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## Effects of Emergence on Hatchling Phenotypes in Loggerhead Sea Turtles (*Caretta caretta*) of the North Pacific

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**ABSTRACT.**—Sea Turtles lay eggs at relatively deep depths on beaches. Although nest emergence is known to be costly for hatchlings, little is known about the positive aspects of emergence. In this study, we investigated the effects of emergence on hatchling phenotypes of Loggerhead Sea Turtles (*Caretta caretta*) in the North Pacific population. We placed the Loggerhead eggs in an incubator (incubator group) and relocated some eggs to a sand tank after the pip was confirmed (emergence group). Immediately after emergence was confirmed in the emergence group, we compared the morphology, terrestrial locomotor performance, and swimming performance of the two groups at the same time. Results showed that hatchlings in the emergence group were smaller than those in the incubator group. Notably, most members of the emergence group were able to completely traverse a 3-m course within 3 min, whereas no members of the incubator group could traverse the course. The emergence group had greater swimming performance than the incubator group. Taken together, these results suggest that emergence may have a positive effect on locomotor performance. Sea turtle nests are occasionally relocated for conservation purposes, and our results suggest that such egg management practices can alter hatchling phenotypes.

Aquatic turtles lay eggs on land and nest depth varies by species. For example, Sea Turtles lay eggs at depths of several tens of centimeters on beaches (Hays et al., 1993; Matsuzawa et al., 1995). Sufficient nest depth is beneficial for hatching success because it provides a stable thermal environment (Maloney et al., 1990; Ischer et al., 2009; Read et al., 2012), sufficient hydric conditions (Foley et al., 2000), and a reduced risk of egg predation (Leighton et al., 2009). In terms of emergence from the nest by hatchlings, however, large nest depth could be costly for hatchlings because it takes 1–7 d to dig through sand toward the surface (Lohmann et al., 1997) with intense activity as evidenced by increases in plasma lactate concentrations (Hamann et al., 2007).

The act of emerging from nests may have a positive effect on hatchling survival probability. Rusli et al. (2015) compared the locomotor performance of Green Sea Turtle (*Chelonia mydas*) hatchlings from in situ nests, hatchery nests, and Styrofoam boxes and found that hatchlings from the Styrofoam boxes showed lower locomotor performance than those from other treatments. Given that hatchlings hatched in Styrofoam boxes did not emerge from the nest (i.e., they did not dig through sand toward the surface), we hypothesized that the experience of emergence is an important factor in determining hatchling locomotor performance. In this study, we investigated the effects of nest emergence on Loggerhead Sea Turtle (*Caretta caretta*) hatchling phenotypes. We placed loggerhead eggs in an incubator and then relocated some of the eggs to a sand tank after confirming the pipping of the eggshell. We then compared morphology, terrestrial locomotor performance, and swimming performance of hatchlings that emerged from the incubator (incubator group) with those that emerged from the sand tank (emergence group).

### MATERIALS AND METHODS

From 8 May to 17 August 2017 and 19 July to 2 August 2021, we patrolled the Nii and Nino beaches located on the west and east sides of the Niyodo River mouth (33°28'N, 133°30'E, datum:

WGS84), Kochi Prefecture, Japan, early in the morning daily to count emergence tracks and nests of Loggerhead Sea Turtles. Four clutches were collected on 30 June 2017 (Clutch 1), 24 July 2017 (Clutch 2), 19 July 2021 (Clutch 3), and 2 August 2021 (Clutch 4). We then transported 30 eggs from Clutch 1 and 2, 113 eggs from Clutch 3, and 60 eggs from Clutch 4 by car to a laboratory approximately 7 km from the beach. We relocated the remaining eggs in each clutch to an open-air hatchery on the same beach, where there was no threat of flooding.

We placed eggs from each clutch in a plastic case and incubated them in an incubator (FR-4B, Isuzu Seisakusho) at a constant temperature of 29.5°C to ensure successful egg hatching. The time between egg collection and placement in the incubator was 60 min. We prepared sand from which the eggs were collected and covered the bottom of each plastic case with this sand. We placed wet *Sphagnum* moss (Besgrow) on the eggs to prevent them from drying out and regularly sprayed the sphagnum moss with water. We positioned a temperature data logger (TidbiT v2: Onset) in the plastic case and monitored the incubation temperature every 30 min.

To collect emerged hatchlings in the laboratory, we created a laboratory emergence system (Fig. 1). We prepared a sand tank (40 × 30 × 55 cm) with holes (6 mm in diameter) drilled along the side, 13 cm from the bottom. This tank was placed in a plastic container (85 cm × 55 cm × 20 cm) filled with water to a depth of 15 cm. A thermostat sensor (ET-600X, Kotobuki Kogei) was placed at the center of each clutch, and the water temperature was maintained using a Micro Power Heater (Kotobuki Kogei). We maintained the temperature in the center of the clutch at approximately 29.5°C by introducing water to the sand through the holes. We set a basking lamp, Intense Basking Spot (GEX), above the sand surface in the sand tank and turned the light on from 0700 to 1900 h to simulate approximate daily thermal changes in a natural nest (Fig. 2).

During the incubation period, the incubator was checked daily in the morning and at night. After observing pipping (only head emerged) for at least one egg, we relocated some unpipped eggs that could be identified visually as alive to the sand tank (Clutch 1:  $n = 13$ , Clutch 2:  $n = 14$ , Clutch 3:  $n = 30$ , Clutch 4:  $n = 28$ ). The upper and lower depths of the clutches that were

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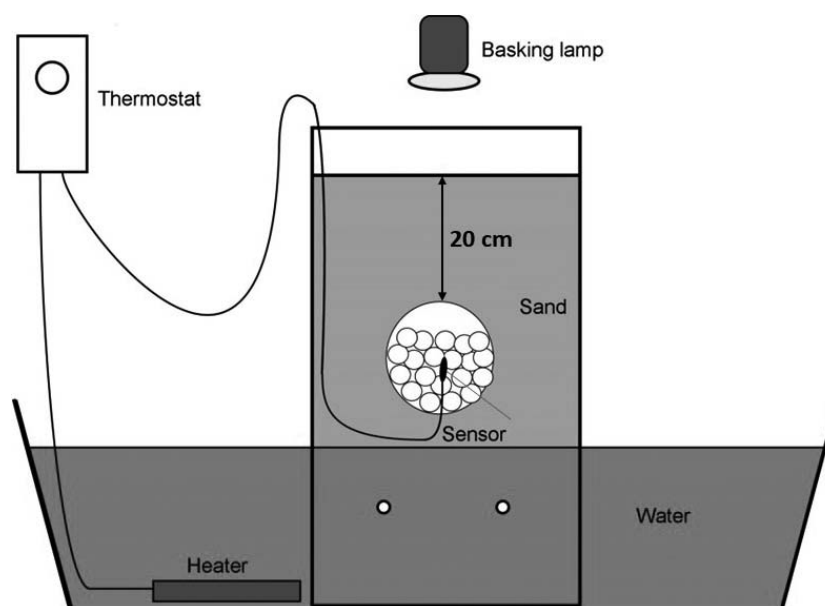


FIG. 1. Illustration of the laboratory system used to simulate natural emergence.

relocated to the sand tank were 20 and 30 cm, respectively. Temperature was measured every 30 min by using a temperature data logger (TidbiT v2) positioned at the center of the clutch. Remaining eggs in the plastic container were allowed to continue incubation in the incubator and were checked daily so that we could observe hatching (a head and a flipper emerging from the shell; Godfrey and Mrosovsky, 1997) and determine the hatching date in the incubator group. After hatching was confirmed, we kept hatchlings in the plastic case in the incubator and did not open it to avoid the potential effect of light until the emergence of hatchlings in the emergence group. The sand tank was also monitored at night. Immediately after turtle emergence, we measured hatchlings, including straight carapace length (SCL; mm), straight carapace width (SCW; mm), and body mass (BM; g), using a Vernier caliper and balance. All hatchlings in the emergence group of each clutch emerged simultaneously. We also measured hatchlings in the incubator group immediately after measuring those of the emergence group.

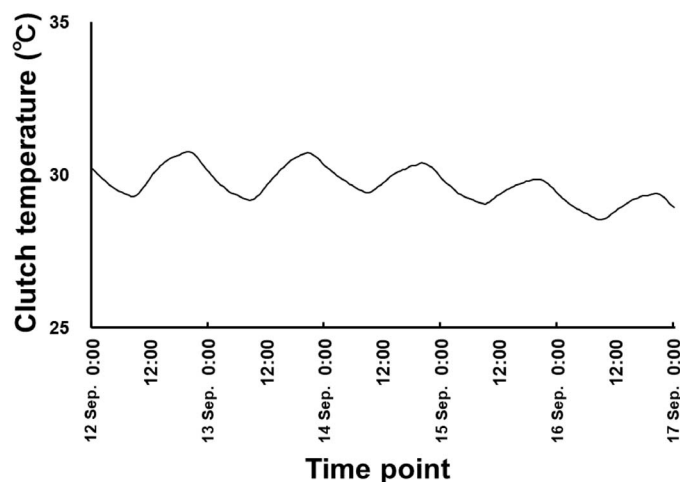


FIG. 2. Typical example of a thermal profile of a clutch in the laboratory emergence system.

We selected four hatchlings that were close to the average size of those in the incubator and emergence groups. As soon as we took measurements, we observed whether hatchlings could completely traverse a 3-m course within 3 min and quantified their crawling speed, as described in previous studies (Kobayashi et al., 2017; Saito et al., 2019). After quantifying the crawling speed, we tested the self-righting response of the hatchlings, as described in previous studies (Kobayashi et al., 2017; Saito et al., 2019). Self-righting responses were scored using the method described by Booth et al. (2013). We quantified the time (s) at which hatchlings successfully self-righted.

As soon as the terrestrial locomotor performance test was completed, we measured the swimming performance of hatchlings at 0, 12, 24, 48, and 72 h after emergence, as described by Booth et al. (2013), Kobayashi et al. (2018), and Fujimoto et al. (2020). Each hatchling was fitted with a harness with a monofilament polyethylene string connected to a force transducer and data acquisition system (MLTFO 50/ST, Pod Expander FE305, and Power Lab 8/35; ADInstruments). Hatchlings swam individually in a plastic tank (70 × 40 × 30 cm) filled with seawater at a mean temperature of 28°C in a dark room. We painted all sides of the tank black, except for one side, where a light (fluorescent lamp, 27 W, approximately 2,400–2,600 lx) guided the hatchlings to swim in one direction. As defined by Wyneken (1997), frenzy swimming consists of powerstroking with dogpaddling while breathing, which can be identified by using a typical force trace (Burgess et al., 2006). Consistent a definition from Pereira et al. (2011), we defined powerstroking of loggerhead hatchlings as a swimming movement at least 5 sec in length with a continuous mean thrust (mN) of at least 20, and we considered other swimming movements to be dogpaddling, based on swimming variables of loggerhead hatchlings. We calculated the mean thrust (mN), maximum thrust (mN), number of powerstrokes (strokes/min), and time spent powerstroking (%) by counting all powerstrokes at 1-min intervals from 0–1, 5–6, and 9–10 min in a 10-min recording period. Recorded values were averaged to obtain a single value for each individual.

TABLE 1. Information regarding experimental clutches and hatchlings<sup>a</sup>.

	Clutch 1		Clutch 2		Clutch 3		Clutch 4	
	Emergence group	Incubator group	Emergence group	Incubator group	Emergence group	Incubator group	Emergence group	Incubator group
Incubation period (d)	-	53	-	48	-	51	-	51
Mean incubation temperature (°C)	-	29.1	-	30.1	-	29.1	-	30.3
Number of eggs	13	17	14	16	30	83	30	30
Number of hatchlings	12	12	14	14	30	57	27	20
Digging period (d)	10	-	10	-	9	-	10	-
Mean temperature from hatch to emergence (°C)	30.4	29.9	29.0	30.8	30.1	31.5	30.0	29.6
Straight carapace length (mm, mean ± SD)								
All hatchlings	41.2 ± 1.4	42.7 ± 0.9	41.3 ± 1.4	42.2 ± 1.6	43.9 ± 0.8	44.7 ± 1.4	43.5 ± 0.8	44.5 ± 1.0
Hatchlings used for locomotor performance	41.9 ± 1.4	43.0 ± 0.9	41.6 ± 0.6	42.1 ± 1.0	44.0 ± 0.7	45.1 ± 0.6	43.5 ± 0.3	44.4 ± 0.3
Straight carapace width (mm, mean ± SD)								
All hatchlings	34.4 ± 1.1	35.9 ± 0.9	34.8 ± 1.8	35.9 ± 1.1	35.3 ± 0.8	36.1 ± 1.1	35.9 ± 0.6	36.8 ± 0.7
Hatchlings used for locomotor performance	34.9 ± 1.0	35.6 ± 0.7	35.3 ± 0.5	35.6 ± 0.5	35.7 ± 0.7	36.6 ± 0.5	35.8 ± 0.4	37.0 ± 0.2
Body mass (g, mean ± SD)								
All hatchlings	14.2 ± 0.8	15.4 ± 0.8	15.4 ± 1.1	15.7 ± 1.0	18.2 ± 0.6	18.2 ± 0.7	17.7 ± 0.6	17.9 ± 0.7
Hatchlings used for locomotor performance	14.6 ± 0.6	15.5 ± 0.3	15.8 ± 0.6	15.6 ± 1.0	18.4 ± 0.2	18.7 ± 0.2	17.7 ± 0.3	18.0 ± 0.4

<sup>a</sup> We placed a clutch of eggs in an incubator (incubator group) and relocated some eggs to a sand tank after the pip was confirmed (emergence group). Immediately after emergence was confirmed in the emergence group, we measured the morphology and locomotor performances of the two groups at the same time.

A two-way analysis of variance, with treatment group and clutch as fixed factors, was used to test for separate effects of emergence and clutch on SCL, SCW, and BM. Considering the potential effect of body size on performance, a two-way analysis of covariance, with treatment group and clutch as fixed factors and SCL as covariate, was used to assess the separate effects of emergence and clutch on self-righting score, self-righting time, and swimming performance. When a significant interaction was confirmed, a simple main effect test was used to confirm which clutch showed a significant difference between groups. Statistical analyses were performed using BellCurve Excel Statistics for Windows (SSRI). Statistical significance was set at  $P < 0.05$ .

TABLE 2. A summary of the  $P$  values<sup>a</sup> from two-way analysis of variance, with group (emergence and incubator) and clutch as fixed factors for straight carapace length, straight carapace width, and body mass and 2-way analysis of covariance for self-righting score and self-righting time.

Straight carapace length	
Group effect	<b>&lt;0.01</b>
Clutch effect	<b>&lt;0.01</b>
Interaction	0.69
Straight carapace width	
Group effect	<b>&lt;0.01</b>
Clutch effect	<b>&lt;0.01</b>
Interaction	0.53
Body mass	
Group effect	<b>&lt;0.01</b>
Clutch effect	<b>&lt;0.01</b>
Interaction	<b>&lt;0.01</b>
Self-righting score	
Group effect	0.61
Clutch effect	0.46
Interaction	0.38
Self-righting time	
Group effect	0.32
Clutch effect	0.06
Interaction	<b>&lt;0.01</b>

<sup>a</sup> Bold indicates statistical significance ( $P < 0.05$ ).

## RESULTS

Information on experimental clutches and hatchlings is presented in Table 1. In all clutches, the duration between pipping and emergence from the sand tank was 9–10 d. The emergence group had significantly smaller SCL and SCW values than the incubator group, with a significant clutch effect (Table 2). For BM, a significant interaction between group and clutch effects was confirmed (Table 2), and a simple main effect test showed that only Clutch 1 showed a significant difference, with a lighter BM in the emergence group than that in the incubator group, indicating that emergence from the sand tank resulted in lower body mass.

Notably, 14 of 16 hatchlings in the emergence group completely traversed the 3-m course within 3 min. However, none of the hatchlings in the incubator group were able to do so. Mean crawling speed in the emergence group was 7.0 cm/sec. No group or clutch effects were observed for self-righting score and self-righting time (Table 2). For self-righting time, a significant interaction between group and clutch effects was confirmed (Table 2), and a simple main effect test showed that Clutch 2 and 3 showed significant differences, with inconsistent tendencies between the clutches. Therefore, emergence from the sand tank was less effective on self-righting time than the other treatment.

A summary of  $P$  values for the four measures of swimming performance at each measurement point for each group is shown in Table 3. The four swimming performance measures decreased toward 72 h (Fig. 3A–D). At the beginning of the swimming performance test, no differences were observed between groups in any of the four categories. However, the four measurements in the emergence group were higher than those in the incubator group at 12 h and 24 h. For the maximum thrust at 24 h, a significant interaction between group and clutch effect was confirmed (Table 3), and a simple main effect test showed that only Clutch 4 showed a significant difference, with a higher maximum thrust in the emergence group than that in the

TABLE 3. A summary of the  $P$  values<sup>a</sup> from two-way analysis of covariance with group and clutch as fixed factors and straight carapace length as the covariate, for the four measures of swimming performance at each measurement point.

	Time since emergence				
	0 h	12 h	24 h	48 h	72 h
Mean thrust					
Group effect	0.11	<b>0.04</b>	< <b>0.01</b>	< <b>0.01</b>	<b>0.01</b>
Clutch effect	0.48	0.06	0.53	0.12	0.53
Interaction	0.63	0.96	0.19	0.08	0.18
Maximum thrust					
Group effect	0.61	< <b>0.01</b>	< <b>0.01</b>	< <b>0.01</b>	<b>0.03</b>
Clutch effect	<b>0.03</b>	< <b>0.01</b>	0.18	<b>0.02</b>	0.90
Interaction	0.47	0.27	<b>0.04</b>	0.08	0.72
Number of powerstrokes					
Group effect	0.21	<b>0.02</b>	< <b>0.01</b>	0.08	0.12
Clutch effect	< <b>0.01</b>	<b>0.01</b>	< <b>0.01</b>	< <b>0.01</b>	< <b>0.01</b>
Interaction	0.12	0.75	0.74	0.55	0.32
Time spent powerstroking					
Group effect	0.09	<b>0.03</b>	<b>0.02</b>	0.07	0.07
Clutch effect	0.10	< <b>0.01</b>	0.28	<b>0.02</b>	< <b>0.01</b>
Interaction	0.10	0.93	0.70	0.25	0.05

<sup>a</sup> Bold indicates statistical significance ( $P < 0.05$ ).

incubator group. The significant differences in mean and maximum thrust between each group remained toward the end of the measurement period (Fig. 3A,B). Partial clutch effects were confirmed for the four swimming performance measures.

#### DISCUSSION

In this study, we used a laboratory emergence system to determine whether emergence affects Loggerhead Sea Turtle hatchling phenotype. Results showed that nest emergence has positive effects on crawling and swimming performance, with less effects on BM and self-righting ability (Fig. 4). We have

interpreted our results cautiously for several reasons. First, hatchling phenotypes were observed in only four clutches, and the small sample size may have caused statistical errors. However, we believe that our results are important for understanding the effects of emergence on hatchling phenotypes of Loggerhead Sea Turtles. We were also cautious about interpreting our results because we measured hatchling phenotypes 9–10 d after observing the pip. Because sea turtle hatchlings generally emerge from their nest after 1–7 d of hatching (Lohmann et al., 1997), hatchlings in this study may have been under unusual physical and physiological conditions. A previous study showed a negative correlation between the

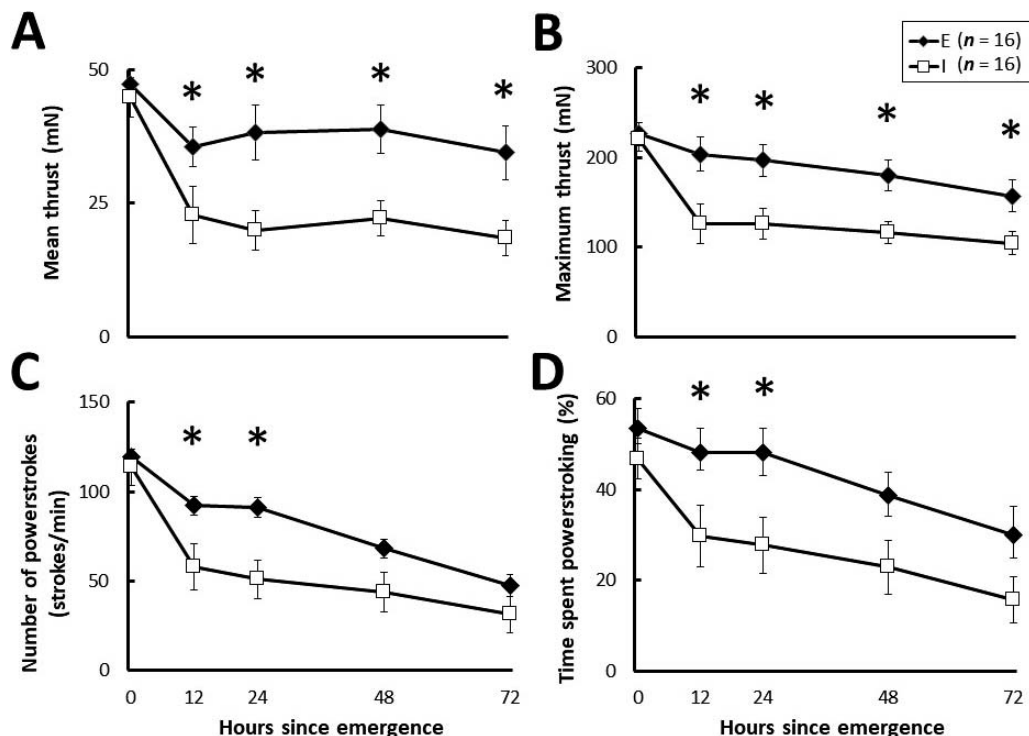


FIG. 3. Swimming performance of Loggerhead Sea Turtle hatchlings after 72 h in emergence and incubator groups. Results are expressed as mean  $\pm$  SE, and asterisks indicate significant group effects on swimming performance between the emergence (E) and incubator (I) groups at each measurement point. (A) Mean thrust. (B) Maximum thrust. (C) Number of powerstrokes. (D) Time spent powerstroking.

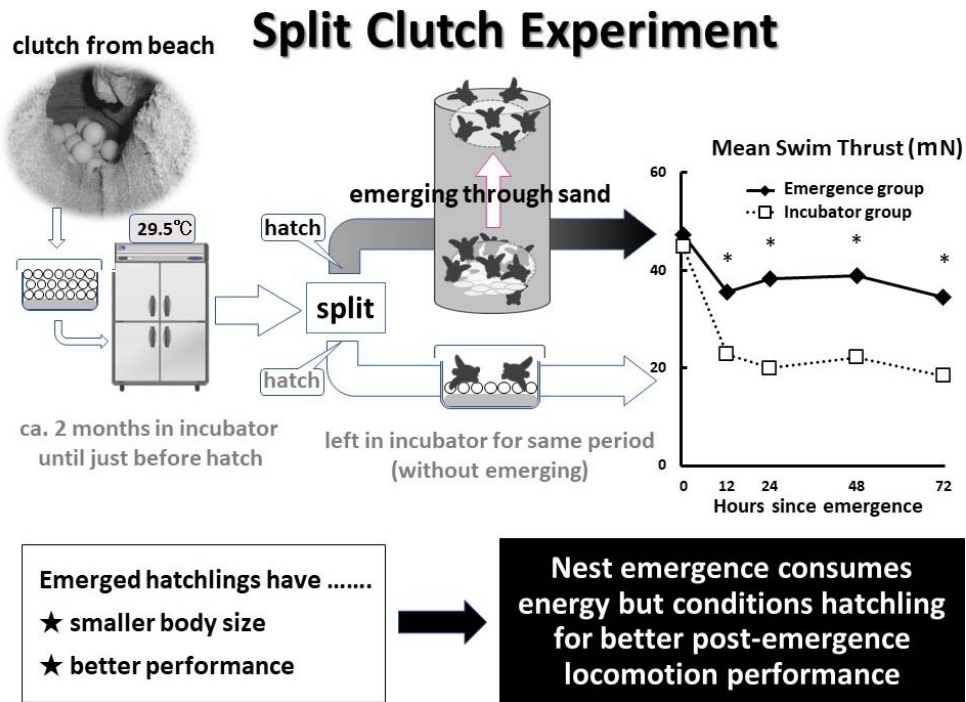


FIG. 4. Graphical abstract of the experimental design and results of this study.

number of hatchlings and the duration of digging in green turtles (Rusli et al., 2016), indicating that the longer digging duration in the emergence group was likely due to the smaller number of hatchlings that emerged ( $n = 12\text{--}30$ ) compared to the number in a natural nest ( $n = 100$ ). The use of an appropriate number of buried eggs should be studied further to elucidate the effects of emergence on hatchling phenotypes in natural environments.

Given that both the incubator and emergence groups were incubated under the same thermal conditions before pipping, smaller hatchling size in the emergence group was likely due to emergence. This result likely occurred because the emergence group had to consume energy to emerge from the sand tank, whereas the incubator group did not and most likely used that energy to increase their carapace size.

Hatchlings in the emergence group exhibited better crawling performance than those in the incubator group. Rusli et al. (2015) reported poor crawling performance in Green Sea Turtle hatchlings that had been incubated in Styrofoam boxes compared with that of turtles that emerged from in situ or beach hatchery nests. Taken together, the positive effect of digging into the sand surface on hatchling crawling performance was consistent between species and can be explained as follows. First, hatchlings in the emergence group may have increased limb muscle growth after locomotion, including digging into the sand surface, whereas hatchlings in the incubator group were assumed to be inactive in the dark and did not experience such growth. Second, Green Sea Turtle hatchlings have been reported to emerge toward the sand surface, coinciding with an increase in plasma corticosterone concentration (Hamann et al., 2007). Corticosterone is related to locomotor activity and energy metabolism (Landys et al., 2006), suggesting that such physiological responses stimulated higher locomotor activity in hatchlings in the emergence group in our study.

There was no difference in swimming performance between the groups at the beginning of the test. Rusli et al. (2015) also found that incubation type did not affect the initial swimming performance of Green Sea Turtle hatchlings. Therefore, the initiation of swimming activity in the frenzy state was not affected by emergence experience in either Loggerhead or Green Sea Turtles. Swimming performance from 12–72 h in the emergence group was higher than that in the incubator group, possibly due to a similar reason as that discussed above for differences in crawling performance. Our results highlight the importance of emergence in hatchling locomotor performance during early life stages.

For conservation purposes, sea turtle nests are sometimes relocated to protect them from threats, such as flooding, erosion, poaching, and predation (Boulon, 1999; Mortimer, 1999; Witherington and Witherington, 2015; Sari and Kaska, 2017; Martins et al., 2021). At our study area, most Loggerhead nests were flooded by storms or high tides unless they were relocated. Given that climate change is a global phenomenon that contributes to increased nest flooding, the number of nesting areas in which eggs need to be relocated to unaffected areas, such as beach hatcheries, will continue to increase. However, in some areas, it is difficult to establish beach hatcheries, and placing eggs in a container for incubation is the only option. Based on our results, hatchlings that hatch on natural beaches and beach hatcheries are likely to have higher terrestrial locomotor and swimming performance from 12–72 h after they initiate swimming than hatchlings hatched from containers. The period of 12–72 h is critical for survival against predators (Gyuris, 1994), indicating that hatchlings hatched in a container may be more vulnerable. In contrast, hatchlings incubated in a container may have higher survival rates because hatchlings with larger carapaces can avoid gape-limited predators (Gyuris, 2000) and hatchlings in the incubator group (no emergence) were relatively large in our study. It remains unclear whether locomotor performance or hatchling size is more important for

survival, and answering this question is necessary to determine appropriate egg management practices for sea turtles when relocation is necessary. Our results indicate that egg management practices can alter hatchling phenotypes.

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