

RESEARCH ARTICLE

High resting metabolic rates with low thermal dependence induce active dives in overwintering Pacific juvenile loggerhead turtles

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ABSTRACT

The metabolic rate and activity of sea turtles generally decreases with decreasing seasonal ambient temperature. Juvenile loggerhead turtles in the Mediterranean Sea made prolonged inactive dives (>400 min), indicating a state of dormancy during the cold winter period. However, seasonal differences in dive duration were not detected in juvenile loggerheads in the western North Pacific, even though the ambient water temperature changed by more than 10°C. Thus, metabolic states might differ among populations, explaining differences in the diving behaviour of juveniles during winter. Here, we tested the hypothesis that the active overwintering behaviour of juvenile loggerheads in the western North Pacific is driven by a high resting metabolic rate (RMR) with low thermal dependence. The RMR of juveniles in the western North Pacific ($N=13$) was 1.4–5.7 times higher ($Q_{10}=1.8$) than that of juveniles in the Mediterranean Sea ($Q_{10}=5.4$). To validate the high RMR values in the western North Pacific, the difference between core body temperature and ambient water temperature (ΔT_b) was estimated from measured RMR and was compared with measured ΔT_b . The measured and estimated ΔT_b matched each other. In addition, most of the dives conducted by the turtles in the western North Pacific were within the calculated aerobic dive limit (cADL) expected from the measured metabolic rate. Our results indicate that high RMR with low thermal dependence induces active diving during the overwintering periods of juvenile loggerheads in the western North Pacific, supporting the suggestion that metabolic states differ among populations.

KEY WORDS: Respirometry, Body temperature, Diving behaviour, Overwintering strategy, Satellite tracking, *Caretta caretta*

INTRODUCTION

Ambient temperature is one of the most important factors influencing the physiological states of ectothermic reptiles. The physiological processes and activities of sea turtles change with ambient water temperature (T_w). For instance, metabolic rates decrease with decreasing T_w in loggerhead sea turtles, *Caretta caretta* (Lutz et al., 1989; Hochscheid et al., 2004), and green turtles, *Chelonia mydas* (Southwood et al., 2003). Loggerhead turtles have the widest geographic range of any species in the family Cheloniidae and are routinely found inhabiting tropical to temperate zones (Wallace et al., 2010). Therefore, this species experiences the widest range of T_w in

various environments. Loggerheads have a clear phylogeographic structure among the major nesting populations in the Atlantic, Indian and Pacific Oceans and the Mediterranean Sea (Bowen et al., 1994). Thus, the behavioural response to T_w might vary in relation to the population in loggerhead turtles. For instance, juvenile loggerhead turtles in the Mediterranean Sea showed median dive durations of 5.5 min in summer and 341 min in winter when the T_w dropped from about 25°C to 15°C (Hochscheid et al., 2005). During winter, most dives were typical resting dives on the sea bottom, indicating that the turtles had entered a state of dormancy (Hochscheid et al., 2007). In contrast, juvenile turtles in the western North Pacific seem to maintain active dives and foraging behaviour throughout the winter season (Narazaki et al., 2015), despite the water temperature dropping by the same degree as that experienced by the turtles in the Mediterranean Sea population (i.e. to an ambient temperature of <15°C). Furthermore, the dive duration of juvenile turtles in the western North Pacific was not significantly affected by T_w (Narazaki et al., 2015). Thus, the juveniles in the western North Pacific might have a specific physiological state allowing them to maintain activity throughout the cold winter season.

Oxygen stores and metabolic rates determine the diving duration of lung breathing animals, such as sea turtles (Kooyman, 1989). The calculated aerobic dive limit (cADL) is estimated from oxygen stores and metabolic rates during dives (Costa et al., 2001). The metabolic rate of sea turtles changes with T_w . Q_{10} is the widely recognized index used to assess the effects of temperature change. The typical Q_{10} value for the metabolic rate of reptiles falls within the range of 2–3 (Bennett and Dawson, 1976); thus, the metabolic rate increases 2- to 3-fold with each 10°C increment in temperature. Juvenile loggerhead turtles in the Mediterranean Sea exhibit a major drop in metabolic rate ($Q_{10}=5.4$) from summer to winter T_w (27.1 to 15.3°C) (Hochscheid et al., 2004). During winter, the prolonged dives (>400 min) of juvenile loggerheads in the Mediterranean Sea would have been within aerobic limits, as the animals returned to the surface to breathe before the cADL was reached (Hochscheid et al., 2005). Thus, a significant reduction in the metabolic rate prolonged the dives of these turtles during the cold winter season. If juveniles in the western North Pacific have high metabolic rates with low thermal dependence, the dive duration might remain short with no seasonal differences. Therefore, the active dives of juvenile turtles in the western North Pacific during the cold winter season could be attributed to their own high metabolic rate with low thermal dependence.

Resting metabolism results in 100% heat production (Calder, 1984). During internesting periods, adult loggerhead turtles are able to maintain their body temperature (T_b) 0.7–1.7°C higher than the T_w through metabolic heat production (Sato et al., 1995). If juvenile loggerhead turtles in the western North Pacific have a higher metabolic rate, they should be able to maintain a temperature difference between their T_b and the T_w , which could be estimated from their metabolic heat.

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List of symbols and abbreviations

A	activity ratio (%)
AIC	Akaike information criterion
cADL	calculated aerobic dive limit (min)
$F_{E_{O_2}}$	oxygen concentration in effluent air
$F_{I_{O_2}}$	oxygen concentration in influent air
GLM	generalized linear model
K	thermal conductivity ($J s^{-1} m^{-1} ^\circ C^{-1}$)
M_b	body mass (kg)
MLE	maximum likelihood estimation
Q	rate of heat production ($J s^{-1} m^{-3}$)
Q_{10}	temperature coefficient
RMR	resting metabolic rate ($ml O_2 min^{-1} kg^{-0.83}$)
SCL	straight carapace length (cm)
SRDL	satellite relay data logger
SST	sea surface temperature
T_b	body temperature
T_w	ambient water temperature ($^\circ C$)
\dot{V}_{O_2}	oxygen consumption rate ($ml O_2 min^{-1} kg^{-0.83}$)
ΔT_b	difference between body and ambient water temperature ($^\circ C$)

It is important to understand the physiological state of juvenile sea turtles during the winter because this affects behavioural patterns, such as diving, which are directly related to the growth and survival rate of juveniles. This study aimed to test the hypothesis that active dives during the overwintering period of juveniles in the western North Pacific are driven by their high resting metabolic rate (RMR) with low thermal dependence. We measured the RMR of juveniles caught in the western North Pacific using a respiratory system in a tank set at various water temperatures (15–25°C). The difference between core T_b and T_w (ΔT_b) was estimated using the measured metabolic rate and a spherical thermodynamic model (Sato, 2014). This information was used to validate the measured metabolic rate by comparing estimated ΔT_b and measured ΔT_b . Dive duration and experienced T_w were tracked using satellite telemetry to determine whether the measured dive duration was correlated with the cADL estimated from the measured metabolic rate. Our results should provide new insights into how metabolic states differ among sea turtle populations.

MATERIALS AND METHODS**Study animals and site**

Juvenile loggerhead turtles, *Caretta caretta* (Linnaeus 1758), were collected between 2009 and 2017. These individuals were incidentally captured by commercial set nets between Miyako and Ofunato on the Sanriku coastal area of Japan (38°55'N to 39°40'N, 141°40'E to 142°05'E). All turtles were promptly transferred 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) from the notch to the tip of the carapace, as well as body mass (M_b). Following morphological measurement, each captured turtle was used for the experiments described below.

Respirometric measurements

The oxygen consumption rate (\dot{V}_{O_2}) of 13 juvenile loggerhead turtles were measured using a respiratory system from July to October in 2016 and 2017 to calculate metabolic rate. Short-term acclimation (ca. 3 h) before measurements did not produce accurate \dot{V}_{O_2} values (Hochscheid et al., 2004). Thus, 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. Juvenile loggerhead turtles are caught at a wide range of T_w (12.0–23.8°C) in our study area (Narazaki et al., 2015). In the present study, all experimental turtles were caught when T_w was relatively low (15.5–20.0°C; Table 1), and the turtles must have previously been living at cold temperatures (around 15°C). Therefore, 1 week of cold acclimation was considered sufficient. The water temperature in the tank was controlled by a thermostat. Turtles L1601, L1612, L1624 and L1627 were not fed during the experimental period when maintained at the same water temperature. The experimental fasting period lasted no longer than 33 days. \dot{V}_{O_2} was measured 4–7 times during each experimental period. After finishing one experimental period, the turtles were moved to a tank with a different water temperature and fed a diet of 250 g Japanese common squid, *Todararodes pacificus*, per day for 1 week. Turtles L1709, L1710, L1715, L1728, L1731, L1740, L1741, L1743 and L1753 were fed during the experimental period, and just one \dot{V}_{O_2} measurement was obtained at each water temperature (15, 20 and 25°C). After measurement, the turtles were moved to a tank with a different water temperature and were kept at this temperature for at least 1 week to acclimate.

In both cases, the experimental tank was covered with a wooden board with a breathing hole. A 60.8 l air chamber (45×45×30 cm high) was placed over this hole, so the turtles could only breathe within the chamber (Fig. 1). Respirometric measurements lasted for 156–410 min and were conducted during the daytime. The exhaled air of each turtle was collected from the air chamber. The air samples were passed through a dehumidifier to remove water vapour and then pumped into an oxygen analyser (Xentra 4100, Servomex Ltd, East Sussex, UK). The flow rate (\dot{V}_E) of the respirometer was fixed at 3.0 l min⁻¹ using a mass flow controller ($\pm 2\%$, Type HM1171A, Tokyo Keiso Co., Ltd, Tokyo, Japan). Effluent air was dried over silica gel, and 200 ml min⁻¹ of the dried effluent air was directed into the oxygen analyser. The oxygen analyser was calibrated using dry air from outside (set to 20.946% oxygen) and pure stock nitrogen (set to 0.000% oxygen). A computer was used to record the oxygen concentration in effluent air ($F_{E_{O_2}}$) every 1 s. The \dot{V}_{O_2} was

Table 1. Individual data for respirometric measurements and body temperature

Turtle ID	Capture date (day/month/year)	Capture T_w ($^\circ C$)	Initial M_b (kg)	Experimental temperature ($^\circ C$)	
				\dot{V}_{O_2}	ΔT_b
L1601	30/6/2016	16.5	35.5	15, 20, 25	15
L1610	16/7/2016	15.5	43.5	–	20
L1612	21/7/2016	16.1	37.5	20	–
L1618	25/7/2016	17.8	38.5	–	20
L1624	1/8/2016	19.0	36.0	15, 25	25
L1627	4/8/2016	18.5	24.0	15	–
L1709	13/7/2017	16.6	33.0	15, 20, 25	15, 20, 25
L1710	13/7/2017	16.6	26.0	15, 20, 25	15, 20, 25
L1715	20/7/2017	17.2	56.0	15, 20	15, 20, 25
L1728	2/8/2017	19.3	46.0	15, 20, 25	15, 20, 25
L1731	3/8/2017	20.0	57.5	15, 20, 25	15, 20, 25
L1740	21/8/2017	17.7	34.0	15, 20, 25	15, 20, 25
L1741	21/8/2017	17.7	51.0	15, 20, 25	15, 20, 25
L1743	21/8/2017	17.4	39.0	15, 20, 25	15, 20, 25
L1753	13/9/2017	20.0	37.0	15, 20, 25	15, 20, 25

T_w , ambient water temperature; M_b , body mass; \dot{V}_{O_2} , oxygen consumption rate; ΔT_b , difference between body and ambient water temperature.

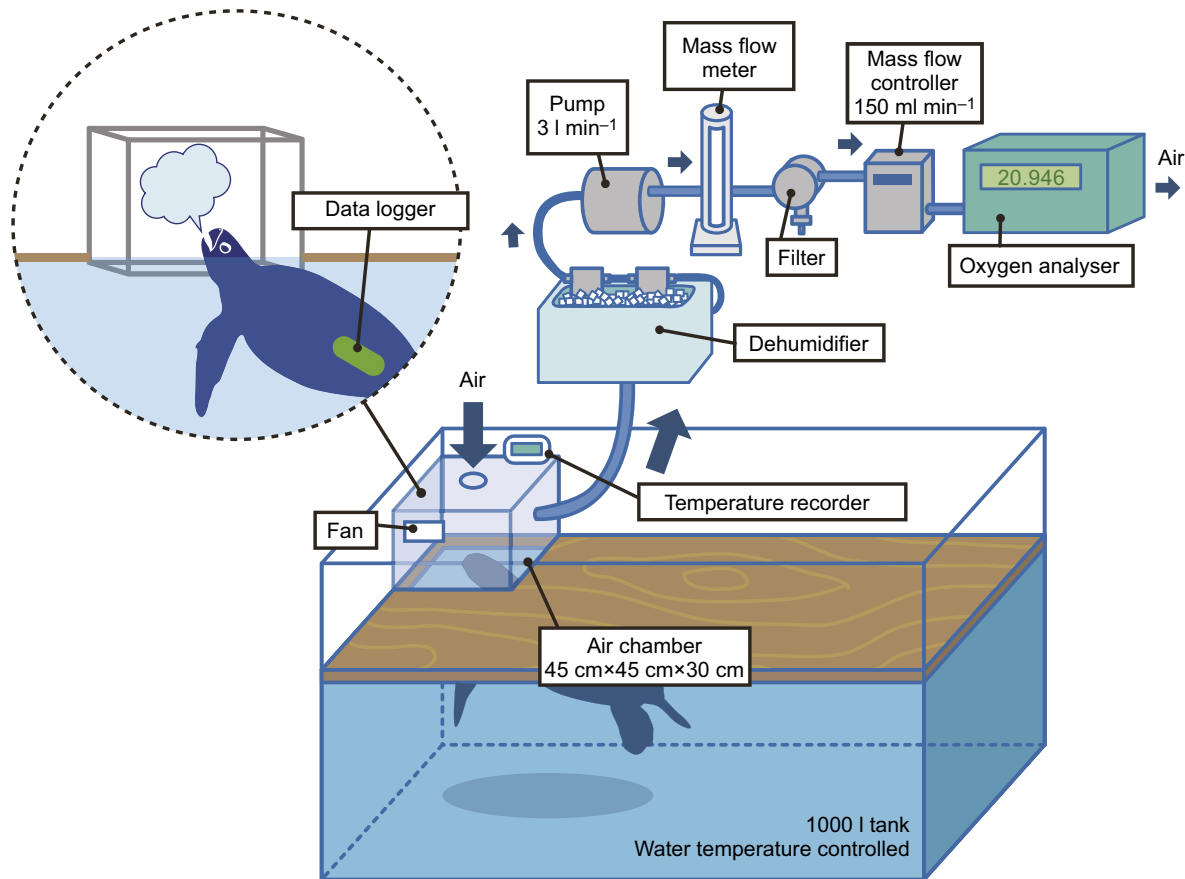


Fig. 1. Experimental design for the respirometry system. Oxygen concentration in the breathing hole was measured using an oxygen analyser after air dehumidification. External (attached to the turtle carapace) and internal (in the stomach) data loggers recorded activity and body temperature, respectively.

calculated using the formula from Withers (1977) as follows:

$$\dot{V}_{O_2} = \dot{V}_E \times (F_{I_{O_2}} - F_{E_{O_2}}) / [1 - (1 - RQ) \times F_{I_{O_2}}], \quad (1)$$

where RQ represents the respiratory quotient and was assumed to be 0.8, following previous studies (Shirai et al., 2012), and the error of energy equivalent fitted was assumed to fall within the usual range (Koteja, 1996). The oxygen concentration in influent air ($F_{I_{O_2}}$) was 20.946%, which is equivalent to an $F_{I_{O_2}}$ of 0.2095. All results are presented at standard temperature (0°C) and pressure (1 atm) under dry (STPD) conditions. Total oxygen consumption (ml O_2) was calculated and averaged over 1 min and converted into a mass-specific rate of oxygen consumption (ml O_2 min⁻¹ kg^{-0.83}). A scaling exponent of 0.83 has been widely used to calculate the metabolic rate of sea turtles (Prange and Jackson, 1976; Southwood et al., 2003; Enstipp et al., 2011).

In general, \dot{V}_{O_2} increases with increasing activity (Hochscheid et al., 2004; Southwood et al., 2003). To monitor activity, we attached a data logger (M190L-D2GT, 15 mm in diameter, 53 mm in length, 18 g in air; Little Leonardo, Tokyo, Japan) along the longitudinal axis on the turtle carapace (Fig. 1). The data logger records water temperature at 1 Hz, depth at 1 Hz and single-axis acceleration (longitudinal) at 16 Hz. Igor Pro software (version 6.36; Wave Metrics Inc., Portland, OR, USA) was used to analyse the acceleration data. Recorded acceleration data included both low-frequency gravity components and high-frequency specific components (mainly caused by dynamic movements, such as flipper beating). We used a filter at a threshold frequency that was unique for each turtle to create a low- and

a high-frequency signal. This filter was defined by a power spectral density plot and a continuous wavelet transform filter in the Ethographer software (version 2.04; Sakamoto et al., 2009). The surge acceleration (longitudinal axis) was divided into two types of behaviour spectrum, namely 'resting' and 'active', using *k*-means clustering and the time ratio of activity (%) was calculated from the active component. When the activity ratio was 0%, the \dot{V}_{O_2} was considered to represent RMR.

Previous studies reported that the \dot{V}_{O_2} of sea turtles is influenced by temperature, activity and fasting duration (Hochscheid et al., 2004; Southwood et al., 2003; Jones et al., 2009). Jones et al. (2009) reported that the \dot{V}_{O_2} of green turtles that had fasted for 10 days was 52% lower than that of fed turtles. A generalised linear model (GLM) with a Gaussian distribution and a log link function was used to evaluate the \dot{V}_{O_2} . The response variable was \dot{V}_{O_2} and the explanatory variables were water temperature, number of days fasting and activity. The most parsimonious model was selected using the Akaike information criterion (AIC). As a result of GLM, \dot{V}_{O_2} was affected by temperature and activity. The following model was applied to estimate \dot{V}_{O_2} :

$$\dot{V}_{O_2} = \alpha \exp(\beta T_w + \gamma A), \quad (2)$$

where *A* is the activity ratio during the experimental period (%). The maximum likelihood estimation (MLE) of the three parameters (α , β , γ) was obtained using the observed \dot{V}_{O_2} , temperature and activity.

Effect of T_w on metabolic rate

The Q_{10} was calculated to examine how T_w affects metabolic rate. The model equation for resting (0% activity) in relation to temperature was used to calculate $\dot{V}_{O_{2,1}}$ at a temperature of 15.0°C (T_1) and $\dot{V}_{O_{2,2}}$ at a temperature of 25.0°C (T_2), which were used to calculate Q_{10} . This calculation was achieved by inserting the calculated values into the equation as follows:

$$Q_{10} = (\dot{V}_{O_{2,2}}/\dot{V}_{O_{2,1}})^{[10/(T_2 - T_1)]}. \quad (3)$$

T_b and T_w measurements

T_b of juveniles was measured from July to October in 2016 and 2017. Following the method used in a previous study (Sato et al., 1994), the turtles were induced to swallow a data logger (M2000-D2GT, 17 mm in diameter, 75 mm in length, 30.3 g in air; Little Leonardo; accuracy of $\pm 0.1^\circ\text{C}$) to record core T_b at 1 Hz. T_w was recorded at 1 Hz by the data logger (M190L-D2GT) attached to the turtle carapace (Fig. 1). The experimental T_w was set between 15 and 25°C.

ΔT_b estimation

Sato (2014) showed that thermoregulatory capabilities of loggerhead turtles are expressed as a temperature difference (ΔT_b) between the core T_b and T_w . We estimated the ΔT_b from the metabolic rate and a spherical thermoregulatory model assuming that turtles are spherical in shape. If the spherical thermodynamic model (see Sato, 2014) was solved under the steady-state condition $\partial T_b(r,t)/\partial t=0$, then:

$$\Delta T_b = \frac{Q}{6K} r_R^2, \quad (4)$$

where Q is the rate of heat production ($\text{J s}^{-1} \text{m}^{-3}$), K is the thermal conductivity ($\text{J s}^{-1} \text{m}^{-1} \text{ }^\circ\text{C}^{-1}$) and r_R is the radius (m) of the spherical model. Q was calculated from the \dot{V}_{O_2} ($\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-0.83}$) in this study using a value of 20.0832 $\text{J ml}^{-1} \text{O}_2$. The thermal conductivity K was assumed to be 1.2 (Sato, 2014). The radius r_R of the spherical model was calculated from the density of the body (1046.5 kg m^{-3}) and the M_b of each individual (Sato, 2014).

Measurement of dive duration and T_w by satellite tracking

To track long-term (>200 days) T_w and dive duration, Satellite Relay Data Loggers (SRDL: Sea Mammal Research Unit, St Andrews, UK) were attached to the carapace of 12 turtles during 2009–2014. Four out of 12 turtles were the same individuals used in Narazaki et al. (2015). All turtles were released in Otsuchi Bay, Iwate, Japan ($39^\circ 21' 05''\text{N}$, $141^\circ 56' 04''\text{E}$). Data on dive duration were processed and compressed onboard and transmitted via the ARGOS system. The information on each dive included dive duration, end of dive time and maximum dive depth. A dive was recorded when the turtle descended below 3 m and ended when the turtle ascended above 3 m or when the saltwater switch was dry at any time. The SRDL also measured T_w every 4 s at a resolution of 0.1°C , providing temperature profiles over the depth range surveyed by the turtles. Of all the temperatures measured, 12 depth–temperature points were selected based on the conventional broken-stick algorithm used for expendable bathythermographs. The resulting data were stored in a buffer where they were made available for transmission for up to 5 days. Therefore, we refer to water temperature recorded at 2 m depth (the shallowest temperature obtained by the SRDL) as an approximate measure of sea surface temperature. Summer and

winter seasons were defined as the periods between 1 May and 31 October, and 1 November and 30 April, respectively, following Narazaki et al. (2015). The differences in T_w , as well as the difference in dive duration between summer and winter, were compared using the Wilcoxon rank sum test. The value for statistical significance was $P < 0.01$.

Estimation of the cADL

Following Costa et al. (2001), cADL (min) was calculated as the total oxygen store (ml O_2) divided by \dot{V}_{O_2} ($\text{ml O}_2 \text{ min}^{-1}$) for each loggerhead turtle. As \dot{V}_{O_2} varied with temperature, monthly average sea surface temperature (SST) derived from the SRDLs was used to calculate the monthly average \dot{V}_{O_2} . In general, lung breathing animals hold oxygen in their lungs, blood and muscle. Based on published values, the lung, muscle and blood of a loggerhead turtle can store 15.5, 5.9 and 0.8 $\text{ml O}_2 \text{ kg}^{-1}$ of oxygen, respectively (Lutz and Bentley, 1985). Summing up these values, the calculated total oxygen store (ml O_2) of each turtle in the present study was $22.2 (\text{ml O}_2 \text{ kg}^{-1}) \times M_b (\text{kg})$. Thus, the average cADL for each month was described by dividing the total oxygen store by the average monthly \dot{V}_{O_2} , which was estimated from the T_w experienced by the turtles.

All statistical analyses were performed with R3.3.2 (R Development Core Team, <http://www.R-project.org>). Means \pm s.d. are presented, unless otherwise indicated.

Ethics statement

All experimental procedures followed the guidelines of the Animal Ethic Committee of the University of Tokyo, Japan, and the protocol of the study was approved by this committee (P12-13, P13-6, P14-3, P15-7, P16-5 and P17-1). 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.

RESULTS

\dot{V}_{O_2} and the effect of T_w

The \dot{V}_{O_2} of 13 turtles was measured (Table 1). When the turtles were captured, seawater temperature around the set nets was between 16.1 and 20.0°C (Table 1). The body mass of the turtles ranged from 24.0 to 57.5 kg ($39.4 \pm 10.4 \text{ kg}$). \dot{V}_{O_2} ranged from 0.19 to 0.49 $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-0.83}$ ($0.31 \pm 0.08 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-0.83}$) at 15°C ($N=12$, 21 trials), from 0.25 to 0.71 $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-0.83}$ ($0.43 \pm 0.13 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-0.83}$) at 20°C ($N=11$, 19 trials), and from 0.44 to 0.94 $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-0.83}$ ($0.63 \pm 0.14 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-0.83}$) at 25°C ($N=10$, 18 trials). \dot{V}_{O_2} increased with increasing water temperature (Fig. 2).

The GLM revealed that \dot{V}_{O_2} was affected by temperature and activity (AIC = -84.16; Table 2). According to the model equation that included the effect of fasting, \dot{V}_{O_2} was decreased by 1.5% over 30 days. However, 'days of fasting' was not included as an explanatory variable in the most parsimonious model (Table 2). The model equation of \dot{V}_{O_2} ($\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-0.83}$) in juvenile turtles in the western North Pacific, including the effect of T_w and A based on MLE, was calculated as:

$$\dot{V}_{O_2} = 0.1098 \exp(0.0581 T_w + 0.0075 A). \quad (5)$$

Using Eqns 3 and 5, we calculated a Q_{10} of 1.8 for the temperature effect from 15 to 25°C. There was a 44.0% decrease in resting \dot{V}_{O_2} under experimental water conditions from 25 to 15°C.

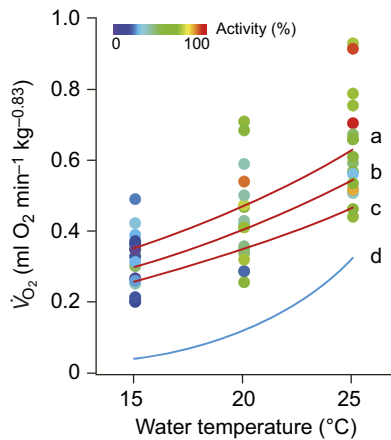


Fig. 2. Oxygen consumption rate (\dot{V}_{O_2}) at various water temperatures. Coloured circles indicate \dot{V}_{O_2} of 13 juvenile turtles in the western North Pacific (58 trials) for each activity level. Red curves indicate \dot{V}_{O_2} estimated for non-fasting turtles using Eqn 5 under different the activity levels: (a) 40% (b) 20% and (c) 0% activity. The blue curve (d) indicates resting \dot{V}_{O_2} of juvenile turtles in the Mediterranean Sea (Hochscheid et al., 2004).

We compared the \dot{V}_{O_2} at various water temperatures experienced by juvenile turtles in the western North Pacific and the Mediterranean Sea (Fig. 2). The data for resting \dot{V}_{O_2} of turtles in the Mediterranean Sea were extracted from a previous study (Hochscheid et al., 2004). The juvenile turtles in the western North Pacific had an RMR that was 1.4–5.7 times higher that of juvenile turtles in the Mediterranean Sea at temperatures ranging between 25 and 15°C (Fig. 2, lines c and d).

Measured and estimated ΔT_b

ΔT_b was measured from 13 juvenile loggerhead turtles, for which M_b ranged from 26.0 to 57.5 kg (41.0 ± 9.3 kg) (Table 1). Both T_b and \dot{V}_{O_2} were measured for 11 out of the 13 individuals. All turtles maintained an average T_b of 0.25–1.11°C above that of the T_w during the experimental period (Fig. 3). The proportion of time spent active during the experimental period ranged from 1.6% to 86.0%.

Measured dive duration and cADL

Dive duration and experienced ambient SST were measured in 12 free-ranging individuals from 2009 to 2014 (Table 3). Tracking

Table 2. Generalized linear model (GLM) investigation of the relationship between \dot{V}_{O_2} , temperature, activity and days of fasting

Model	AIC	Δ AIC
$\dot{V}_{O_2} \sim \text{days of fasting}$	-30.81	53.35
$\dot{V}_{O_2} \sim \text{null}$	-32.57	51.59
$\dot{V}_{O_2} \sim \text{activity} + \text{days of fasting}$	-58.32	25.84
$\dot{V}_{O_2} \sim \text{activity}$	-59.79	24.37
$\dot{V}_{O_2} \sim \text{temperature} + \text{days of fasting}$	-77.26	6.74
$\dot{V}_{O_2} \sim \text{temperature}$	-79.10	5.06
$\dot{V}_{O_2} \sim \text{temperature} + \text{activity} + \text{days of fasting}$	-82.19	1.97
$\dot{V}_{O_2} \sim \text{temperature} + \text{activity}$	-84.16	

AIC, Akaike information criterion. Bold indicates the most parsimonious model.

duration ranged from 216 to 517 days (334 ± 83 days). The turtles ranged from 63.3 to 82.5 cm in SCL (74.2 ± 8.0 cm) and 33.5 to 81.5 kg (62.3 ± 15.5 kg) in M_b . All turtles experienced a winter period. Dive duration was obtained for a total of 46,669 dives. T_w during tracking was significantly lower in winter ($19.3 \pm 2.6^\circ\text{C}$) compared with that in summer ($22.0 \pm 3.1^\circ\text{C}$) (Wilcoxon rank sum test: $W=3826734$, $P<0.01$). Mean dive duration was significantly longer during winter periods (23.5 ± 28.7 min) and shorter during summer periods (17.8 ± 20.5 min) (Wilcoxon rank sum test: $W=257303654$, $P<0.01$), but most of the ranges overlapped; 75.9% and 67.3% of dives in summer and winter, respectively, lasted less than 30 min (Fig. 4). The maximum recorded dive duration was 300 min (turtle ID: L1408) when the daily T_w was 12.8°C in winter (Fig. 5). After the longest dive, there was a long surface time of more than 30 min. The cADL was calculated using \dot{V}_{O_2} based on Eqn 5. Turtles have been shown to actively dive in all seasons (Narazaki et al., 2015), so they were assumed to be constantly active during dives. Thus, the activity was considered to be 100% for Eqn 5. Given this assumption, dive durations of 42,478 dives out of 46,669 dives (91.0%) performed by the 12 turtles were shorter than the cADL, indicating that most of the dives of each individual ended before the cADL was reached (Table 3). Turtles allocated most of the dive time to short dives (<100 min) and the percentage of time spent for such short dives was 69.0% to 96.1% for 12 turtles in winter (Fig. 6). The dive duration, SST, cADL and dive profile in summer and winter of two individuals (turtle ID: L0910, L0912) are shown in Fig. 7 as typical examples. Fig. 8 shows how water temperature affects the cADL of juvenile turtles (50 kg) in the western North Pacific and the Mediterranean Sea.

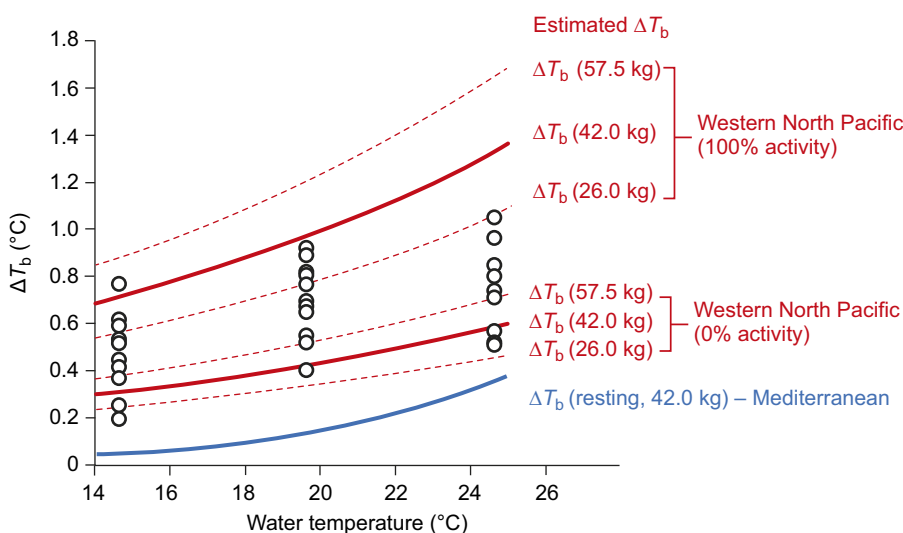


Fig. 3. Relationship between estimated and measured difference between core body and ambient temperature (ΔT_b). The estimated ΔT_b (red lines) for each body mass and activity level (0% to 100%) and measured ΔT_b (open circles) from 13 juvenile turtles in the western North Pacific (31 trials) are shown. Solid and dashed red lines show average body mass and maximum and minimum body mass, respectively. The solid blue line indicates estimated ΔT_b from RMR of juvenile turtles in the Mediterranean Sea (Hochscheid et al., 2004).

Table 3. Summary of satellite-tagged loggerhead turtles

ID	M_b (kg)	SCL (cm)	Day of release (day/ month/year)	No. of days monitored	No. of dives	Dives <cADL (%)
L0910	33.5	58.5	20/8/2009	403	2495	94.4
L0912	40.5	63.3	20/8/2009	239	5176	84.9
L1004	59.0	77.8	23/7/2010	311	5022	96.6
L1005	77.7	82.5	23/7/2010	255	3629	92.3
L1209	57.0	72.8	11/9/2012	216	3382	89.4
L1215	58.0	73.2	30/9/2012	309	2037	95.2
L1305	72.0	77.6	14/7/2013	289	3447	91.3
L1310	81.5	78.2	14/7/2013	360	4005	94.9
L1408	48.0	64.3	4/8/2014	352	3140	84.4
L1410	70.0	80.4	17/8/2014	366	4832	89.9
L1411	73.5	80.7	17/8/2014	517	6368	88.1
L1452	76.5	80.9	24/9/2014	397	3136	96.0

The cADL of juvenile turtles in the Mediterranean Sea was calculated using eqn 5 in Hochscheid et al. (2004) as routine \dot{V}_{O_2} . The cADL of turtles in the western North Pacific changed from 77.7 to 43.4 min between 15 and 25°C. By comparison, the cADL of turtles in the Mediterranean Sea changed from 395.9 to 73.8 min.

DISCUSSION

Juvenile loggerhead turtles in the Mediterranean Sea that made prolonged inactive dives lasting more than 400 min during winter might enter a state of dormancy (Hochscheid et al., 2005, 2007). In contrast, Narazaki et al. (2015) reported that juvenile loggerhead turtles in the western North Pacific conducted active dives throughout the winter, even though the water temperatures reached values as low as 10.3°C. In the present study, we tested the hypothesis that active dives during the overwintering periods of juvenile loggerheads in the western North Pacific are driven by high RMRs with low thermal dependence. We confirmed this hypothesis, showing that juvenile turtles in the western North Pacific had higher RMR (1.4–5.7 times) with lower thermal dependence than juvenile turtles in the Mediterranean Sea for water temperatures between 25 and 15°C (Fig. 2). In addition, the juveniles in the western North Pacific maintained their ΔT_b by using their metabolic heat (Fig. 3). The juvenile loggerheads in our study did not show a clear fasting effect for metabolic rate. Although the metabolic rate of green turtles decreases by 52% over 10 days of

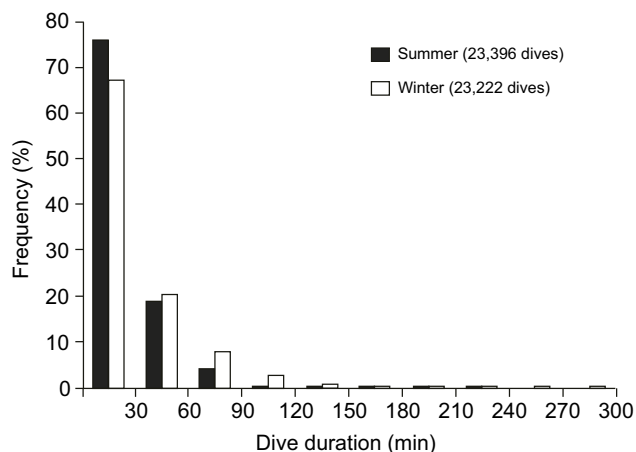


Fig. 4. Frequency distribution of dive duration from 12 turtles. Dive duration is shown in summer (May–October) and winter (November–April).

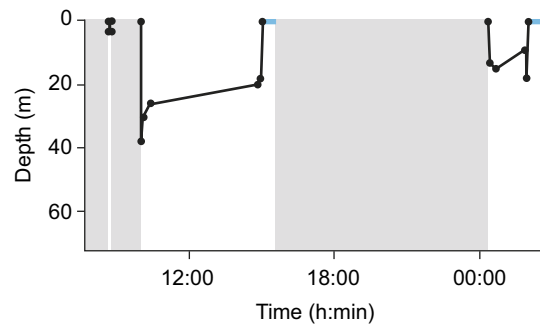


Fig. 5. Record of the longest dive profiles (300 min). The longest dive was recorded for turtle L1408 experiencing a sea surface temperature (SST) of 12.8°C in February. The pre- and post-dive periods are also indicated. After the 300 min dive, there was long post-dive surface time of more than 30 min (indicated by blue lines). No dive profile data were transmitted during the shaded periods.

fasting (Jones et al., 2009), the metabolic rate of loggerhead turtles in the present study decreased by 1.5% over 30 days. Thus, the effect of digestive heat seems to be modest for juvenile loggerheads in the western North Pacific.

Validation of high metabolic rate for juvenile turtles in the western North Pacific

The high RMR value was verified using two independent approaches, ΔT_b and cADL. The resting metabolic rate results in 100% heat production (Calder, 1984). Adult female loggerhead turtles in the western North Pacific maintain core temperature 0.7–1.7°C above T_w throughout the interesting period (Sakamoto et al., 1990; Sato et al., 1994). This temperature difference was maintained by turtles using their own metabolic heat (Sato et al., 1995). We found that the T_b of juvenile turtles in the western North Pacific was also maintained above T_w , with observed ΔT_b being derived from their own metabolic heat (Fig. 3). Therefore, juvenile loggerhead turtles in the western North Pacific seem to be able to maintain higher ΔT_b than juveniles in the Mediterranean Sea by producing heat from their own high metabolic rate. In other words, metabolic heat production of juveniles in the Mediterranean Sea does not maintain as high a ΔT_b as that for juveniles in the western North Pacific (Fig. 3).

Juvenile turtles tracked for more than 200 days in the western North Pacific conducted most dives (42,478 out of 46,669, 91.0%, $N=12$) within the cADL (Fig. 7, Table 3). Thus, juvenile turtles in the western North Pacific performed aerobic dives within the estimated duration when considering their oxygen stores and high metabolic rate. Sea turtles rarely perform anaerobic dives (Hochscheid et al., 2005; Okuyama et al., 2012). If they exceed the aerobic threshold during dives, prolonged post-dive surface time is necessary to clear accumulated lactic acid (Kooyman et al., 1980). Very long dives (>100 min) were exceptional in turtles in the western North Pacific (Fig. 6), but some dives (4191 out of 46,669 dives) did exceed the cADL. There was a long surface time (>30 min) after the longest dive (300 min; turtle ID: L1408), but there was not always a long surface time after long dives that exceeded the cADL. Turtles might control the dive duration and subsequent post-dive surface time to clear lactic acid generated from dives exceeding cADL, similar to the strategy used by Galápagos fur seals (Hornig, 2012). Most of the turtles in the western North Pacific live offshore (Narazaki et al., 2015) and conduct gradual ascent dives in midwater during winter (Fig. 7). In contrast, Hochscheid et al. (2005, 2007) reported that most turtles in the

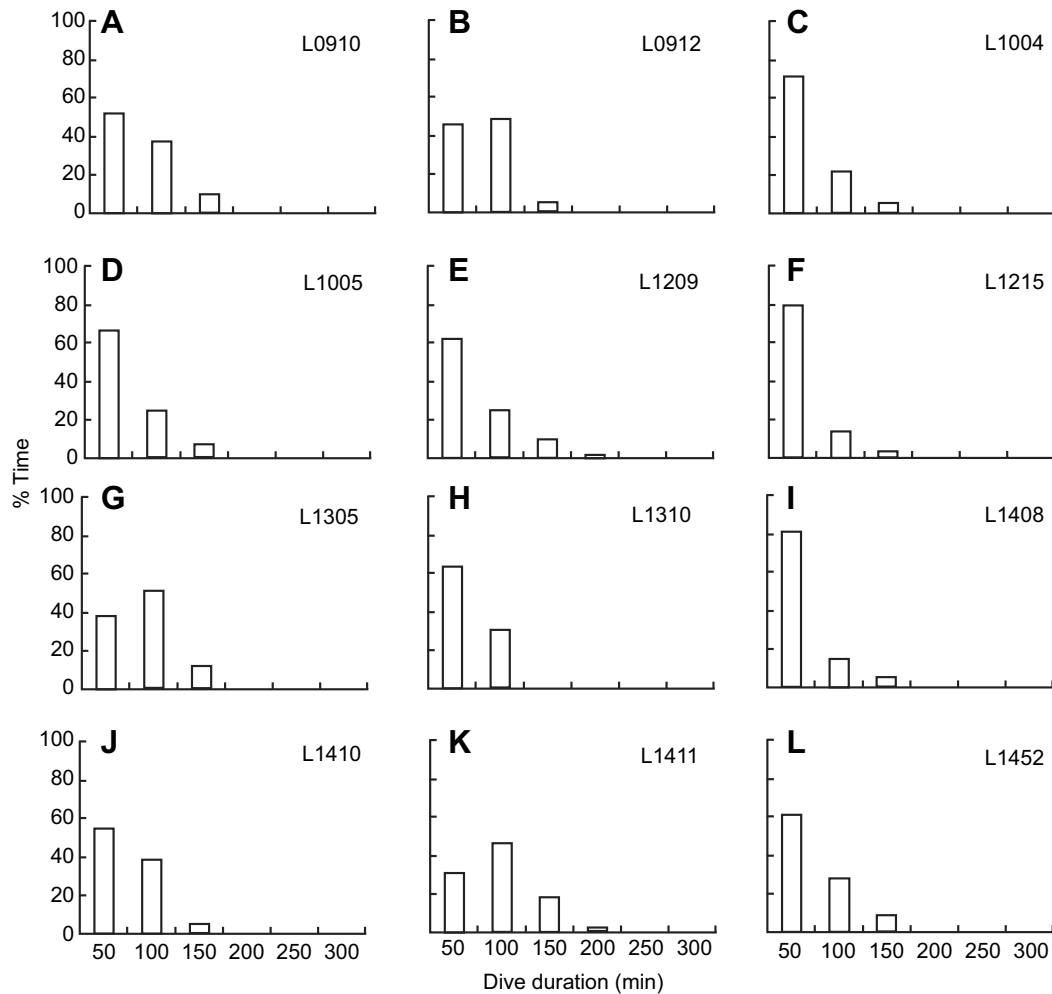


Fig. 6. Dive time allocation for 12 overwintering juvenile turtles. Bars indicate the time allocation to dives for each individual (A–L) during winter (November–April).

Mediterranean Sea stayed in coastal areas and conducted U-shaped dives to rest at the sea bottom in winter. The differences in dive shape between the two populations probably depend on overwintering habitats (oceanic versus neritic). In winter, a high proportion of dives performed by juvenile loggerheads in the Mediterranean Sea lasted more than 180 min (85–95%; Hochscheid et al., 2007) whereas the majority of dives by juveniles in the western North Pacific lasted less than 100 min (69.0–96.1%; Fig. 6) and long dives (>180 min) were rarely conducted. