Mean head width, head height, and head length were 8.7 ± 1.2, 8.2 ± 1.1, and 11.5 ± 1.5 cm, respectively. Bite force was lower in magnitude than reported for loggerhead turtles as predicted but still strong enough to process algal and plant matter, as well as crush many hard prey items. Simultaneous measurements of body and head size, and the use of non-linear reduced major axis regression, show that bite force scaled isometrically relative to body size and head size. Simple correlation showed that all logged transformed morphometrics were good predictors of logged bite performance, but an AICc-based weighted regression showed that body mass, followed by head width and head height, were better predictors of bite force than carapace size.

1. Introduction

Performance measures are valuable in understanding trophic relationships since behavioral performance links morphology with resource use, trophic niche partitioning, competition, and ultimately fitness (Arnold, 1983; Dumont, 1999; Herrel et al., 2001a,b, 2002; Kiltie, 1982; Marshall et al., 2012; Perez-Barbera and Gordon, 1999; Wainwright and Reilly, 1994). Variation in bite force among related taxa should reflect variation in trophic challenges and in fitness (Wainwright, 1991). For example, bite force of lizards and some turtles have been correlated with both head morphology and trophic ecology (Herrel et al., 2001a,b, 2002; Marshall et al., 2012; McBrayer, 2004; Pfaller et al., 2010). Bite force in vertebrate herbivores is presumed to be high and this is supported by both morphological and performance data in some amniotes (e.g., turtles, Claude et al., 2004; lizards, Herrel et al., 1998,1999; King, 1998; turtles, Herrel et al., 2002; turtles and lizards, Herrel and O'Reilly, 2006; reptiles, birds, and mammals, Reilly et al., 2001; anomodonts, Rybczynski and Reisz, 2001; turtles, Stayton, 2006; lizards, Throckmorton, 1976). Despite the fact that numerous vertebrate groups are known to couple changes in jaw morphology with feeding performance (e.g., chondrichthyans (Huber et al., 2005, 2006; Habegger et al., 2012), ray-finned fishes (Hernandez and Motta, 1997; Hjelm et al., 2003; Svanbäck and Eklöv, 2002; Wainwright and Richard, 1995), lizards (Ballinger et al., 1977; Capel-Williams and Pratten, 1978; DeMarco et al., 1985; Herrel

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et al., 1999, 2006; Paulissen, 1987), mammals (Binder and Van Valkenburgh, 2000; Wroe et al., 2005), freshwater turtles (Herrel and O'Reilly, 2006; Herrel et al., 2002; Pfaller et al., 2010) and loggerhead turtles (*Caretta caretta*, Marshall et al., 2012)), the number of feeding performance studies of herbivores is relatively few.

Sea turtles are a model system to study feeding performance due to their long, complex life histories and ontogenetic shifts in both habitat and diet. Sea turtles exhibit interesting and often drastic ontogenetic changes in diet and feeding capability during their lifespan. As with most other sea turtles, green turtles (*Chelonia mydas*) have a complex life history that involves a juvenile oceanic phase followed by an ontogenetic shift in both habitat and diet as they approach sexual maturity. In their oceanic phase they are omnivorous (Bjorndal, 1985; Bolten, 2003; Musick and Limpus, 1997; Reich et al., 2007), consuming a range of planktonic material including crustaceans, jellyfish and ctenophores. In the eastern Pacific Ocean, green turtles make a shift to neritic habitats at ~44 cm curved carapace length (CCL; Limpus et al., 2005) or ~40 SCL (CCL to SCL conversion for eastern Pacific green turtles; Seminoff et al., 2003). Once green turtles recruit to neritic habitats they become marine algae and sea grass specialists as adults (Bjorndal, 1985, 1997; Howell, 2012; Mortimer, 1981a,b; Seminoff et al., 2002a). Recent work on the diet of green turtles in the Gulf of Mexico, using both stomach content and stable isotope analyses, showed multiple shifts in diet and habitat (Howell, 2012). In some populations green turtles also consume mangrove leaves and shoots; the importance of this dietary component is often underappreciated (Limpus, 1998; Limpus, and Limpus, 2000; Pendoley and Fitzpatrick, 1999).

