

RESEARCH ARTICLE

Analysis of why sea turtles swim slowly: a metabolic and mechanical approach

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ABSTRACT

Animals with high resting metabolic rates and low drag coefficients typically have fast optimal swim speeds in order to minimise energy costs per unit travel distance. The cruising swim speeds of sea turtles (0.5–0.6 m s⁻¹) are slower than those of seabirds and marine mammals (1–2 m s⁻¹). This study measured the resting metabolic rates and drag coefficients of sea turtles to answer two questions: (1) do turtles swim at the optimal swim speed?; and (2) what factors control the optimal swim speed of turtles? The resting metabolic rates of 13 loggerhead and 12 green turtles were measured; then, the cruising swim speeds of 15 loggerhead and 9 green turtles were measured and their drag coefficients were estimated under natural conditions. The measured cruising swim speeds (0.27–0.50 m s⁻¹) agreed with predicted optimal swim speeds (0.19–0.32 m s⁻¹). The resting metabolic rates of turtles were approximately one-twentieth those of penguins, and the products of the drag coefficient and frontal area of turtles were 8.6 times higher than those of penguins. Therefore, our results suggest that both low resting metabolic rate and high drag coefficient of turtles determine their slow cruising speed.

KEY WORDS: Optimal swim speed, Cost of transport, Metabolic rate, Drag coefficient, Stroke frequency, Loggerhead turtle, Green turtle

INTRODUCTION

Aquatic animals are subjected to higher drag because they move in a denser environment than terrestrial animals moving through air. The mechanical work of swimming is a product of distance and drag, where drag is proportional to the squared speed. Some aquatic animals such as sea turtles, marine mammals, seabirds and fish perform long-distance migrations throughout their life cycle (e.g. Hays and Scott, 2013; Rasmussen et al., 2007; Watanabe et al., 2015). Therefore, in order to save energy for migration, it is important to choose an appropriate swim speed that minimises energy costs. Quantitative estimates of migration energy costs and the factors that determine swim speed provide important insights into the migration strategies and energy budgets of aquatic animals (e.g. Hatase and Tsukamoto, 2008; Watanabe et al., 2015). Previous research indicated that the cruising swim speeds of endothermic aquatic animals, ranging from seabirds weighing 0.5 kg to marine mammals weighing 90,000 kg, are proportional to body mass^{0.09} (Watanabe et al., 2011), but converge in a relatively narrow range of 1–2 m s⁻¹

(Sato et al., 2007). This means that, during travel, endothermic aquatic animals swim at a speed that minimises the energy cost per unit distance (Watanabe et al., 2011; Sato et al., 2010), which is defined as the ‘optimal swim speed’. Aquatic animals swimming faster or slower than the optimal swim speed would have extra energy costs owing to increased drag or prolonged transit times, respectively.

The optimal swim speed and cost of transport (COT) at each speed can be estimated by calculating the mechanical cost and basal metabolic cost for the animal during swimming (Sato et al., 2010). For example, when an emperor penguin (30 kg) dives to a depth of 400 m at various angles, the optimal swim speed converges between 1.5 and 2.0 m s⁻¹ regardless of the pitch angle (Sato et al., 2010). This speed is consistent with the measured cruising swim speed of penguins (1.8–2.3 m s⁻¹) (Sato et al., 2010). However, the cruising swim speed of ectothermic animals is generally slower than that of endothermic animals (Watanabe et al., 2011). For example, the cruising speed of loggerhead turtles (*Caretta caretta*) is 0.5–0.6 m s⁻¹ at approximately 20°C (Narazaki et al., 2009; 2013). Assuming that sea turtles swim at their optimal swim speed, this slow cruising swim speed might be related to their lower resting metabolic rate and higher drag coefficients. If the resting metabolic rate is low, the optimal swim speed is expected to be slow (Watanabe et al., 2011). According to a previous study, the resting metabolic rates of sea turtles (except leatherback turtles, *Dermochelys coriacea*) are close to those of reptiles (Wallace and Jones, 2008). The drag coefficients of turtles are also likely to affect their optimal swim speeds (Watanabe et al., 2011). Because they have a carapace, sea turtle morphology is significantly different from that of streamlined aquatic mammals and seabirds. If sea turtles have higher drag coefficients than marine endothermic animals, this may also reduce their optimal swim speed. However, no previous study has quantitatively verified whether the cruising speed of sea turtles matches their optimal swim speed.

In this study, an energy model used to estimate the COT of penguins (Sato et al., 2010) was modified to estimate the optimal swim speed for sea turtles. In order to investigate the factors affecting the slow cruising swim speeds of sea turtles, two questions were examined: (1) do turtles swim at the optimal swim speed?; and (2) what factors regulate the optimal swim speed of turtles? We combined morphological and respirometric measurements, as well as behavioural data collected in the field, to provide quantitative estimates of the optimal swim speed of sea turtles. To answer question (1), we also tested how the cruising swim speed and stroke frequency of sea turtles changes with body mass.

MATERIALS AND METHODS

Ethics

This study was conducted as a part of a tag and release programme, in which loggerhead and green turtles caught by set nets through by-catch in the Sanriku Coast were handed over to researchers by fishermen. All experimental procedures were covered by the

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List of symbols and abbreviations

A	activity ratio (%)
AIC	Akaike information criterion
a	multiplier for entrained water attached to the surface of the turtle
m_b	body mass (kg)
C_d	drag coefficient of gliding animals
COT	cost of transport
GLMM	generalised linear mixed model
D	drag (N)
E_V	mechanical energy cost (J)
h	heading angle
H	moving distance (m)
k	basal metabolic rate (W)
L	body length
M_V	basal metabolic energy cost (J)
MLE	maximum likelihood estimation
ρ	pitch angle
S	frontal area of turtle from head-on angle (m ²)
SCL	straight carapace length (cm)
SI	straightness index
T_w	ambient water temperature (°C)
U	swimming speed (m s ⁻¹)
U_{opt}	optimal swimming speed (m s ⁻¹)
\dot{V}_{O_2}	oxygen consumption rate (ml O ₂ min ⁻¹ kg ^{-0.83})
ε_A	efficiency with which chemical energy is translated into muscular work
ε_p	propeller efficiency with which muscular movement is translated into forward thrust
λ	ratio of drag of an active swimmer to that of a passive object
ν	kinematic viscosity of water (m ² s ⁻¹)
ρ_w	sea water density (1027 kg m ⁻³)

guidelines of the Animal Ethics Committee of the University of Tokyo, and the protocol of the study was approved by this committee (P12-13, P13-P14-3, P15-7, P16-5, P17-1, P-18-5, and P19-6).

Study site and morphological measurements

Loggerhead [*Caretta caretta* (Linnaeus 1758)] and green turtles [*Chelonia mydas* (Linnaeus 1758)] were collected in June to November between 2005 and 2019 at the Sanriku coastal area in the western North Pacific. This study site is a summer-restricted foraging ground for loggerhead and green turtles (Fukuoka et al., 2015; Narazaki et al., 2015). All experiments were conducted using wild loggerhead and green turtles incidentally captured in set nets between Miyako and Ofunato in the Sanriku coastal area (38°55′ to 39°40′N, 141°40′ to 142°05′E). Captured turtles were transferred promptly to tanks at the International Coastal Research Center, Atmosphere and Ocean Research Institute, The University of Tokyo (39°21′05″N, 141°56′04″E). Following the definition of Bolten (1999), we measured the straight carapace length (SCL: cm) from the notch to the tip of the carapace. We also measured the body mass (m_b : kg) and frontal area (S : m²) of loggerhead and green turtles. The latter was measured photogrammetrically from photographs taken at a head-on angle using Photoshop (Adobe Systems, Inc., San Jose, CA, USA).

Respirometric measurements of sea turtles

The metabolic rates of 13 juvenile loggerhead turtles were obtained from a previous study (Kinoshita et al., 2018); those of juvenile green turtles were measured in the present study using the same respirometric method under 15, 20 and 25°C. The turtles were kept

in an experimental water tank (155×115×60 cm deep) filled with water at a temperature of 15, 20 and 25°C for at least 1 week before measurements were taken. Here, 1 litre of oxygen was considered to be equivalent to 20.1 kJ. The oxygen consumption rate (\dot{V}_{O_2}) of 12 juvenile green turtles (m_b : 7.5–84.0 kg) captured in the Sanriku coastal area was measured using a respiratory system from July to October in 2017 and 2019 (Table S1). We then derived a model equation of the oxygen consumption rate (ml O₂ min⁻¹ kg^{-0.83}) in green turtles that included the effect of temperature and activity. All turtles were fed a diet of 250 g of Japanese common squid every 3 days. A generalised linear mixed model (GLMM) with a Gaussian distribution and log link function was used to evaluate \dot{V}_{O_2} . The response variable was \dot{V}_{O_2} and the explanatory variables were water temperature and the activity ratio measured by a behavioural data logger (15 mm diameter, 53 mm long, 18 g in air; M190L-D2GT, Little Leonardo Co., Tokyo, Japan) during respirometric measurement. The most parsimonious model was selected using the Akaike information criterion (AIC). The GLMM results revealed that \dot{V}_{O_2} was affected by both temperature and activity ratio. The following model was applied to estimate \dot{V}_{O_2} :

$$\dot{V}_{O_2} = \chi \exp(\psi T_w + \omega A), \quad (1)$$

where A is the activity ratio (%), indicating the active time ratio during experiments (Kinoshita et al., 2018). The maximum likelihood estimation (MLE) of the three parameters χ , ψ and ω in Eqn 1 was obtained using the observed \dot{V}_{O_2} , water temperature (T_w) and activity ratio.

Measuring cruising swim speed and stroke frequency

The cruising swim speed and stroke frequency of 15 loggerhead and 9 green turtles were measured using behavioural data loggers (26 mm diameter, 175 mm long, 140 g in air; W1000-3MPD3GT, Little Leonardo Co.) in the field from 2010 to 2019 (Table 1; Table S2). The data loggers were programmed to record depth, temperature, swim speed, tri-axis (lateral, longitudinal and dorso-ventral) magnetism at 1 Hz, and tri-axis acceleration at 16 or 32 Hz. The data loggers needed to be retrieved to obtain the data; therefore, we used an automatic time-scheduled release system (e.g. Narazaki et al., 2009; Watanabe et al., 2004). The resulting time-series data were analysed using IGOR PRO (WaveMetric, Inc., Lake Oswego, OR, USA). Aquatic animals generally exhibit various swim speeds and stroke frequencies during descent and ascent as a result of their own buoyancy (Sato et al., 2002). Thus, the cruising swim speed and stroke frequency were extracted from gradual ascent phases when the sea turtles appeared to attain neutral buoyancy at the bottom of gradual ascent dives (Minamikawa et al., 2000) (Fig. 1). Recorded acceleration data included both low-frequency gravity components and high-frequency specific components (mainly caused by dynamic movements, such as flipper beating). We filtered the longitudinal high-frequency components from the data as information on flipper stroking activity. This filter was defined by a power spectral density and a continuous wavelet transform filter in IGOR Pro.

The swim speed was measured by the rotation of the propeller in front of the data logger. As there is a strong correlation between propeller rotation speed and swim speed (Akamatsu et al., 2002; Kawabe et al., 2004), a speed correction experiment was conducted to derive a corrective equation for calculating swim speed from the propeller rotation speed. However, the equation assumes that the water flow impacts the propeller from a head-on angle, yet it was impossible to align the data logger exactly parallel to the longitudinal axis of the turtle. Therefore, the difference in heading

Table 1. Individual information from logger-deployment experiment

Turtle ID	SCL (cm)	m_b (kg)	Frontal area of turtle+tags (m ²)	Average C_d	Experimental duration (h)	Temperature (°C)
Loggerhead turtle						
L1005	82.5	77.7	0.1302	0.31	111.9	21.9
L1310	78.2	81.5	0.1366	0.27	60.0	17.3
L1401	72.4	54.0	0.1031	0.32	59.5	21.0
L1411	80.7	65.0	0.1170	0.32	57.5	20.5
L1644	69.4 ^a	68.0	0.1177	0.31	100.2	20.7
L1740	62.0	34.0	0.0778	0.37	58.1	18.2
L1901	85.2	87.0	0.1421	0.32	21.3	15.7
L1904	68.5	49.5	0.0972	0.49	33.7	21.9
L1913	59.0	30.0	0.0690	0.41	41.0	22.2
L1914	61.8	40.0	0.0815	— ^b	91.0	18.0
L1915	67.3	47.0	0.0939	— ^b	52.5	22.0
L1916	42.8	14.0	0.0406	— ^b	86.1	21.8
L1918	82.0	91.0	0.1446	0.34	57.8	20.3
L1922	69.7	49.0	0.0966	0.52	50.8	19.9
L1935	63.9	38.0	0.0730	0.31	61.7	21.8
Green turtle						
G1210	44.3	11.5	0.0361	0.47	41.1	22.8
G1356	48.4	15.0	0.0416	0.22	152.8	22.5
G1454	47.3	16.5	0.0434	0.25	68.3	20.0
G1514	48.8	15.0	0.0416	0.25	135.8	20.3
G1506	72.2	55.5	0.0807	0.70	35.6	20.1
G1605	45.2	13.0	0.0390	0.50	157.3	18.1
G1742	43.7	12.0	0.0368	0.46	91.9	18.4
G18105	49.2	16.0	0.0448	0.64	86.2	19.9
G1921	47.6	15.0	0.0379	— ^b	82.8	21.8

Experimental duration excludes the first 12 h after release. Temperature is the mean water temperature experienced during the experiment. SCL, straight carapace length; m_b , body mass; C_d , drag coefficient. ^aThe carapace was partly missing in this turtle. ^bNo horizontal glide.

(h ; deg) and pitch angle (p ; deg) had to be calculated. Considering the attachment angle, the swim speed of each turtle was obtained as follows:

$$\text{Actual swim speed} = \frac{\text{Swim speed calculated from the propeller}}{\cos p \cdot \cosh h} \quad (2)$$

where actual and calculated swim speed are both in m s^{-1} . The difference in the heading angle (h) was measured from a photograph taken from above when the data logger was attached. The difference in pitch angle (p) was measured from the gravity acceleration in the dorso-ventral axis of the data logger.

Furthermore, the straightness of each dive (straightness index: SI) was calculated to extract the travelling periods because animals swimming for non-travelling purposes do not always swim at a cruising speed (Watanabe et al., 2019). SI was calculated by

dividing the horizontal distance between the start and end of the dive by the distance the sea turtle actually moved. SI takes a value of 0–1; the closer it is to 1, the more linearly the sea turtle is interpreted to have travelled (Zar, 1998). To calculate SI for each dive, 3D paths were calculated using data on depth, swim speed, and tri-axis acceleration and magnetism obtained from the data logger. The 3D paths were reconstructed every 1 s using a dead-reckoning method (http://bre.soc.i.kyoto-u.ac.jp/bls/index.php?3D_path, accessed 15 March 2019). In this study, dives with $\text{SI} > 0.7$ were considered to have a travelling objective and were used to extract the swim speed and stroke frequency. To account for post-release stress in the turtles, the first 12 h of each deployment were excluded from the analysis.

Estimation of drag coefficient

Movements of aquatic organisms are affected by drag, which can be calculated from deceleration rates during horizontal glides

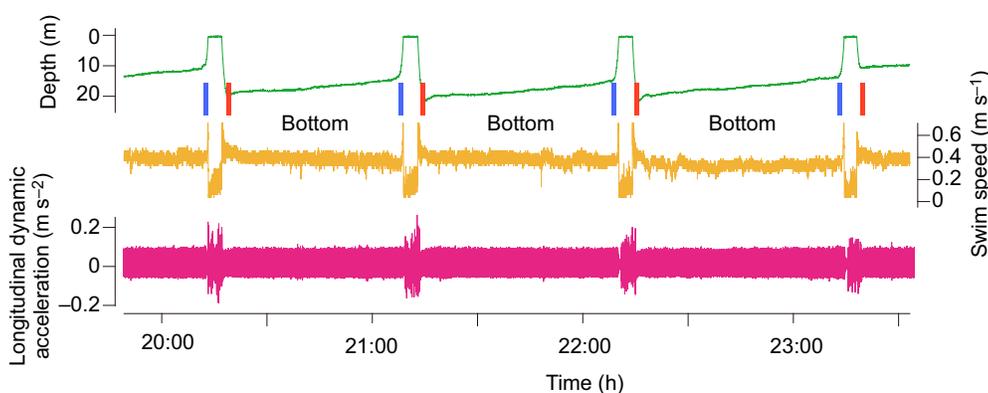


Fig. 1. Example of time-series behavioural data showing each gradual ascent dive from a loggerhead turtle. The green, yellow and pink lines indicate depth, swim speed and longitudinal dynamic acceleration, respectively. The regions labelled 'bottom' were considered to represent the gradual ascent phase; the cruising swim speeds were calculated by averaging swim speed during the gradual ascent phase in each dive. Red and blue lines indicate the beginning and end of the gradual ascent phase, respectively. Data were obtained from turtle L1411 on 18 August 2014.

(Watanabe et al., 2006). We randomly extracted 3–11 deceleration phases per individual from periods when the turtles stopped stroking and swam horizontally, which were determined from the behavioural data (Fig. S1). Drag (D) was calculated using the deceleration rate as follows:

$$D = m_b a (U_t - U_{t+1}), \quad (3)$$

where a is a multiplier for entrained water attached to the surface of the turtle (total mass = $m_b a$). The value for a was set to 1.06 based on measurements of a prolate spheroid of fineness ratio 5.0 (Skrovan et al., 1999; Miller et al., 2004; Watanabe et al., 2006). U_t and U_{t+1} are swim speeds (m s^{-1}) with a resolution of 0.019 m s^{-1} at t and $t+1$ (s), and were averaged to describe the mean glide speed (U). The drag coefficient (C_d) based on the frontal area was then given by:

$$C_d = 2D / (\rho_w S U^2), \quad (4)$$

where ρ_w is the sea water density (1027 kg m^{-3}) and S is the frontal area of the turtle (m^2) calculated from morphological measurements.

Biomechanical model for optimal swim speed of turtles

The total energy cost of diving animals is divided into the basal metabolic cost and mechanical cost (Sato et al., 2010) (Fig. S2). Sato et al. (2010; see their eqns 2.13) indicate the total energy cost of emperor penguins diving at various pitch angles; their model included the work against buoyancy. However, in the case of sea turtles, swim speed was measured during horizontal swimming at the depth of neutral buoyancy. Therefore, we simplified the equation by excluding the work against buoyancy:

$$\frac{E_V}{\epsilon_p \epsilon_A} + M_V = \left(\frac{\rho_w \lambda C_d S U^2}{2} \right) \frac{H}{\epsilon_p \epsilon_A} + \frac{kH}{U}. \quad (5)$$

Here, E_V is the mechanical energy cost (J) required to transit a distance H (m); ϵ_p is the propeller efficiency with which muscular movements are translated into forward thrust; and ϵ_A is the efficiency with which chemical energy is translated into muscular work. The mechanical energy cost E_V can be converted to the metabolic COT using both efficiencies ϵ_p and ϵ_A : $E_V / (\epsilon_p \epsilon_A)$ (Hind and Gurney, 1997). M_V is the basal metabolic cost (J) during travel; λ is the ratio of the drag of an active swimmer to that of a passive object (Hind and Gurney, 1997); S is the frontal area (m^2), obtained by morphological measurement; U is the swim speed (m s^{-1}); k is the measured resting metabolic rate (W) of the green turtles used in this study and the quoted resting metabolic rate of loggerhead turtles obtained from a previous study (eqn 5 in Kinoshita et al., 2018); and C_d is the measured value of horizontal glide (Eqn 4). The constant values of ϵ_p , ϵ_A and λ were assumed to be 0.85, 0.17 and 0.576, respectively (Hind and Gurney, 1997).

We also estimated the optimal swim speed of each turtle following the method employed in a previous study (Sato et al., 2010). The total energy cost [$E_V / (\epsilon_p \epsilon_A) + M_V$] reaches a minimum at a range of swim speeds. Differentiating Eqn 5 by the swim speed, U , gives the optimal swim speed that results in the minimum cost, U_{opt} :

$$\frac{d(E_V / \epsilon_p \epsilon_A + M_V)}{dU} = \left(\frac{\rho_w \lambda C_d S H}{\epsilon_p \epsilon_A} \right) U + k H U^2 = 0 \quad (6)$$

and

$$U_{\text{opt}} = \left(\frac{\epsilon_p \epsilon_A k}{\rho_w \lambda C_d S} \right)^{1/3}. \quad (7)$$

We then verified whether the estimated optimal swim speed and measured cruising swim speed obtained by field experiments were the same. We also examined the factors that caused a reduction in the optimal swim speed of sea turtles by replacing k , C_d and S with the values from a previous study on penguins (Sato et al., 2010).

Relationship between m_b , optimal swim speed and stroke frequency

Eqn 7 can be used to examine the theoretic scaling of speed at minimum COT (U_{COTmin}). ϵ_p , ϵ_A , λ and ρ_w are considered independent of m_b (Hind and Gurney, 1997). We assumed that k is proportional to $m_b^{0.83}$ (e.g. Southwood et al., 2003; Kinoshita et al., 2018). Little information is available on the size dependency of ϵ_p , ϵ_A and λ (Hind and Gurney, 1997). ϵ_p , ϵ_A and λ may be related to each other (Hind and Gurney, 1997); if so, $(\epsilon_p \epsilon_A) / \lambda$ in Eqn 7 could be regarded as a single dimensionless parameter representing the total swimming efficiency that converts the mechanical drag power of non-oscillating bodies into the metabolic drag power of active swimmers. C_d was assumed to be proportional to the Reynolds number (Re) $^{-1/5}$, which is an approximation for turbulent flow (Vogel, 1994). Re is a dimensionless number that characterises the scale effect of flow (Vogel, 1994) and is calculated as LU/v , where L is body length (m) and v is the kinematic viscosity of water ($\text{m}^2 \text{ s}^{-1}$) (independent of m_b). In this study, L was taken to be SCL. Adding all these assumptions to Eqn 7 results in the following proportional expression:

$$U_{\text{opt}} \propto (m_b^{0.83} / m_b^\alpha / m_b^\beta U_{\text{opt}})^{-1/5} / m_b^\gamma. \quad (8)$$

The scaling exponents α and β were calculated using the relationship of morphological features (S , SCL) versus m_b in this study. The slope of the regression of m_b and cruising swim speed was estimated by Eqn 8 and compared with the measured slope of m_b versus cruising swim speed obtained in the field experiment. We also examined the slope of the relationship between stroke frequency and m_b . Stroke frequency is the reciprocal of the flipper stroke cycle and was described as: stroke frequency = $1/\text{stroke cycle} = \text{reciprocation speed of flipper}/\text{reciprocation distance of flipper}$. The reciprocation distance is an index of length and is expected to be proportional to $m_b^{1/3}$ as stroke frequency is proportional to the reciprocation speed of flipper $\times m_b^{-1/3}$. The drag and propulsion of the swimming turtle are therefore balanced. As shown in Eqn 4, the drag is proportional to U^2 , so propulsion is considered to be proportional to the (speed of moving flippers) 2 . Therefore, the U and speed of moving flippers are in a proportional relationship, so U is proportional to the reciprocation speed of flipper. Therefore:

$$\text{Stroke frequency of flipper} \propto U m_b^{-1/3}. \quad (9)$$

Assuming that the optimal swimming speed is proportional to m_b^γ , the following expression is obtained as the relational expression between the optimal stroke frequency and m_b :

$$\text{Optimal stroke frequency} \propto m_b^\gamma m_b^{-1/3} \propto m_b^\delta, \quad (10)$$

where γ was obtained from Eqn 8. We calculated the proportional coefficient of the optimal flipper frequency and m_b and compared it with that of the value measured in the field.

Statistics

Analysis of covariance (ANCOVA) was used to determine whether there were differences in body mass and other parameters (SCL, S , cruising swim speed and stroke frequency) between green and

loggerhead sea turtles. m_b was defined as a covariate. The relationship between each morphological feature and m_b was calculated by major axes analyses with the SMATR package in order to estimate the scaling relationships (Warton et al., 2006). All statistical analyses were performed with R3.3.2 (R Development Core Team, <http://www.R-project.org>). Mean±s.d. values are presented unless otherwise indicated. The significance level of all statistical tests was set to 0.05.

RESULTS

\dot{V}_{O_2} of green turtles

The \dot{V}_{O_2} of 12 green turtles (29 trials) was measured in this study (Table S1). The body mass of the green turtles ($n=12$) ranged from 7.5 to 84.5 kg (16.6 ± 20.4 kg) and the \dot{V}_{O_2} of green turtles ranged from 0.19 to 0.94 ml O₂ min⁻¹ kg^{-0.83} at 15–25°C. The GLMM revealed that the \dot{V}_{O_2} of green turtles was affected by temperature and activity (AIC=-40.65; Table S3). The model equation of \dot{V}_{O_2} (ml O₂ min⁻¹ kg^{-0.83}) in juvenile green turtles, which included the effect of water temperature (T_w) and activity (A) based on MLE, was calculated as:

$$\dot{V}_{O_2} = 0.1200 \exp(0.0506T_w + 0.0026A). \quad (11)$$

The value when A was set to 0 (%) was considered the resting metabolic rate (ml O₂ min⁻¹ kg^{-0.83}) of green turtles.

Morphological measurement of two sea turtle species

The straight carapace length (SCL; cm) of 415 loggerhead (m_b 14.0–109.0 kg) and 150 green turtles (m_b 7.0–104.0 kg), as well as the frontal area (S ; m²) of 23 loggerhead (m_b 14.0–97.0 kg) and 7 green turtles (m_b 9.0–84.0 kg) were related to m_b ; however, morphological differences were observed between the two species in both SCL and S ($P<0.05$). Therefore, the regression analysis was divided into species (Table 2). The regression equations calculated by major axes analyses were as follows:

$$SCL_{\text{loggerhead}} = 17.955m_b^{0.343} \quad (12)$$

($R^2 = 0.92$, $F = 4875.4$, $P < 0.05$; Fig. 2A),

$$SCL_{\text{green}} = 19.208m_b^{0.330} \quad (13)$$

($R^2 = 0.98$, $F = 7367.2$, $P < 0.05$; Fig. 2B),

$$S_{\text{loggerhead}} = 0.005m_b^{0.736} \quad (14)$$

($R^2 = 0.91$, $F = 218.1$, $P < 0.05$; Fig. 2C),

$$S_{\text{green}} = 0.009m_b^{0.511} \quad (15)$$

($R^2 = 0.97$, $F = 177.2$, $P < 0.05$; Fig. 2D).

Cruising swim speed and stroke frequency from field measurements

From 2010 to 2019, a total of 1794.9 h (range 21.3–152 h per individual) of behavioural data were obtained from 15 loggerhead and 9 green turtles (Table 1; Table S2). The SCL and m_b of the instrumented turtles was 42.8–85.2 cm and 14.0–91.0 kg for loggerhead turtles and 43.7–72.2 cm and 11.5–55.5 kg for green turtles, respectively. The mean water temperature during the experiment was 15.7–22.8°C for loggerhead turtles and 18.1–22.8°C for green turtles, and the temperature range of respirometric measurements covered the temperature experienced in the field by the turtles. The mean cruising swim speed during the gradual ascent phase was 0.27–0.50 m s⁻¹ for 13 loggerhead turtles (m_b 30.0–91.0 kg) and 0.27–0.47 m s⁻¹ for 9 green turtles (m_b 11.0–55.5 kg). Data for two of the loggerhead turtles could not be obtained because of a propeller problem. The relationship between the cruising speed and m_b of loggerhead and green turtles was not significantly different between the two species ($P=0.92$). The cruising speed for both species was proportional to $m_b^{0.131}$ (Fig. 2E):

$$\text{Cruising swim speed} = 0.221m_b^{0.131}. \quad (16)$$

The cruising swim speed was typically faster with larger m_b ($R^2=0.22$, $F=77.8$, $P<0.05$). The stroke frequency during the gradual ascent phase obtained from 14 loggerhead turtles (m_b 14.0–91.0 kg) and 9 green turtles (m_b 11.0–55.5 kg) was 0.20–0.36 Hz and 0.27–0.40 Hz, respectively. Data for one loggerhead turtle could not be obtained owing to a data problem. The relationship between stroke frequency and m_b of loggerhead and green turtles was not significantly different between the two species ($P=0.67$). The stroke frequency for both species was proportional to $m_b^{-0.131}$ (Fig. 2F):

$$\text{Stroke frequency} = 0.491m_b^{-0.131}. \quad (17)$$

The stroke frequency was typically faster with smaller m_b ($R^2=0.29$, $F=157.8$, $P<0.05$).

Estimated energy cost of swimming and optimal swim speed

The frontal area (S) of turtles including the tag area was 0.0361–0.1446 m², and the estimated averaged drag coefficient (C_d) was 0.22–0.70 (Table 1; Table S2). Some turtles (ID: L1914, L1915, L1916 and G1921) did not indicate deceleration during the horizontal dive; therefore, C_d could not be estimated. According to Eqn 7, the optimal swim speed estimated from 12 loggerhead turtles (m_b 30.0–91.0 kg) and 8 green turtles (m_b 11.5–55.5 kg) ranged from 0.25 to 0.31 m s⁻¹ and 0.19 to 0.37 m s⁻¹, respectively. The predicted optimal swim speed of each

Table 2. Summary of allometric relationships in morphological and behavioural comparisons

Relationship	Turtle species	N	Scaling exponents (α , β , γ , δ)		
			Measured	95% CI	Predicted
Morphology					
SCL versus m_b^β	Loggerhead	415	0.343	0.333–0.352	
	Green	150	0.330	0.323–0.338	
S versus m_b^α	Loggerhead	24	0.736	0.633–0.840	
	Green	7	0.511	0.412–0.609	
Behaviour					
U versus m_b^γ	All ^a	22	0.131	0.016–0.251	0.05–0.13 ^b
SF versus m_b^δ	All ^a	23	-0.131	-0.213 to -0.049	-0.28 to -0.21 ^c

Allometric equations were calculated using mean values of straight carapace length (SCL; cm); frontal area (S ; m²); body mass (m_b ; kg); swim speed (U ; m s⁻¹); and stroke frequency (SF; Hz s⁻¹) in two turtle species. ^aIncludes loggerhead and green turtles (no significant difference between species). ^bEstimated from measured scaling exponent (γ) of morphological and metabolic features. ^cDifferent from 95% confidence interval (CI) for measured scaling exponent (δ).

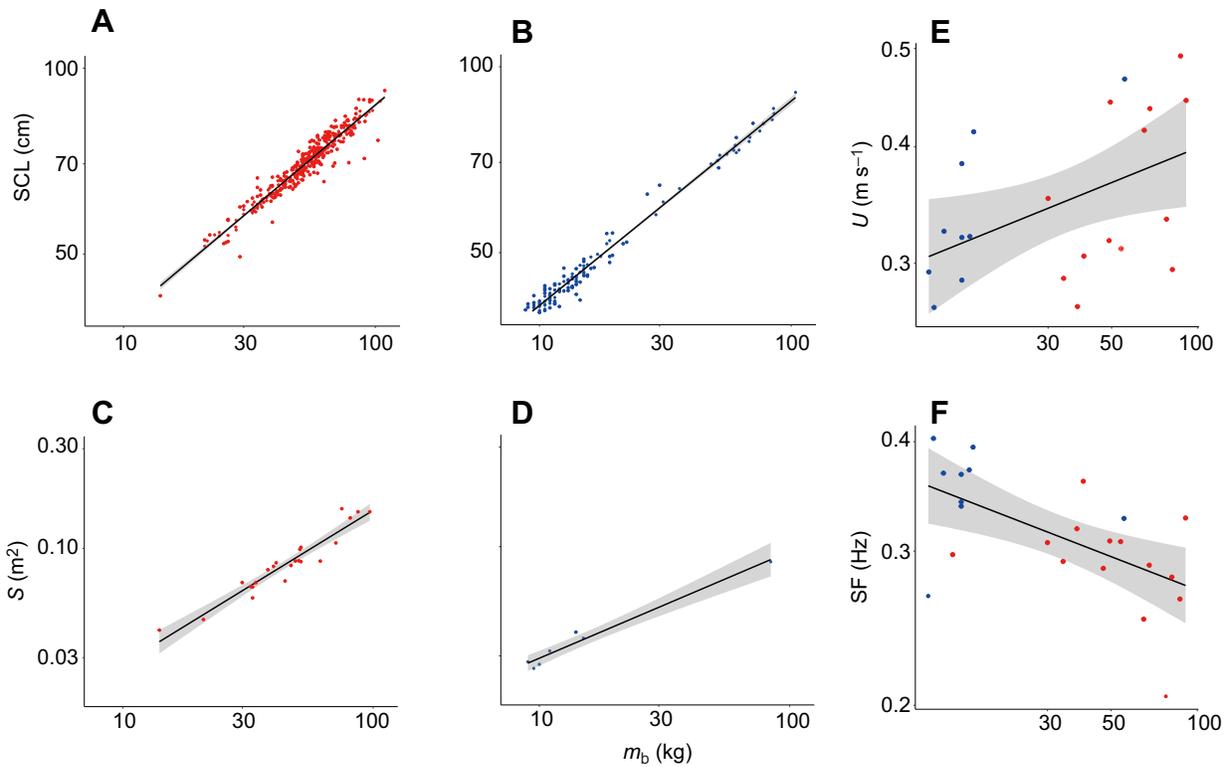


Fig. 2. The relationship between body mass (m_b) and morphology and behaviour. Relationship between m_b and straight carapace length (SCL) from (A) 415 loggerhead turtles and (B) 150 green turtles; frontal area (S) from (C) 23 loggerhead turtles and (D) 7 green turtles; (E) swim speed (U) from 13 loggerhead turtles and 9 green turtles; and (F) stroke frequency (SF) from 14 loggerhead turtles and 9 green turtles. All panels are double logarithmic plots. The red and blue dots indicate loggerhead and green turtles, respectively. The solid line and grey areas indicate the regression line and 95% confidence interval (CI), respectively.

individual agreed with the histogram-derived mode of the measured cruising swim speed (Fig. 3). For 16 out of 20 turtles, the majority of measured cruising speeds (80%) converged around the optimal swim speed, with less than a 30% increase from the total cost (J) of swimming at the optimal speed. However, the measured cruising swim speeds of L1901, L1904, L1918 and G1506 were slightly mismatched.

In addition, the energy cost was estimated under two model conditions: (1) the k value for sea turtles was replaced with that of seabirds (McKechnie et al., 2006), and (2) the k and $C_d S$ values for sea turtles were replaced with those of penguins (Clark and Bemis, 1979). The m_b of all individuals was assumed to be 30 kg. In model 1, the optimal swim speed was 0.9 m s^{-1} (Fig. 4, green line), which was faster than that of sea turtles but did not reach the optimal swim speed of penguins ($1.8\text{--}2.3 \text{ m s}^{-1}$). In model 2, the optimal swim speed was equal to that of penguins (Fig. 4, yellow line). The difference in cost between the models with horizontal and vertical descent (yellow and orange lines, respectively) was due to the cost of buoyancy.

Estimated relationship between m_b and optimal swim speed

SCL and S were proportional to $m_b^{0.343}$ and $m_b^{0.736}$ for loggerhead turtles, and to $m_b^{0.330}$ and $m_b^{0.511}$ for green turtles, respectively (Table 2). Therefore, the slopes of the optimal swim speed of sea turtles, estimated using Eqn 8 with reference to the morphological data of loggerhead turtles and green turtles, were as follows. For loggerhead turtles:

$$U_{\text{opt}} \propto (m_b^{0.83}/m_b^{0.736}(m_b^{0.343}U_{\text{opt}})^{-1/5})^{1/3} \propto m_b^{0.05}, \quad (18)$$

and for green turtles:

$$U_{\text{opt}} \propto (m_b^{0.83}/m_b^{0.511}(m_b^{0.330}U_{\text{opt}})^{-1/5})^{1/3} \propto m_b^{0.13}. \quad (19)$$

According to Eqns 18 and 19, the estimated optimal swim speed of sea turtles was in the range $m_b^{0.05}\text{--}m_b^{0.13}$. This result was statistically consistent with the measured slope being proportional to $m_b^{0.131}$ ($F=2.2$, $P=0.16$; $F=1.4$, $P=0.97$). In addition, if the optimal swim speed is proportional to $m_b^{0.05}\text{--}m_b^{0.13}$, the estimated stroke frequency of sea turtles can be calculated using Eqn 9 as follows:

$$\text{Optimal stroke frequency} \propto m_b^{0.05-0.13} \times m_b^{-1/3} \propto m_b^{-0.28}\text{--}m_b^{-0.21}. \quad (20)$$

Therefore, the optimal stroke frequency for sea turtles was estimated as proportional to $m_b^{-0.28}\text{--}m_b^{-0.21}$. This prediction was somewhat statistically inconsistent with the measured slope, which was proportional to $m_b^{-0.131}$ ($F=4.0$, $P=0.06$; $F=13.5$, $P<0.05$).

DISCUSSION

Do sea turtles swim at the optimal swim speed?

The optimal swim speed, which was estimated from the resting metabolic rate, C_d and S of each individual, agreed with the measured cruising speed in most individuals (Fig. 3). It was considered that sea turtles chose the optimal speed at which the energy cost per unit travel distance was minimised. According to Jones et al., (2013), the drag cost of tag attachment depends on the shape of the tag (square or teardrop), species (loggerhead or green)

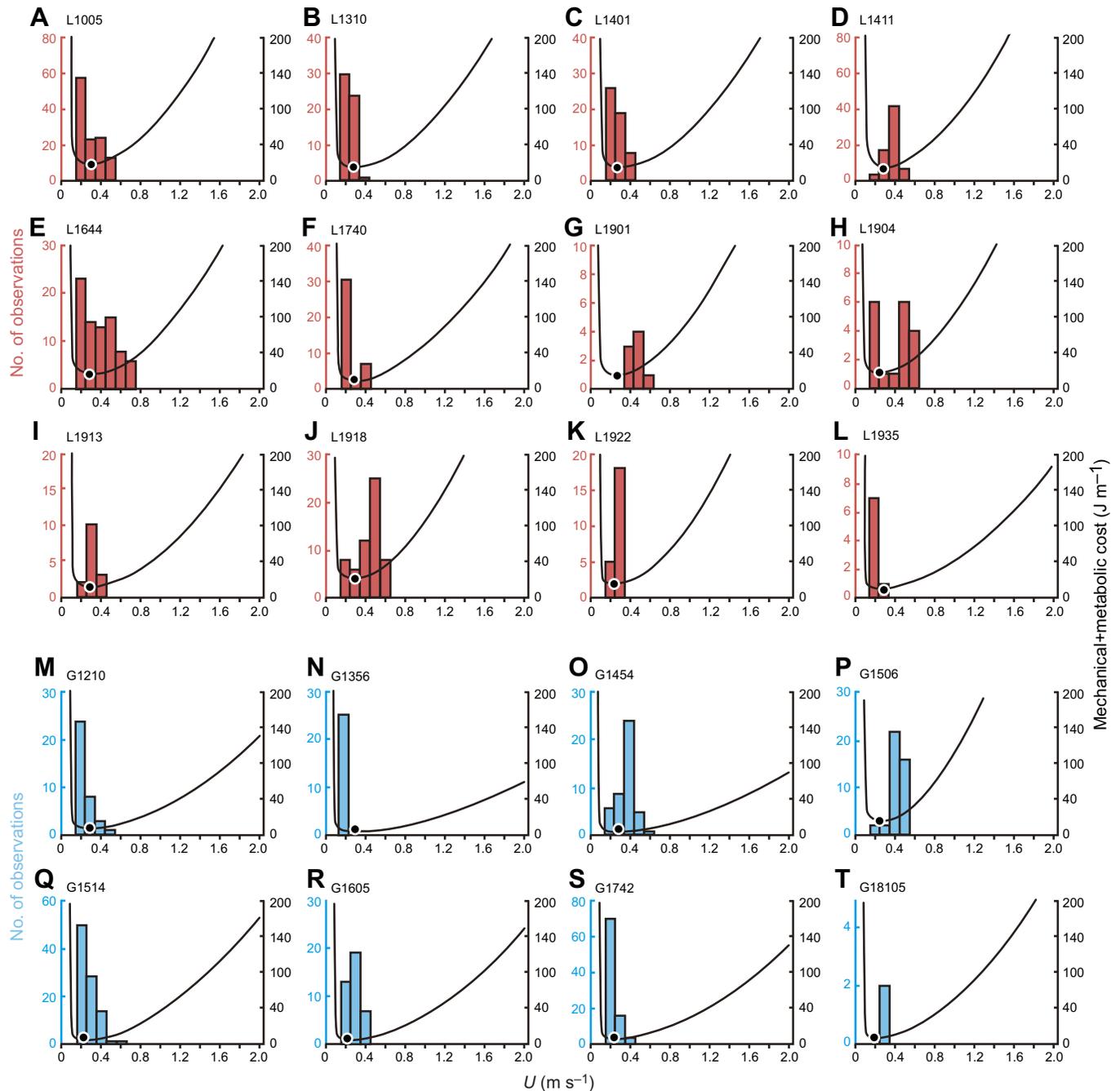


Fig. 3. Cruising swim speed of loggerhead and green turtles. Histograms indicate the number of observations of cruising swim speeds (U) during gradual ascent dives of 12 loggerhead turtles (A–L) and 8 green turtles (M–T). The black curves are total energy (mechanical+metabolic) cost of each swim speed. The filled circle indicates the optimal swim speed.

and the individual's frontal area. For example, the C_d of loggerhead turtles in our study would be expected to have an approximately 20–30% increase in the smallest turtle (L1913: 30.0 kg) and an approximately 10–20% increase in the largest turtle (L1901: 87.0 kg) because of tag attachment. For green turtles, the C_d would be expected to have an approximately 40–50% increase in the smallest turtle (G1742: 12.0 kg) and an approximately 40–50% increase in the largest turtle (G1506: 55.5 kg). If C_d was increased by 40% using the tag deployment condition of L1913 and G1506, the minimum COT (J m^{-1}) would have increased by 12% and 13%, respectively. However, the estimated optimal swim speeds did not

change much (from 0.26 to 0.24 m s^{-1} in L1913, and from 0.24 to 0.21 m s^{-1} in G1506). Therefore, the effect of tags on cruising swim speed seems to be very small, and correspondence between measured and estimated swim speeds is robust. Jones et al. (2013) measured the drag coefficient (with reference to the frontal area) of cast of turtles without tags and front flippers and found that $C_d=0.11$ –0.22, which is slightly lower than the value in our study ($C_d=0.22$ –0.70). The difference might be due to the absence of tag attachments and to the removal of the front flippers in their study. The λ value also affected the cruising swim speed. In the present study, the optimal swim speed was calculated with $\lambda=0.567$ (Hind

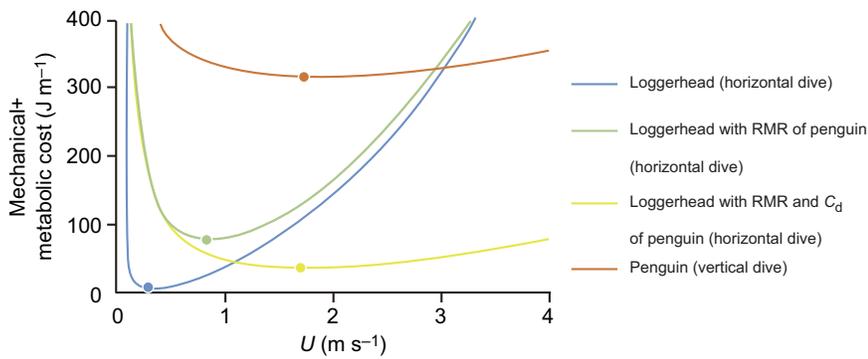


Fig. 4. Energy costs of loggerhead turtles and emperor penguins under various conditions. The blue lines indicate the energy cost when turtles swim horizontally with neutral buoyancy. The green and yellow lines indicate the energy cost when turtles swim horizontally (neutral buoyancy) with the same metabolic rate as seabirds and with the same resting metabolic rate (RMR) and drag coefficient (C_d) as penguins, respectively. The orange line indicates the energy cost when penguins descend vertically (pitch angle -90 deg) (Sato et al., 2010). All individuals were assumed to be 30 kg. Coloured circles indicate the optimal swimming speed in each model.

and Gurney, 1997) according to a previous study (Sato et al., 2010), where λ is the ratio of the drag coefficient during active swimming and gliding, which in some cases was set to more than 1 (Ribak et al., 2005). According to Eqn 7, it was predicted that the optimal swim speed of sea turtles would increase when λ was smaller than 0.576 and decrease when λ was larger than 0.576. However, even when λ was set in the range 0.2–3.0 (Weihs, 1974; Hind and Gurney, 1997), the optimal swim speed of sea turtles converged between 0.14 and 0.36 m s^{-1} (e.g. for a 50.0 kg loggerhead). Therefore, it is inferred that the variation of λ does not affect the main conclusion that sea turtles exhibit slower optimal swim speeds than seabirds and marine mammals. In the respiratory experiments, the percentage of activity time was calculated from the longitudinal-axis acceleration of turtles in the tank, and the optimal swim speed was estimated from the metabolic rate at 0% activity as the resting

metabolic rate. If the active metabolic rate had been considered when estimating the swim speed, the effect of degree of activity would have remained. However, in the present study, as resting metabolic rate was used in the estimation of optimal swim speed (Eqn 7), there should be no large deviation in our results. Four out of 20 turtles (L1901, L1904, L1918 and G1506) showed varying cruising swim speeds. In particular, the mean cruising swim speed of turtle L1901 was 0.50 m s^{-1} , although its estimated optimal swim speed was 0.27 m s^{-1} . This might have been due to a difference in the individual metabolic status and drag costs. Furthermore, the cruising swim speed was calculated from the phase of travel that occurred at least 12 h after release, but it is possible that some turtles exhibited unusual behaviours, such as prolonged stress after release or escape from captivity. In similar field experiments (Narazaki et al., 2009; 2013), the swim speed immediately after release tended to be faster (0.5–0.6 m s^{-1}) than in the present study (0.27–0.50 m s^{-1}). It was difficult to consider these individual-level conditions in our study. Although there are still points left to consider, we found that most turtles swam at their optimal swim speed.

Relationship between m_b , cruising swim speed and stroke frequency

The cruising swim speed of 13 loggerhead and 9 green turtles was proportional to $m_b^{0.131}$ and tended to be slightly faster for larger individuals (Fig. 2E). The optimal swim speed of sea turtles was predicted to be proportional to $m_b^{0.05}$ – $m_b^{0.13}$, which is statistically consistent with the observed results. Therefore, it was inferred that the optimal swim speed of sea turtles was consistent with the relationship between their own morphology, resting metabolic rate and m_b . It has been reported that the cruising swim speed of marine mammals and seabirds also increases in proportion to $m_b^{0.09}$, with larger individuals tending to have slightly faster cruising swim speeds (Watanabe et al., 2011). The relationship between cruising swim speed and m_b was not significantly different from the relationship predicted for optimal swimming speed, which was proportional to $m_b^{0.05}$ (Watanabe et al., 2011). Therefore, it can be considered that aquatic mammals, birds and reptiles adopt optimal swim speeds commensurate with their own resting metabolic rate and morphology, even among different taxa.

The stroke frequency of sea turtles was proportional to $m_b^{-0.131}$, with smaller turtles tending to exhibit more frequent strokes (Fig. 2F). It has been reported that marine mammals and birds exhibit stroke frequency proportional to $m_b^{-0.29}$ (Sato et al., 2007). Considering the relationship between optimal swim speed and m_b , the stroke frequency of sea turtles was estimated to be proportional to $m_b^{-0.28}$ – $m_b^{-0.21}$ according to Eqn 20. The measured slope (stroke frequency $\propto m_b^{-0.131}$) and the estimated slope (stroke frequency $\propto m_b^{-0.28}$ – $m_b^{-0.21}$) were close, but not statistically coincident (Table 2). The stroke frequency was affected not only by m_b

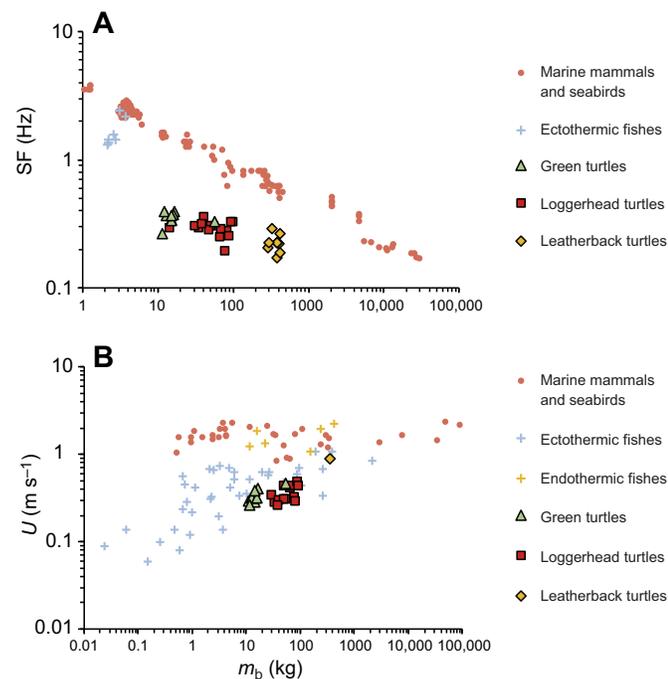


Fig. 5. Double logarithmic plots of dominant stroke frequency and cruising swim speed in relation to body mass. (A) The dominant or average stroke frequency (SF) of marine mammals and seabirds, ectothermic fishes, green turtles, loggerhead turtles and leatherback turtles. (B) The cruising swim speeds (U) of marine mammals and seabirds, ectothermic fishes, endothermic fishes, green turtles, loggerhead turtles and leatherback turtles. Stroke frequency data were obtained from published data for marine mammals, seabirds and leatherback turtles (Sato et al., 2007). Cruising swim speed data for marine mammals, seabirds, leatherback turtles and fishes were obtained from Watanabe et al. (2011, 2015).

but also by the resting metabolic rate. In this study, we measured the stroke frequency under a T_w of 15.7–22.8°C (Table 1). The variation in stroke frequency might have been caused by the resting metabolic rate related to the water temperature difference of 7°C. In addition, the size of the attached loggers might also have had an effect. From the result of stroke frequency versus m_b , it was concluded that sea turtles with smaller body sizes were more likely to exhibit higher frequency strokes. In terms of the relationship between m_b and stroke frequency, the stroke frequency of sea turtles is lower than that of mammals and birds with the same m_b (Fig. 5A; Sato et al., 2007). The resting metabolic rate in reptiles is generally 10–30 times lower than in mammals and birds (Else and Hulbert, 1985; Berner, 1999). The stroke frequency may be related to the fact that animals minimise energy costs when balancing the mechanical and physiological costs (see Eqns 5 and 7). Therefore, a lower stroke frequency and relatively slower swim speed can achieve a low total travelling energy cost for migrating turtles.

Two factors affecting the cruising swim speed of sea turtles

The optimal swim speeds of sea turtles were lower than those of penguins because of their lower metabolic rate, higher C_d and S (Fig. 4). Leatherback turtles, a family of sea turtles, have an intermediate resting metabolic rate between that of mammals and reptiles (Wallace et al., 2005; Wallace and Jones, 2008). Furthermore, only leatherback turtles belong to the family of Dermochelidae within sea turtles, and their morphological features are quite different from those of the Cheloniidae family, as the five longitudinal ridges on their carapace enhance hydrodynamic performance (Bang et al., 2016). Estimating optimal swim speed of leatherback turtles by Eqn 5 based on previous studies of metabolic rate, C_d and S (Wallace et al., 2005; Jones et al., 2013), the optimal swim speed for leatherback turtles weighing 30 kg and 300 kg was 0.6 and 0.8 m s⁻¹ (Fig. S3, green and yellow lines). These speeds are close to the measured cruising swim speeds (0.6–0.9 m s⁻¹) of leatherback turtles (267–363 kg) (Southwood et al., 2005; Sato et al., 2007). It is inferred here that leatherback turtles also swim at optimal swim speed.

Although the C_d in fish, which are ectothermic species, is similar to that of aquatic mammals and birds (Vogel, 1994), the swim speed of fishes (excluding species with regional endothermy) range from 0.06 to 1.1 m s⁻¹ (Watanabe et al., 2015; Fig. 5B), which is slower than the swim speed of aquatic mammals and birds (1–2 m s⁻¹). However, in case of tuna and sharks with regional endothermy, swim speed is faster than that of fishes without regional endothermy (1.09–2.25 m s⁻¹; Watanabe et al., 2015; Fig. 5B), and these speeds are comparable with those of aquatic mammals and birds. Therefore, the lower swim speed of ectothermic fishes may be due to their own lower resting metabolic rate. The COT has been widely calculated in fishes, birds and mammals (Sato et al., 2010; Watanabe et al., 2015; 2019; Castellini and Mellish, 2015). In the present study, we calculated the COT of sea turtles to estimate the optimal swim speed, and then compared this with measured cruising speed. We suggest that the cruising swim speed at minimum COT is selected regardless of taxonomic group.

Sea turtles have a carapace, which may result in greater drag costs than those experienced by penguins, which have more streamlined bodies. The high drag coefficient of sea turtles leads to a steep increase in the energy cost when the swim speed increases (Fig. S3, blue line) because the mechanical cost is proportional to U^2 (Eqn 5). Therefore, the ability of sea turtles to swim at an optimal swim speed might be more constrained than for penguins. However, turtles sometimes swim faster than their optimal swim speed. For example, a loggerhead turtle (m_b : 65.0 kg) swam at

0.88 m s⁻¹ (maximum 1.26 m s⁻¹) for 5 min while chasing a blue crab (*Portunus* sp.) (Fukuoka et al., 2016). The energy cost of fast swimming during this chase was approximately 3.5 times higher than that at the optimal swim speed; therefore, it was unlikely to be sustainable.

Ecological implications of cruising swim speed

Sea turtles exhibit slower cruising speeds than aquatic birds and mammals (Sato et al., 2007; Watanabe et al., 2011); however, their speeds are optimal for minimising their energy costs. If turtles swam at the same speed as aquatic mammals and birds (i.e. 2.0 m s⁻¹), the energy costs would be more than 15 times higher. Aquatic mammals and birds must eat high-energy food such as fish in order to satisfy their own high-energy demands (basal metabolic rate). Conversely, the basal energy demands of sea turtles are approximately one-tenth those of birds and mammals (Wallace and Jones, 2008). The main prey of turtles is low energy density and slow-moving organisms such as jellyfish, seaweed and benthic animals (Narazaki et al., 2013; Fukuoka et al., 2016; 2019). Compared with aquatic birds and mammals, sea turtles are able to survive at low energy costs; therefore, they may have adopted a corresponding strategy of slow swimming.

Cruising swim speed might be related to the annual migratory range of aquatic animals. Watanabe et al. (2015) showed that fishes with high resting metabolic rates tended to have faster cruising swim speeds and a wider annual migration range, which was defined as the maximum value of the linear distance on the Earth's surface between the two furthest points on an individual's migration loop. Leatherback turtles, which have a higher resting metabolic rate than loggerhead and green turtles (Wallace et al., 2005), exhibit a wider annual migration range of 4900 km (James et al., 2005). This trend can also be observed between intraspecific populations of loggerhead turtles. Loggerhead turtles in the western North Pacific have resting metabolic rates 1.4–5.7 times higher than those of the Mediterranean population (Kinoshita et al., 2018) and a reported maximum annual migration range of 3377 km (Narazaki et al., 2015), which is substantially larger than the migration range of the Mediterranean population (2100 km; Broderick et al., 2007). Although no studies have measured the cruising speed of the Mediterranean population, it is expected to differ among populations. Comparison of the annual migration range of loggerhead and green turtles shows that the latter exhibit a relatively narrow migration range (Fukuoka et al., 2015; Narazaki et al., 2015), although loggerhead and green turtles have a comparable metabolic rate and cruising speed. This may be because green turtles are predominantly herbivorous. However, the mean migration distance to breeding and foraging sites for green turtles (806 km) is significantly longer than that for loggerhead turtles (618 km) (Hays and Scott, 2013). Therefore, it is likely that green turtles are also capable of migrating long distances. In summary, resting metabolic rate is closely related to the cruising speed of sea turtles and may induce differences in annual migration range at the interspecies and interpopulation levels. Different migratory ranges may change the type, quality and quantity of food eaten, as well as the energy balance, which may provide a basis for life history polymorphisms.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: C.K.; Methodology: C.K., K.S.; Software: C.K., T.F., T.N., Y.N.; Formal analysis: C.K.; Investigation: C.K., T.F., T.N.; Resources: T.F., T.N., Y.N.; Writing - original draft: C.K.; Writing - review & editing: T.F., T.N., Y.N., K.S.; Visualization: C.K.; Supervision: K.S.; Project administration: C.K., T.F., T.N.; Funding acquisition: C.K., T.F., K.S.

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Supplementary information

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