

## Differences in the Skull Morphology between Juvenile and Adult Green Turtles: Implications for the Ontogenetic Diet Shift

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**Abstract:** Skull morphology was compared between juvenile and adult green turtles by geometric morphometrics. The size of the orbit and length of the supraoccipital in relation to the centroid size were larger in juveniles than in adults, while the relative sizes of the infratemporal fossae and parietal were larger in the latter than in the former. The difference in the relative length of the supraoccipital did not predict the maintenance of functional equivalence of trophic structures, probably reflecting a functional trophic change with growth.

**Key words:** Sea turtle; *Chelonia mydas*; Ontogeny; Diet shift; Geometric morphometrics

The green turtle (*Chelonia mydas*) is a long-lived species that is globally distributed in tropical and subtropical waters (Pritchard, 1997). This species is highly migratory and undergoes ontogenetic habitat and diet shifts (Bolten, 2003). Of these, the habitat shift occurs from

pelagic juveniles to subsequent neritic life stages, and a change also occurs in feeding behavior that entails a shift from omnivorous diet of neustonic and planktonic material to predominantly herbivorous diet consisting of macroalgae, seagrass, and mangrove material (Bjorndal, 1997).

Feeding behavior may be constrained by the growth of the skull, with different growth rates in lengths, surface areas, and volumes (Emerson and Bramble, 1993). Of those various functions of the tetrapod skulls, prey acquisition and food processing are particularly important to survival (Birch, 1999). Therefore, the ontogenetic habitat and diet shift of green turtles may possibly be accompanied by changes in skull shape.

To verify this prediction, we applied geometric morphometric methods (Zelditch et al., 2004) for comparisons of the skull shape between juvenile and adult green turtles in the Western Pacific. Here we report some of the growth-related morphological differences in the skulls accordingly. We also discuss the functional implications of such ontogenetic changes briefly.

### MATERIALS AND METHODS

The skulls of 39 green turtles were examined. Of these, 18 specimens, obtained from the Ogasawara Islands, Tokyo, Japan, and deposited in the collection of the Kyoto University Museum (N. Kamezaki's private numbers, 80, 82, 91, 136, 141, 143, 150, 153, 155, 182, 199, 234, 237, 244, 247, 287, 292, and 1112) were adults with straight carapace lengths (SCLs) ranging from 85.5 to 102.5 cm (Hatase et al., 2006). The other 21 specimens (34.7–51.2 cm SCL; H. Nishizawa's private collection) were juveniles that were stranded and died on Ishigaki Island, Okinawa Prefecture, Japan. For green turtles, the Ogasawara Islands is known as a major nesting ground around Japan (Kamezaki and Matsui, 1997; Hatase et al., 2006), whereas the coastal water around Ishigaki Island is a major feeding area of juveniles (Nishizawa et al., 2010). The lack of specimens with SCLs of 52–85 cm and <35 cm

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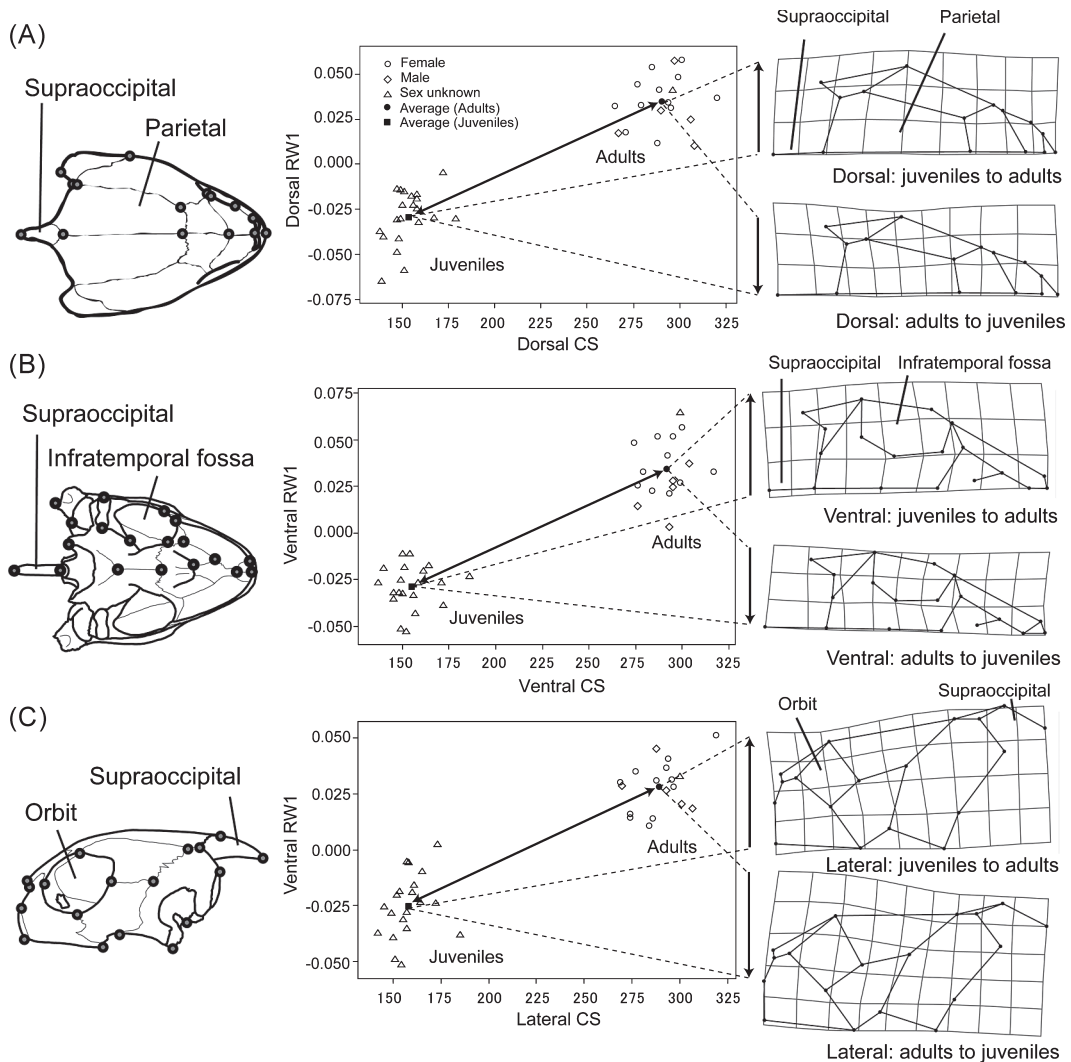


FIG. 1. Geometric morphometrics of skulls of adult and juvenile green turtles (*Chelonia mydas*). Landmarks used to describe skull shape (left), scatter plots of centroid size (CS) versus relative warp1 (RW1) (middle), and deformation between average shapes of juvenile and adult skulls (right) in dorsal (A), ventral (B), and lateral (C) views.

is likely to reflect rarity of individuals of these size ranges in both regions, presumably due to the life history pattern of habitat use in the East Asian green turtle populations.

The skulls of green turtles were photographed in lateral, dorsal, and ventral views using a Canon EOS Kiss digital X camera. Then, 15, 19, and 18 landmarks were, respectively, digitized on photographs from these

views (Fig. 1) using tpsDig (Rohlf, 2006). For one of the skulls examined, data from the lateral view were excluded from the analyses due to its apparent damage on several landmark locations defined in this view.

To understand the patterns of variation, we examined the overall shape variation by relative warp analysis using tpsRelw (Rohlf, 2007). The sex had been determined for a few speci-

mens, but in the relative warp analysis, we could not detect any differences between females and males; therefore, no inter-sexual differences were assumed throughout the analyses. Centroid size (CS), defined as the square root of the sum of the squared distances from landmarks to the centroid (Zelditch et al., 2004), was used as the standard measure of size. To understand the shape differences between adults and juveniles, partial warp scores were compared by MANOVA implemented in Minitab 14 (released in 2004 from Minitab Inc., State College, Philadelphia, Pennsylvania, USA). Deformation between the average configurations of adults from Ogasawara and juveniles from Ishigaki were illustrated using thin-plate splines in TpsSpline version 1.20 (Rohlf, 2004).

## RESULTS AND DISCUSSION

The relationships between CS and relative warp 1 (RW1) and the deformations between adult and juvenile skulls based on lateral, dorsal, and ventral views are illustrated in Fig. 1. The  $\log_{10}$  CS was strongly correlated with  $\log_{10}$  SCL, supporting the adequacy of CS as a measure of total body size. The best-fit lines indicated that the skull size relative to the body size decreased with an increase in the latter (dorsal:  $\log_{10}$  CS =  $0.81 \log_{10}$  SCL - 0.13, with  $r^2 = 0.99$ ; ventral:  $\log_{10}$  CS =  $0.81 \log_{10}$  SCL - 0.14, with  $r^2 = 0.99$ ; lateral:  $\log_{10}$  CS =  $0.77 \log_{10}$  SCL - 0.06, with  $r^2 = 0.99$ ).

The MANOVA results indicated that the skull shape was significantly different between adults and juveniles (dorsal: Wilks' lambda = 0.016,  $p = 0.035$ ; ventral: Wilks' lambda = 0.016,  $p = 0.035$ ; lateral: Wilks' lambda = 0.007,  $p = 0.002$ ). Figure 1 shows grids depicting the deformations between the average configurations of adult and juvenile skulls. The deformation grids showed that the relative size of the orbit and relative length of the supraoccipital are larger in juveniles than in adults, while the relative sizes of the infratemporal fossae and parietal are larger in adults than in juveniles.

In their general review of the consequences of scaling and allometry on the evolution and function of vertebrate skulls, Emerson and Bramble (1993) predicted that the sensory capsules and braincase should show negative allometry during growth. The observed smaller relative size of the orbit of adult green turtle skulls is consistent with this prediction. This difference may reflect the relative importance of vision during the juvenile stage.

In addition, Emerson and Bramble (1993) also predicted that the trophic structures in the facial and rostral regions should scale with isometry or positive allometry. In turtles, the infratemporal fossae and parietal, to which adductor muscles insert or attach, have clear trophic functions (Schumacher, 1973). Therefore, the relatively larger infratemporal fossae and parietal in adult green turtles also seems to be consistent with Emerson and Bramble's (1993) second prediction. Nevertheless, although the supraoccipital serves as the attachment site for the adductor muscles in turtles (Schumacher, 1973), its relative length was smaller in adults than in juveniles of the present species. The positive allometric or isometric growth of trophically important structures may be related to the requirement for maintenance of functional equivalence with increasing body size (Emerson and Bramble, 1993; Larson, 2002). In this regard, apparently negative allometry of the supraoccipital length in green turtles is puzzling. This may possibly reflect a functional trophic change with growth. In turtles, elongation of the posterior part of the skull is important for the insertion of the musculus depressor mandibulae (Claude et al., 2004), which are involved in the depression of the lower jaw and suction feeding (Aerts et al., 2001). In fact, the elongation is thought to enhance this mode of feeding in freshwater turtles (Claude et al., 2004). Thus, our results suggest that the juvenile green turtle is more adapted for suction feeding than adults, although examinations of biomechanically relevant muscles are needed to verify this explanation.

In this study, juvenile specimens were obtained

from Ishigaki Island, whereas adult specimens were from the Ogasawara Islands. Therefore, geographic variation might have actually contributed to the differences in skull shape between those juveniles and adults. However, considering that approximately 20% of the juveniles around Ishigaki Island are likely to have hatched in and migrated from the Ogasawara Islands (H. Nishizawa, in preparation), crucial effect of geographic variation on the present results is much unlikely.

Green turtles are highly migratory and undergo ontogenetic habitat and diet shifts (Bolten, 2003). After leaving the nesting beach as hatchlings, they are thought to migrate pelagically, feeding on a broad range of planktonic materials, including crustaceans, jellyfish, and ctenophores (Bjorndal, 1997). After the pelagic early juvenile stage (ca 25–35 cm SCL), they recruit to neritic habitats (Reich et al., 2007), where their dietary habit shifts from omnivorous, consuming neustonic material, to predominantly herbivorous, feeding on macroalgae, seagrass, and mangrove material (Bjorndal, 1997). Most specimens in our study had SCLs >35 cm and thus were likely to have settled in a neritic habitat already. Based on the stable isotope analysis, Arthur et al. (2008) demonstrated that pelagic juvenile green turtles do not exhibit a well-defined dietary shift on recruitment, but instead undergo a gradual transitional stage thereafter. Their observations are apparently consistent with the implication from our study that the juvenile green turtles retain features adaptive to suction feeding for a while even after settling in a neritic habitat.

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