Although most adult green turtle populations are reported as primarily herbivorous (Balazs, 1980; Bjorndal, 1997), mounting evidence shows that green turtles in the eastern Pacific Ocean consume a mixed diet of sea grasses, algae and often animal matter that include sponges, gelatinous zooplankton, and also mollusks and red crabs (Amoroch and Reina, 2007; Carrión-Cortez et al., 2010; Lopez-Mendilaharsu et al., 2005; Seminoff et al., 2002b). The level of carnivory in green turtles is likely a function of the habitat where the turtles forage (Amoroch and Reina, 2008). Grazing by green turtles is known to impact the benthic community upon which they feed by altering the nutrient cycling of sea grass beds (Moran and Bjorndal, 2007; Thayer et al., 1982), and the greater benthic community.

Sea turtles exhibit several interesting adaptations to trophic niches that include durophagy (loggerhead turtles), spongivory (hawksbill turtles) and herbivory (green turtles). Among reptiles, turtles have radiated into herbivorous niches more often (King, 1998; Reilly et al., 2001). Although green turtles in the eastern Pacific Ocean may consume a more mixed diet, green turtles are notable in that they are considered to be the only herbivorous sea turtle (Balazs, 1980; Bjorndal, 1985; Lemons et al., 2011; Mortimer; 1981a). The serrated morphology of the tomia and rhamphotheci of green turtles is thought to be important to their grazing behavior, but functional data are lacking to support or refute this hypothesis. There have been no studies that characterize green turtle bite performance, or the scaling relationships of bite performance to body and head size. Therefore, the objectives of this study were to 1) measure bite performance in green turtles over a portion of their ontogeny after recruiting to neritic habitats, 2) characterize how bite performance scales to body size and head morphometrics, and 3) determine which body or head morphometric best predicts bite force. We hypothesized that bite force would be less than that reported for loggerhead turtles at the same life history stage (Marshall et al., 2012) and that head width and height would be the best predictors of bite force in green turtles.

2. Methods

Bite force, mass, morphometrics, and behavioral observations were collected from seventy-three subadult and adult green turtles captured in Punta Abreojos, Baja California Sur, Mexico ($n = 64$) and the eastern coast of Japan ($n = 9$; Otsuchi, Iwate Prefecture, Japan). In Baja California Sur, working with local Mexican fishermen who participate in the sea turtle conservation efforts through Grupo Tortuguero, turtles were collected using two 100 m entanglement nets with 40 cm mesh size (stretched diagonally). Nets were checked every 90 min to reduce the risk of stress to sea turtles that were caught. Each net was positioned approximately 1/4 mile from the other, and was set over a 4-day period. Green turtles captured in Japan were part of a tag and release program in which turtles caught as by-catch in set nets near Otsuchi were turned over by local fishermen to the International Coastal Research Center, Atmosphere and Ocean Research Institute, the University of Tokyo. Turtles were retained in an outdoor flow-through saltwater holding facility from 1 week to 2 months. These turtles participated in a variety of studies before being and after being released offshore away from the fishery gear in the many bays of Iwate prefecture (e.g., Narazaki et al., 2009, 2013).

2.1. Morphometrics

Mass (kg), standard carapace length (SCL), and straight carapace width (SCW) were collected for all turtles. Digital calipers were used for collecting the greatest head width (HW), greatest head height (HH) and greatest head length (HL). Greatest head width was measured at the widest part of the skull, which also coincided with the location of the adductor mandibulae. The greatest head height was measured from the dorsal-most parietal to the ventral-most dentary near the jaw joint. The greatest head length was measured from the anterior-most tip of the snout to the posterior-most part of the supraoccipital.

2.2. Bite force and motion analysis

Forty-one subjects met the criteria of aggressive motivated biting and were included in the BF analyses (Mexico, $n = 39$; Japan, $n = 2$). Methods for maximal bite force (Max BF) collection are described in detail by Marshall et al. (2012) and elsewhere (Aguirre et al., 2002; Herrel et al., 1999, 2001a,b). In summary, bite force was measured *in vivo* using a force transducer (Kistler FSH 9203 & 9312A, Amherst, NY) fitted into an apparatus with customized sea turtle bite force plates. Once bitten upon, the upper bite plate transferred the force to the piezoelectric force transducer and signals were amplified by a handheld charge amplifier (Kistler FSH 5995, Amherst, NY) and recorded. Bite measurements always occurred at the anterior tip of the jaws (Fig. 1) and placement was rigorously controlled with stops on the bite plates.

Fig. 1. An adult green turtle biting on the bite force apparatus.