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# Factors Affecting the Fitness Rate of Sea Turtle Hatchlings: Systematic Literature Review

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## Abstract
*The fitness rate is an important indicator for improving survival in the early stages of hatchling's life. This study aimed to determine the fitness rate of sea turtles based on the morphological profile and locomotor performance which includes crawling, self-righting, and swimming performance. The research method used is systematic literature reviews. We found 24 articles published during 2010-2020, which were accessed through Google Scholar, Science Direct, and Springer Link. The results showed that the factors that influence the morphological profile and locomotor performance are sun exposure (12.5%), nest temperature (33.3%); incubation technique (8.3%), sand grain size (8.3%). In addition, the morphological profile and locomotor performance were affected by phenotypic variations of 8.3% and 12.5%; parental origin and nest environment of 8.3% and 4.2%. Factors that only affect locomotor performances are release time and nest digging (4.2%), emergence order, sand temperature, emergence time, nest distance to the sea (4.2%), water temperature (8.3%). Nests that are slightly exposed to sunlight, optimal temperature (30 °C), use coastal hatchery incubation techniques, have a fine sand size (0.5-1 mm), and have phenotypic variations in the form of modal scute patterns produce hatchlings with carapace sizes bigger and greater locomotor performance. Furthermore, higher locomotor performance is obtained if the hatchlings are released immediately after emerge and immediately dug, first emerge hatchlings, have a sand temperature (<36 °C), time to leave the nest before 08.00, nest closer to the sea, warm water temperature (30 °C), and has good environmental conditions.*

Keywords: *Fitness Rate, Morphological Profile, Locomotor Performance, Sea Turtle Hatchlings, Systematic Literature Review*

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## INTRODUCTION

The turtle population continues to decline due to various threats both on land and at sea, such as heat stress, predation, coastal debris, and human exploitation (Triessnig et al., 2012). Leatherback Turtles declined by 95% in the last 30 years in the Indo-Pacific region (Tapilatu et al., 2017). Female Green Turtles and Hawksbill Turtle populations are estimated to have decreased by 48–67% and >80%, respectively, over the last three generations (c. 130 years) (Broderick et al., 2006).The strategies commonly used in turtle conservation are translocation of eggs to hatcheries, which are widely considered useful in protecting eggs from threats such as poachers, natural predators, and environmental stresses (Mortimer, 1999). Even though protected hatcheries as a conservation method is still a matter of debate because it has the potential to get undesirable results such as adversely affecting embryonic development (Patino-Martinez, Marco, Quiñones, Abella, et al., 2012), decreased hatchling fitness (Patino-Martinez, Marco, Quiñones, & Hawkes, 2012), and improper release method of hatchlings will result in a high mortality rate (Mortimer, 1999). As a result, moving eggs to hatcheries is considered a last option when in situ conservation is not the best option (International Union for Conservation of Nature (IUCN), n.d.). However, this does not mean that hatcheries can not positively contribute because its effectiveness depends on management methods (Tisdell & Wilson, 2005).

Greater quality of hatchlings will increase the survival rate by minimizing contact with predators (Gyuris, 1994). Fitness rate is used as an indicator of the quality of hatchlings indicated by locomotor performance which is influenced by hatchling's size, since larger hatchlings have more extended flipper and thus more significant power stroke (Janzen, 1993; Janzen et al., 2007). In addition, larger hatchlings are less susceptible to predators, so that in many natural situations, the larger hatchlings have an advantage (Gyuris, 1994).

Many researchers critically evaluate hatchery procedures. Therefore, we conducted a comprehensive review of the various factors that can affect the fitness level of hatchlings. Furthermore, the study focused on (i) morphological profile and (ii) locomotor performance which includes crawling performance, self-righting performance, and swimming performance. This information is essential for successful hatchery management worldwide.

## METHODOLOGY

### 1.1. Literature search

This study used a systematic literature review research design following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyzes) statement as a guide (Moher et al., 2009). A systematic literature review is a review of clearly formulated questions using systematic and explicit methods to identify, select, critically assess relevant research, and collect and analyze data from the studies included in the review. Statistical methods (meta-analysis) allow it to be used to analyze and summarize the results of the included studies. Meta-analysis refers to the use of statistical techniques in a systematic review to integrate the results of included studies. This method was chosen based on existing literature and the latest recommendations in the marine sector (Liquete et al., 2013; O'Leary et al., 2015).

The literature search was conducted by accessing (

Table 1) on Google Scholar (https://scholar.google.com/), Science Direct (https://www.sciencedirect.com/), and Springer Link (https://link.springer.com/) as the top-ranked peer-reviewed research journal articles database and search engine (Aithal & Aithal, 2016). Reviewed journal articles published in the years 2010-2020 with the following keyword combinations in the title, abstract, or text content used in the search: *"fitness rate," "morphology", "locomotion performance", "crawling performance", "self-righting performance", "swimming performance", "sea turtle hatchlings".* We also searched using the bahasa Indonesia equivalent. Next, the keywords were entered into a search engine.

Table 1. Main characteristics of Google Scholar, Science Direct, and Springer Link (Gusenbauer & Haddaway, 2020)

| Characteristics | Google Scholar | Science Direct | Springer Link |
|---|---|---|---|
| Search Settings | Full index | Full index | Full index |
| Subject | Multidisciplinary | Multidisciplinary | Multidisciplinary |
| Size | 389,000,000+ | 15,000,000+ | 12,731,539 |
| Covered items | Preprint articles (eg from arXiv [physics], journal articles, books, patents, conference proceedings, theses, presentations, web-pages, non-peer-reviewed sources | Peer-reviewed journal, book, handbook, reference works, and book series | Articles, chapters, conference articles, reference work entries, books, protocols, conference proceedings, book series, journals, reference works, video segments, and videos |
| Open Access Content | Mixed | Proprietary | Proprietary |
| Full Text | Yes | No | No |
| Search Option | | | |

The literature search resulted in 1,816 articles and 921 articles after duplicates were removed (Figure 1). Specifically for literature searches on Google Scholar, we limit the first 1000 publications as ordered by relevance, considering that Google Scholar will not display more than the first 1000 publications in the search. Grey literature such as non-English and non-bahasa Indonesia websites, books, and publications were excluded from the review if found. Complete list of identified publications maintained with open-source reference management software Mendeley (https://www.mendeley.com/).

### 1.2. Selection Criteria

The selection of articles went through two stages with the main selection criteria, namely articles discussing factors that influence the morphology and locomotor performance of sea turtle hatchlings. In the first stage, there were 921 articles based on titles, keywords, and abstracts. A total of 872 articles were eliminated at this stage (Figure 1) according to the exclusion criteria in

Table 2. The remaining 49 abstract articles contain information on factors that influence the morphology and locomotor performance of sea turtle hatchlings. As a general rule, if

the abstract is unclear or there is uncertainty surrounding the inclusion, then the abstract is submitted for the next screening stage.

The next stage is full-text screening of 49 articles selected from abstract screening. The exclusion criteria here are the same as the abstract screening stage listed above, with the additional exclusion factor of the grey literature and books further found (

Table 2). Books and the 'grey literature' were excluded because new, credible and innovative solutions were expected to be represented in recent peer-reviewed research articles. 'Grey literature' is defined in this study as any document or website that has not been expert reviewed or did not come from a reputable company or organization. A total of 25 articles were excluded at the full-text screening stage. After this final screening stage, a total of 24 articles were entered into the final data collection and quantitative analysis (Figure 1). All publications included in the final qualitative or quantitative synthesis are listed in the S1 Appendix and SINTA.

Table 2. Articles exclusion criteria at abstract and full-text screening stages with number excluded for each reason shown

| Exclusion Criteria | Abstract Screening | Full Text Screening |
|---|---|---|
| The article focuses on turtles and reptiles, not sea turtles | 63 | 1 |
| The article does not discuss the factors that influence the morphology of sea turtle hatchlings | 98 | 9 |
| The article does not discuss the factors that affect the locomotor performance of sea turtle hatchlings | 179 | 11 |
| This article focuses on the metabolism of sea turtles | 54 | 4 |
| Book or grey literature publication | 478 | 0 |

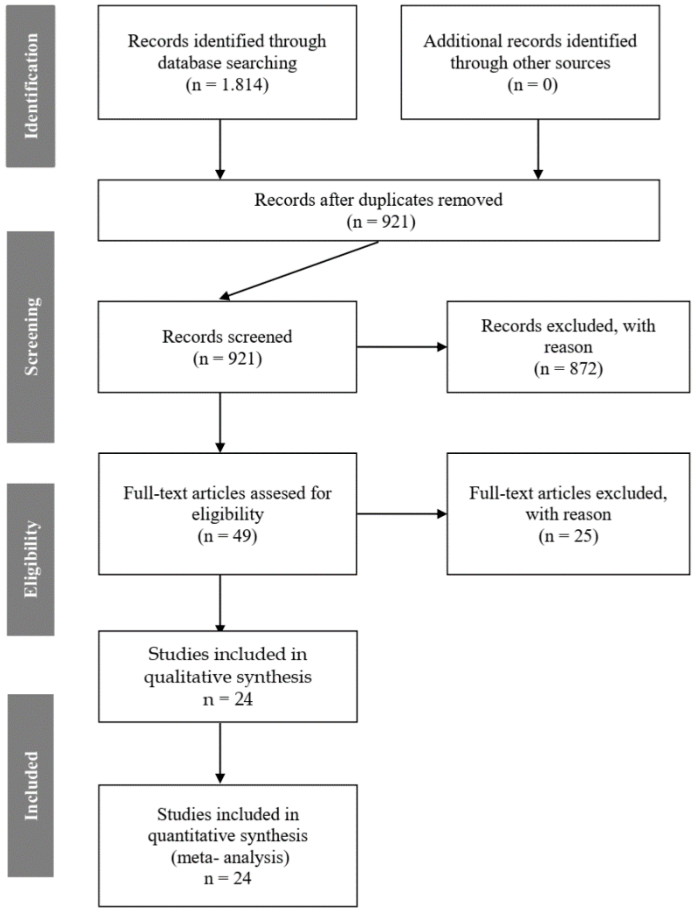


**Figure 1.** Flow chart of the review article selection process and the number of articles excluded at each stage. This follows the PRISMA statement guidelines on reporting review process [10]

### 1.3. Data Extraction

After the screening process, the final total of 24 remaining articles will be analyzed and extracted. The data taken from the article focused on the factors that influence fitness rate, including morphology and locomotor performance of sea turtle hatchlings. Specifically, the following information was taken from each article: (1) species; (2) study site; (3) years; (4) factors were observed in the literature; (5) hatchling morphology; (6) locomotor performance; (7) references. The information is entered into a table so that the extraction results are easy to read and observe. Furthermore, the extraction results are converted to percent, displayed on a graphic image Figure 2.

## RESULT AND DISCUSSION

### 1. Result

The literature search resulted in 24 research articles published between 2010-2020 (Figure 2a). These articles are related to various factors that influence the fitness rate of sea turtle hatchlings based on their morphological profile and locomotor performance. The influence of factors on the morphological profile seen from the morphometric measurements and locomotor performance of the hatchlings is indicated by crawling performance, self-righting performance, and swimming performance.

The research articles reviewed (Figure 2b) focused on the loggerhead turtles (n = 11; 45.8%), olive ridley turtle (n = 5; 20.8%), green turtles (n = 5; 20.8%), leatherback turtles (n = 3; 12.5%), and flatback turtles (n = 2; 8.3%). The studies in the literature (Figure 2c) were predominantly conducted in Australia (n = 8; 33.3%); Japan and Malaysia (n = 3; 12.5%); Costa Rica, Indonesia, USA, and Mexcico (n = 2; 8,3); Trinidad and Tobago and South Africa (n = 1; 4.2%). Based on the literature (Figure 2d) external factors that affect the morphological profile consist of sun exposure (n = 3; 12.5%); nest temperature (n = 8; 33.3%); incubation technique (n = 2; 8.3%); sand grain size (n = 3; 12.5%); phenotypic variation (n = 3; 12.5%); parental origin and nest environment (n = 2; 8.3%). The literature that focuses on the factors that influence locomotor performance, consist of sun exposure (n = 3; 12.5%); nest temperature (n = 8; 33.3%); incubation technique (n = 2; 8.3%); sand grain size (n = 2; 8.3%); phenotypic variation (n = 3; 12.5%); release time and nest digging (n = 1; 4.2%); emergence order, sand temperature, emergence time, distance of nest to sea (n = 1; 4.2%); water temperature (n = 1; 4.2%), parental origin and nest environment (n = 1; 4.2%). Summary of all studies on factors affecting the fitness rate of sea turtle hatchlings are shown in Table 3.

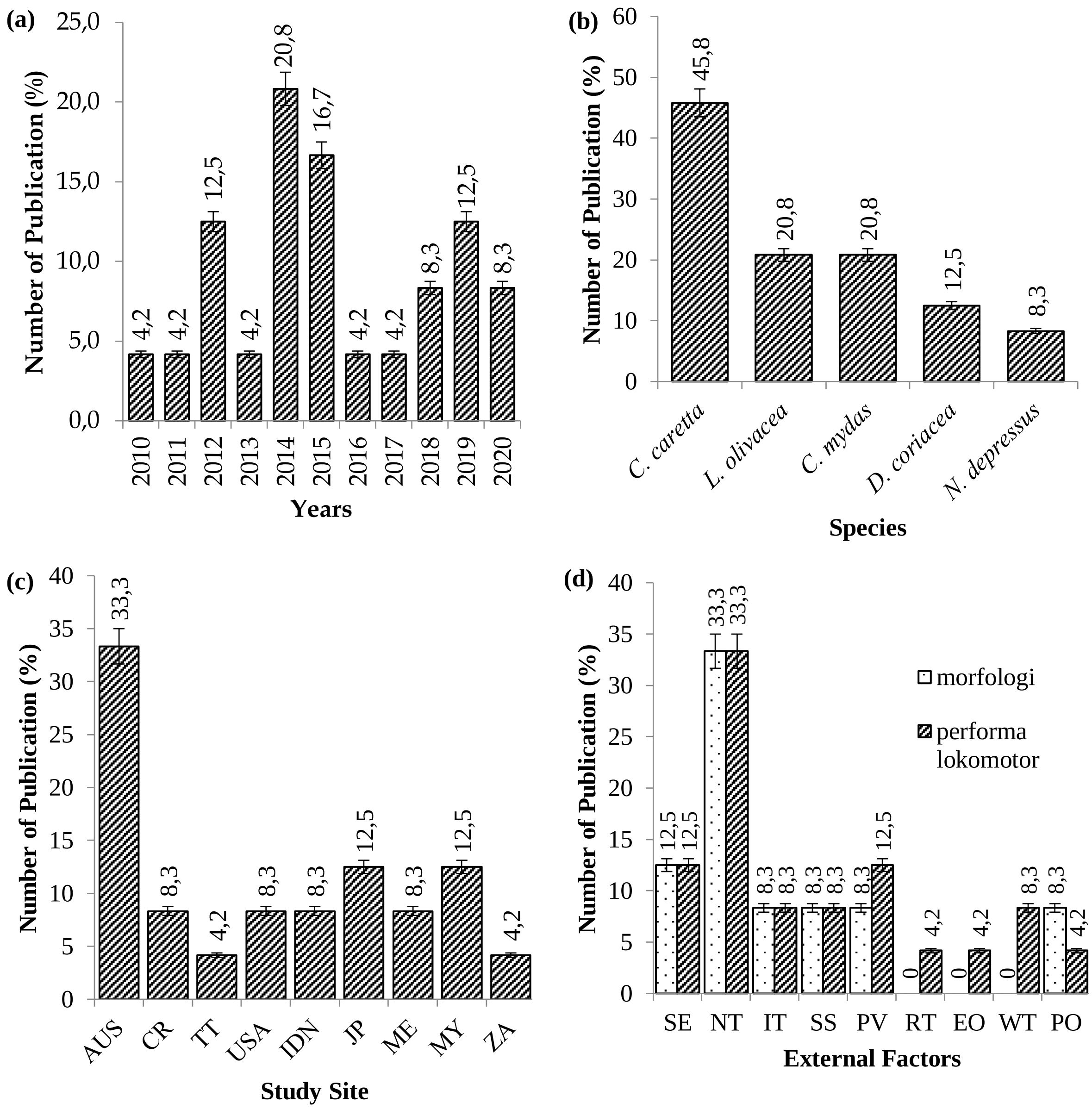


**Figure 2.** Number of publication based on tracing every (a) year (2010-2020), (b) species, (c) study site (AUS, Australia; CR, Costa Rica; TT, Trinidad and Tobago; USA, United States; INA, Indonesia; JP, Japan; MEX,

Mexico; MY, Malaysia; ZA, South Africa), (d) factors affecting morphology and locomotor performance (SE, sun exposure; NT, nest temperature; IT, incubation technique; SS, sand grain size; PV, phenotype variation; RT, release time and nest digging; EO, emerge order, sand temperature, emergence time, nest distance to sea; WT, water temperature; PO, parental origin and nest environment)

Table 3. Summary of all studies on factors affecting the fitness rate of sea turtle hatchlings

| Species | Study Site/ Years | Factors Observed in the Literature | Morphology | Locomotor Performance | | | References |
|---|---|---|---|---|---|---|---|
| | | | | Crawling Performance | Self-righting Performance | Swimming Performance | |
| ***Sun exposure*** | | | | | | | |
| *C. caretta* | Australia /2009-2010 | Classification of nest conditions:<br>• unshaded<br>• least shade<br>• intermediate shade<br>• most shade | • Cooler nests (shaded) produce hatchlings with larger carapaces<br>• Incubation temperature does not affect body mass | Low temperature nest has greater performance | Low temperature nest has greater ability and propensity | - | (Wood et al., 2014) |
| *D. coriacea* | Costa Rica/ 2013-2015 | Classification of nest conditions:<br>• unshaded<br>• shaded | Shaded nest increases body size and mass | Shaded nest has greater performance | Shaded nest has greater performance | Shaded nest has greater performance | (Rivas et al., 2019) |
| *C. caretta* | Australia /2017-2018 | Classification of nest conditions:<br>• shaded + no vegetation<br>• shaded + vegetation<br>• unshaded + vegetation<br>• unshaded + no vegetation | • No effect on body mass<br>• Shaded nests has larger carapace | Unshaded nests has poorer performance | Unshaded nests has poorer performance | - | (Staines et al., 2019) |

Table 3. Summary of all studies on factors affecting the fitness rate of sea turtle hatchlings (*Continued*)

| Species | Study Site/ Years | Factors Observed in the Literature | Morphology | Locomotor Performance | | | References |
|---|---|---|---|---|---|---|---|
| | | | | Crawling Performance | Self-righting Performance | Swimming Performance | |
| ***Nest temperature*** | | | | | | | |
| *D. coriacea* | Trinidad and Tobago/ 2018 | Installation of Temperature Data-Loggers (TDLs) in each nest at different depths | Higher incubation temperatures produce smaller hatchlings | Hatchlings from lower temperature nests have faster terrestrial speeds and total run times | - | - | (Mickelson & Downie, 2010) |
| *C. caretta* | Australia /2010-2011 | Differences in incubation sites:<br>• La Roche Percée beach<br>• Mon Repos beach | • Incubation temperature has no effect on body mass<br>• Mon Repos hatchlings have a larger front flipper and carapace size | Mon Repos hatchlings crawl almost twice as fast | Mon Repos hatchlings have greater ability and propensity | - | (Read et al., 2012) |
| *L. olivacea* | Indonesia/2009-2010 | Classification of nest conditions:<br>• natural nests<br>• protected nests<br>• hatchery nests | High nest temperatures reduce the size | High incubation temperature (T3dm>34 °C) reduces performance | High incubation temperature (T3dm>34 °C) reduces ability and propensity | - | (Maulany et al., 2012) |
| *C. caretta* | USA/ | The hatchlings were incubated in five incubators with a | Hatchlings from 27 °C and 31 °C temperature | 27 °C incubation temperature has | 27 °C and 31 °C incubation temperature has | 27 °C incubation temperature has | (Fisher et al., 2014) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | 2011-2012 | temperature of 27 °C - 32.5 °C | have smaller carapace curved length than 28 °C – 30 °C | the lowest performance | lower performan-ce than medium temperature (28 °C – 30 °C) | the lowest performance | |

Table 3. Summary of all studies on factors affecting the fitness rate of sea turtle hatchlings (*Continued*)

| **Species** | **Study Site/ Years** | **Factors Observed in the Literature** | **Morphology** | **Locomotor Performance** | | | **References** |
|---|---|---|---|---|---|---|---|
| | | | | **Self-righting Performance** | **Self-righting Performance** | **Swimming Performance** | |
| *L. olivacea* | Indonesia/2013-2014 | Classification of nest conditions:<br>• feminine (30-33 °C) produce female<br>• masculine (26-27 °C) produce male | Masculine temperature has smaller carapace curved length | - | Masculine temperature has greater performance | Higher power stroke and survival rate at feminine temperatures | (Dima et al., 2015) |
| *C. caretta* | Australia /2010-2012 | Classification of nest conditions:<br>• full sun<br>• half shade<br>• full shade | Nests with temperatures T3dm> 34 °C produced smaller hatchlings | Nests with temperatures T3dm < 34 °C produced faster hatchlings | No difference in propensity and ability between the two groups | • T3dm <34 °C hatchling has faster swimming speed in the first 20 minutes<br>• After 4 hrs the performance in both groups decreased | (Sim et al., 2015) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *L. olivacea* | Mexico/ 2013-2016 | Classification of nest conditions:<br>• 24 °C<br>• 26 °C<br>• 28 °C<br>• 30 °C<br>• 32 °C<br>• 34 °C | • 30 °C has wi-dest carapace than ranges of 26–27 °C and 32–33 °C<br>• Maternal origin has a significant effect on hatchling morphology | - | - | Intermediate temperatures highest performance compared to low and high temperatures, especially at low temperatures | (Mueller et al., 2019) |

Table 3. Summary of all studies on factors affecting the fitness rate of sea turtle hatchlings (*Continued*)

| **Species** | **Study Site/ Years** | **Factors Observed in the Literature** | **Morphology** | **Locomotor Performance** | | | **References** |
|---|---|---|---|---|---|---|---|
| | | | | **Self-righting Performance** | **Self-righting Performance** | **Swimming Performance** | |
| *C. caretta* | Japan/ 2015 | Nest classification based on the nesting season:<br>• early<br>• late | The carapace size index differed significantly between nests in each group but not significantly different between the two groups of the nesting season | Early nesting season has higher performance | • Early nesting season has higher performance<br>• Self-righting ability is positively related to the incubation period and negatively related to incubation temperature | Early nesting season has higher performance | (Kobayashi et al., 2017a) |

***Incubation technique***

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *C. mydas* | Malaysia /2009 | Classification of incubation techniques:<br>• *in situ*<br>• hatchery<br>• styrofoam box | In situ has the longest carapace length and styrofoam box has wider carapace width | Styrofoam box has poorer performance | - | Hatchery has best performance | (Rusli et al., 2015) |
| *L. olivacea* | Mexico/ 2012-2013 | Classification of incubation techniques:<br>• polystyrene boxes<br>• coastal hatchery | Hatcthling from hatchery nest has larger body size | Polystyrene boxes have slower ability | No significant differences between the two incubation techniques | - | (Hart et al., 2016) |

Table 3. Summary of all studies on factors affecting the fitness rate of sea turtle hatchlings (*Continued*)

| Species | Study Site/ Years | Factors Observed in the Literature | Morphology | Locomotor Performance | | | References |
|---|---|---|---|---|---|---|---|
| | | | | Self-righting Performance | Self-righting Performance | Swimming Performance | |
| ***Sand grain size*** | | | | | | | |
| *C. mydas* | Malaysia /2018 | Sand classification for nests: <br>• coarse sand <br>• medium sand <br>• fine sand | No difference in carapace size and hatchling period | Medium sand has greater performance | Medium sand has greater performance | Medium sand has greater performance | (Stewart et al., 2019) |
| *C. caretta* | Japan/ 2014-2015 | Sand classification for nests: <br>• 0.5–1mm (fine sand) <br>• 1–2mm (coarse sand) | Fine sand has larger hatchlings | Coarse sand nests reduce performance | Coarse sand nests reduce performance | Coarse sand nests reduce performance | (Saito et al., 2019) |
| *Phenotypic Variation* | | | | | | | |
| *C. caretta* and *N. depres-sus* | Australia /2010-2010 | Classification of scute pattern: <br>• *modal* <br>• *minor non-modal* <br>• *major non-modal* | • Modal scute patterns are the heaviest in both species <br>• Carapace length *of C. caretta* did not differ significantly <br>• *N. depressus* modal scute | The three types of scute patterns in the two species were not significantly different | No significant differences in the three types of scute patterns in the two species | • *C. caretta*, the three scute patterns were not significantly different <br>• *N. depressus* with modal scute patterns indicates a higher swimming | (Sim, Booth, & Limpus, 2014) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | | patterns are longer than major non-modal scute patterns | | | performance in first 40 minutes | |

Table 3. Summary of all studies on factors affecting the fitness rate of sea turtle hatchlings (*Continued*)

| **Species** | **Study Site/ Years** | **Factors Observed in the Literature** | **Morphology** | **Locomotor Performance** | | | **References** |
|---|---|---|---|---|---|---|---|
| | | | | **Self-righting Performance** | **Self-righting Performance** | **Swimming Performance** | |
| *N. depres-sus* | Australia /2010-2011 | Comparison of variations in scute patterns based on: <br>• Bare Sand Island Beach <br>• Mon Repos Beach Island | Mon Repos Island has larger eggs sizes and hatchlings | No differences between Mon Repos and Bare Sand Island | There were no differences between Mon Repos and Bare Sand Island | Major non-modal scute patterns on Bare Sand Island than Mon Repos nests has lower performance | (Sim, Booth, Limpus, et al., 2014) |
| *C. caretta* and *D. coriacea* | South Africa/ 2010-2018 | Effect of body size on: <br>• egg size <br>• number of eggs | - | Crawling speed was not significantly correlated with any of the research attributes | - | Flipper size is the main factor driving swimming speed and is independent of species | (Le Gouvello et al., 2020) |
| ***Release time and nest digging*** | | | | | | | |
| *C. mydas* | Malaysia /2004-2005 | • Hatchlings are held for 1, 3, and 6 hours <br>• Digging time: | - | • Decreased ability for hatchlings that were held longer | • Decreased ability for hatchlings that were held longer | • Decreased ability for hatchlings that were held longer | (Van de Merwe et al., 2013) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | a. hatchlings emerge on the main nest<br>b. hatchlings emerge individu-ally after 5 days<br>c. dug as soon as the main nest emerges<br>d. dug 5 days after the main nest emerges | | • Hatchlings that are removed from their nests 5 days later experience a significant reduction in ability | • Hatchlings that are removed from their nests 5 days later experience a significant reduction in ability | • Hatchlings that are removed from their nests 5 days later experience a significant reduction in ability | |

Table 3. Summary of all studies on factors affecting the fitness rate of sea turtle hatchlings (*Continued*)

| **Species** | **Study Site/ Years** | **Factors Observed in the Literature** | **Morphology** | **Locomotor Performance** | | | **Reference s** |
|---|---|---|---|---|---|---|---|
| | | | | **Self-righting Performance** | **Self-righting Performance** | **Swimming Performance** | |
| ***Emergence order, sand temperature, emergence time, distance of nest to sea*** | | | | | | | |
| *L. olivacea* | Costa Rica/2006-2010 | Comparison of several factors:<br>• emergence order (first, intermediate, last)<br>• sand temperature<br>• emergence time<br>• nest distance to sea (debris) | - | • First emerge hatchlings run faster<br>• Hatchlings run faster on sand with lower temperatures (<36 °C).<br>• Speed decreases after 08.00 (37–38 °C) | - | - | (Burger & Gochfeld, 2014) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | | | • Debris slows down speed | | | |
| ***Water temperature*** | | | | | | | |
| *C. mydas* | Australia /2007-2008 | Classification of nest conditions:<br>• open space<br>• shaded areas | - | - | - | • Hatchlings from cooler nests swim better<br>• Hatchlings swimming in 30 °C water have a greater swing frequency than those swimming in 26 °C water | (Booth & Evans, 2011) |

Table 3. Summary of all studies on factors affecting the fitness rate of sea turtle hatchlings (*Continued*)

| **Species** | **Study Site/ Years** | **Factors Observed in the Literature** | **Morphology** | **Locomotor Performance** | | | **References** |
|---|---|---|---|---|---|---|---|
| | | | | **Self-righting Performance** | **Self-righting Performance** | **Swimming Performance** | |
| *C. caretta* | Japan/ 2015 | • Classification of incubation conditions at 31 °C (warm) and 27,5 °C (cold)<br>• Water temperature classification of | - | - | - | • Higher performance at warm incubation temperature (31 °C) and lower ability to maintain performance | (Kobayashi et al., 2018) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | 30 ° C (warm) and 27 ° C (low) | | | | than lower temperature (27.5 °C)<br>• Higher swimming ability in warm water temperatures (30 °C) | |
| *Parental origin and nest environment* | | | | | | | |
| *C. mydas* | Australia /<br>2008-2009 | Maternal origin nest is mixed into one nest and placed in different environmental conditions | Maternal origin has a greater effect on mass and carapace size | - | Nest environment has a stronger effect | Nest environment has a stronger effect in the first 30 minutes | (Booth et al., 2012) |

### 2.1. Factors affecting morphological profile

Several factors that influence the morphological profile of sea turtle hatchlings is shown in Figure 2d. External factors that influence the morphological profile include sun exposure, incubation nest temperature, incubation technique, sand grain size, phenotypic variation, parental origin, and nest environment. A summary of these factors is shown in Table 3.

#### 2.1.1 Sun exposure

The factor of sun exposure in the nest during the incubation period based on the two reviewed literature did not affect body mass of hatchlings (Staines et al., 2019; Wood et al., 2014). However, research conducted by (Rivas et al., 2019) showed different results due to differences in body mass in each treatment, those are shaded nests without shade. Differences in egg quality, such as differences in the proportion of egg yolk and albumen in eggs (eggs with proportionately larger egg yolks produce larger and heavier hatchlings) can explain that each nest can produce a different mass and size of hatchlings depending on the incubation environment (Booth & Evans, 2011).

Nests that are shaded or exposed to less sunlight have lower sand temperatures resulting in larger hatchlings of loggerhead and leatherback turtles (Booth, 2014; Booth & Evans, 2011; Rivas et al., 2019; Staines et al., 2019; Wood et al., 2014). This could be due to the longer incubation period in the shaded nest, allowing more yolk to be converted into hatchling tissue, resulting in larger hatchlings with less yolk residue (Booth, 2006). Hatchlings that have less yolk residue must struggle to survive in an environment with a limited diet, whereas hatchlings that are smaller from nests exposed to sunlight have greater food storage by larger remaining yolk and may be more susceptible to predators but will last longer in food-limited environments (Booth et al., 2004; Cavallo et al., 2015; Reid et al., 2009).

#### 2.1.2 Nest Temperature

The nest temperature during incubation is the most discussed factor in the literature. Higher temperatures (> 30 °C) produce hatchlings with smaller body size and carapace width (Booth & Astill, 2001; Fisher et al., 2014; Mickelson & Downie, 2010; Read et al., 2012; Sim et al., 2015) due to embryo development is faster at higher temperatures and takes less time to convert egg yolk nutrients into the tissue before hatchling occurs (Booth, 2017). The difference in results on the effect of nest temperature on carapace size was shown in this study (Dima et al., 2015) which states that the size of the carapace is smaller at masculine temperatures (26-27 °C), which is thought to be related to the increase in the efficiency of the conversion of energy reserves (egg yolk) in the tissue due to the long incubation period and duration of embryogenesis of olive ridley turtle. Nests with an intermediate temperature (~ 30 °C) were optimal for hatchling development compared to temperature ranges of 26–27 °C and 32–33 °C (Mueller et al., 2019). The size of the hatchlings is an important survival variable because the larger hatchlings has lower chance being preyed upon by predators (Gyuris, 1994; Janzen et al., 2007).

The body mass of hatchlings was not correlated with incubation temperature (green turtles: (Booth & Evans, 2011); loggerhead turtles: (Fisher et al., 2014; Sim et al., 2015); leatherback turtles: (Booth & Astill, 2001)) but is more influenced by genetic and maternal features such as egg size (Glen et al., 2003; International Union for Conservation of Nature (IUCN), n.d.) where the larger eggs produce larger hatchlings (Van Buskirk & Crowder, 1994). Warmer nests have a shorter incubation period, but have a larger yolk residue than hatchlings from colder nests with a longer incubation period (Booth, 2006;

Booth & Astill, 2001; Ischer et al., 2009). This may explain why there was a difference in hatchling size but not mass since the total mass of hatchlings and egg yolk would be similar (Sim et al., 2015).

### 2.1.3 Incubation technique

There are two techniques for incubating turtle eggs, namely in situ and ex-situ methods. In situ method is a practice carried out by marking and leaving the incubation nest naturally after being laid by female turtles. Meanwhile, ex-situ method is the relocation of the egg nest immediately after female turtles laying the egg. The removed eggs will be buried in a protected coastal hatchery or in Styrofoam boxes (Kraemer & Bennett, 1981a). The carapace size of hatchlings originating from nests in the hatchery (30,5 °C) is greater than the incubation in the box (29,9 °C) (Hart et al., 2016). These results are similar to previous research (Rusli et al., 2015), which states that hatchlings carapace size is greater in natural/in situ incubation and coastal hatchery than polystyrene boxes. Nest environmental factors can cause differences in hatchling body size including temperature, humidity, and oxygen levels available to developing embryos (Kraemer & Bennett, 1981a).

### 2.1.4 Sand Grain Size

The difference in sand grain size is based on the diameter in the incubation nest, namely fine sand (0.88 mm), medium (0.54 mm), and coarse (0.34 mm) did not affect the carapace size of the green turtle hatchlings (Stewart et al., 2019). Different results were stated (Saito et al., 2019), which explains that the loggerhead turtle hatchlings originating from fine sand nests (0.5–1 mm) have a larger body size than coarse sand nests (1–2 mm). These are because coarse sand has a high permeability for gas respirators (Ackerman, 1977), thereby reducing nest humidity (Bustard & Peter Greenham, 1968). Drier conditions in coarse nests make the nest temperature warmer causing the incubation period to be faster (Ackerman, 1977). Moreover, the incubation period affects hatchling size (Booth et al., 2004).

### 2.1.5 Phenotypic Variation

Phenotypic variations include differences in scute patterns with classification, namely modal scute patterns, minor non-modal scute patterns, and major non-modal scute patterns. Loggerhead turtle hatchlings do not significantly correlate with body size, while the flatback turtle hatchlings with modal scute patterns have a larger body size than other scute patterns (Sim, Booth, & Limpus, 2014; Sim, Booth, Limpus, et al., 2014). The difference in body size in flatback turtles can be caused by the location of the nesting beaches which have a high predation rate and more nutritious food which allows large turtles to survive. Larger hatchlings have better survival chances because body size provides an advantage to avoid predation, either directly through gape-limited predators or indirectly through locomotor performance, such as speed and endurance (Janzen et al., 2007).

### 2.1.6 Parental Origin and Nest Environment

Parent origin has a greater effect on carapace mass and size than does the nest environment (Booth et al., 2012; Tezak et al., 2020). The phenotype of hatchlings is influenced by maternal origin includes genetic effects (both maternal and paternal) which is complicated because one egg can be fertilized by a different male (Pearse & Avise, 2001), and non-genetic effects such as differences in egg size and/or differences in provisioning of nutrients and water to eggs. It is usually impossible to separate environmental influences from the nest in natural nests because the factors of nest and maternal origin are completely confounded. The only way to separate these factors is to use split clutch manipulation (Booth et al., 2012).

### 2.2 Factors Affecting Locomotor Performance

Various factors affect locomotor performance in sea turtle hatchlings. External factors that affect locomotor performance (Figure 2d) are sun exposure; incubation nest temperature; incubation technique; sand grain size; phenotype variation; release time and nest digging; emergence order, sand temperature, emergence time, distance of nest to sea; water temperature; parental origin and nest environment. The results of the review of each factor is shown in Table 3.

#### 2.2.1 Sun Exposure

Hatchlings from unshaded nests have a lower crawling performance and self-righting propensity (Staines et al., 2019; Wood et al., 2014) and poor swimming performance compared to shade nests (Rivas et al., 2019). Most likely due to sub-lethal physiological effects on nest with high temperature (Bolten, 2003). In unshaded nests there is an increase in the intensity of direct sun exposure so that the nest conditions are warmer.

Crawling performance and self-righting propensity effect on the time the hatchlings spend on the beach (Paitz et al., 2010). The longer hatchlings spend onshore increases the risk of desiccation and overheating from sun exposure as well as predation (Davenport, 1997; Steyermark & Spotila, 2001). The impact of sun exposure will affect individual survival during the early stages of hatchling life (Dial, 1987; Janzen et al., 2007).

#### 2.2.2 Nest Temperature

Hatchlings incubated at lower temperatures (<31 °C) have faster crawling ability than higher ones (Kobayashi et al., 2017b; Maulany et al., 2012; Mickelson & Downie, 2010; Read et al., 2012; Sim et al., 2015), but when the temperature <28 °C crawling ability will decrease (Fisher et al., 2014). Turtle eggs incubated at lower temperatures tend to produce male hatchlings whose body size is larger, including larger flippers (Booth et al., 2004; Burgess et al., 2006). Larger hatchlings have a better chance of avoiding predation by gape-limited predators, such as predators who cannot consume hatchlings because their mouths cannot be opened wide enough to swallow hatchlings (Davenport, 1997; Gyuris, 1994).

Hatchlings originating from nests with high temperatures (> 31 °C) have a lower self-righting ability, and propensity than masculine temperatures (<31 °C) (Dima et al., 2015; Maulany et al., 2012; Read et al., 2012), nest with intermediate temperature provides best performance (28 - 30 °C) (Fisher et al., 2014). Larger hatchlings, apart from improving the fitness, also increase their chances of avoiding gape-limited predators (Burgess et al., 2006).

Some literature states that the highest swimming performance is obtained from hatchlings that are incubated at low temperatures compared to high temperatures (Fisher et al., 2014; Mueller et al., 2019) and come from an earlier nesting season (Kobayashi et al., 2017a). After 4 hours, the performance of the two temperature groups decreased (Sim et al., 2015). Different results suggest a higher front flipper power stroke and survival rate at feminine temperatures (Dima et al., 2015) due to more rapid muscle fatigue at lower incubation temperatures (Burgess et al., 2006). Lower temperatures produce hatchling with a smaller egg yolk reserve because a more extended incubation period allows more yolk to be converted into tissue (Booth, 2006). Thus hatchling fitness appears to be two-sided between egg yolk size and residue; Larger hatchlings may have a greater chance of survival due to faster movement through predatory-rich coasts and nearshore zones (Booth, 2006; Gyuris, 1994), but smaller hatchlings can travel further from shore before slowing down in search of food or rest because yolk residue are not used during embryonic development, emergence and offshore travel (Ischer et al., 2009).

#### 2.2.3 Incubation Technique

Incubation techniques are method used to hatch eggs after being laid by female turtles. Three incubation techniques are most commonly used: natural/in situ incubation, coastal hatchery, polystyrene box, or cooler plastic (Rusli et al., 2015). Self-righting ability did not significantly affect all incubation techniques and hatchlings from slower incubation in the box have slower crawling speed (Hart et al., 2016), and swimming performance of hatchlings in hatchery nests is the highest (Rusli et al., 2015). The literature discusses incubation techniques by laying eggs into nests in hatchery and boxes. The limited size of the box causes shallow nest depth with lower temperatures, thus affecting the fitness level of hatchlings. These results contradict (Booth & Evans, 2011), who found that eggs incubated at lower temperatures resulted in hatchlings that swam greater than those incubated at warmer temperatures. This suggests other factors (besides temperature) in the incubation technique that may play a role in hatchling fitness.

#### 2.2.4 Sand Grain Size

Green turtle hatchlings emerging from medium sand nests have higher crawling, self-righting, and swimming performance than hatchlings from coarse and fine sand (Stewart et al., 2019), which is consistent with the results of the loggerhead turtle hatchlings (Saito et al., 2019). Coarse sand nests reduce fitness levels because the energy required for hatchlings when emerging is higher. Poorly sorted coarse sand can inhibit hatchlings because the tendency of this sand to collapse makes it more difficult to dig out of the nest (Mortimer, 1990)

#### 2.2.5 Phenotypic Variation

The entire literature that discusses the effect of phenotypic variation shows no significant difference in all variables used for the study of crawling and self-righting ability. The female turtle size is directly proportional to the number of eggs in the nest, not the size of the eggs, and swimming speed does not depend on the species (Le Gouvello et al., 2020). According to previous research, it was stated that turtle nesting maximizes nest size rather than egg size in heterogeneous environments (Smith & Fretwell, 1974).

There are three classifications of scute patterns for hatchlings: modal scute patterns, minor non-modal scute patterns, and major non-modal scute patterns. There was no significant difference in swimming ability in the three types of sea turtle hatchlings (Sim, Booth, & Limpus, 2014), but the flatback turtle hatchlings with modal scute patterns showed a higher proportion and swimming performance than the major non-modal scute patterns, only in the first 40 minutes (Sim, Booth, Limpus, et al., 2014). This difference may occur considering the history of life: the loggerhead turtle hatchlings have a period of inter-oceanic migration, while the flatback turtle remains on the continental shelf (Bolten, 2003). Flatback hatchlings also have less intense frenzy periods, and their swimming effort is reduced more rapidly than that of the loggerhead and green turtles (Pereira et al., 2011).

#### 2.2.6 Release Time and Nest Digging

The nests that were dug immediately after the first hatchlings emerged with the same speed and body condition as hatchlings that naturally emerge from the nest. There is a decrease in ability that occurs in hatchlings which shows that they are in the hatchery for longer. Hatchlings that were removed from the nest 5 days after their first appearance caused a significant decrease in fitness (Van de Merwe et al., 2013). There was a 50% reduction in walking speed and a 5.5% reduction in the body condition of the dug hatchlings 5 days after the appearance of the main nest indicating severe dehydration and/or residual yolk consumption. Sea turtle hatchlings consume ~ 50% of the remaining yolk in the 3-5 days needed to emerge after hatchling (Kraemer & Bennett, 1981b)

### 2.2.7 Emergence Order, Sand Temperature, Emergence Time, Distance Of Nest To Sea

Literature related to the effect of hatchling Emergence order, sand temperature, emergence time, nest distance to the sea was found in only one publication. Hatchlings that emerge first will crawl faster (Burger & Gochfeld, 2014). The hatchlings will crawl faster on the sand with low temperatures (<36 °C), and the speed decreases after 08.00 (37–38 °C). Loggerhead turtle hatchlings stopped appearing to the surface when the sand reached temperatures over 32,4 °C (Moran et al., 1999), whereas hatchlings in the Ostional continued to appear when the sand temperatures were well above this, although they stopped appearing at around 38 °C. At extreme sand temperatures (40 °C) it is even possible to die of hatchlings or stress due to excess heat. Debris on the beach will prolong the time for hatchlings to reach the sea because hatchlings can get entangled in the trash, increased exposure to predators and the scorching sun with high sand temperatures reaching 40 °C can cause hatchlings to stress and die (Triessnig et al., 2012).

### 2.2.8 Water Temperature

Apart from the temperature of the nest, a factor affecting the level of fitness is the water temperature. Swimming performance in hatchlings is higher in warm water temperatures (30 °C) (Booth & Evans, 2011; Kobayashi et al., 2018). Since reptiles are ectothermic, their heartbeat depends on the temperature of the environment. Warm water temperature will increase muscle metabolism and delivery capacity by the cardiovascular system (Booth & Evans, 2011). Increased rates of nutrient and oxygen delivery and increased rates of removal of metabolic waste products and carbon dioxide from muscles, will facilitate increased muscle activity. Increasing muscle temperature will also increase the rate of biochemical reactions in the muscles, increasing metabolism and muscle performance during the frenzy and post-frenzy periods (Lillywhite et al., 1999).

### 2.2.9 Parental Origin and Nest Environment

Nest environmental conditions have a stronger influence than the parental origin on the self-righting ability and propensity of hatchlings and their ability to swim in the first 30 minutes (Booth et al., 2012). The locomotor performance of hatchlings is similar to previously reported for green turtle hatchlings from the same island (Heron Island) (Booth, 2009; Booth & Evans, 2011; Burgess et al., 2006; Ischer et al., 2009). Parental origin has been found to affect the crawling and swimming abilities of freshwater turtles (Janzen, 1993), and in tuatara (*Sphenodon* sp.), parental origin affects hatchling speed at 1 month of age (Nelson et al., 2006). The partial correlation between nest temperature and locomotor performance was significant, whereas between egg mass and locomotor performance was not significant, indicating that the influence of the nest was more important than the effect of parental origin in affecting the locomotor ability of hatchlings (Booth et al., 2012).

## CONCLUSION

Factors that influence the fitness rate of sea turtle hatchlings based on the morphological profile and locomotor performance found in the literature are sun exposure, nest temperature, incubation technique, sand grain size, phenotypic variation. All factors do not affect the body mass of hatchlings, because the total mass of hatchlings and yolk sac will be similar. Nests that are slightly exposed to sunlight, optimal temperature (28-30 °C), use coastal hatchery incubation techniques, have a fine sand grain size (0.5-1 mm), and have phenotypic variations in the form of modal scute patterns produce hatchlings with larger carapace sizes and greater locomotor performance thus increasing the chance of avoiding. Moreover, parental origin has a strong influence on the mass and size of the hatchlings. Factors that only affect locomotor performances are release time and nest digging; emergence order, sand temperature, emergence time, distance of nest to sea; water temperature. Furthermore, greater locomotor performance is obtained if the hatchlings are released immediately after emerge and immediately dug, first emerge hatchlings, have a sand temperature (<36 °C), time to leave the nest before 08.00, nest closer to the sea, warm water temperature (30 °C), and have good environmental conditions.

The majority of topics discussed in the literature focus on external factors during the incubation period. Further research is needed during the early post-hatchling period to see the possibility of factors affecting the long-term fitness rate of hatchlings and changes in variables that initially differ significantly (e.g. carapace curved length) to become insignificant. This post-hatchling handling recommendation is an important aspect to improve the efficiency and effectiveness of turtle hatchery management around the world.

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## CONFLICT OF INTEREST

There is no conflict of interest related to the writing or publication of this article.

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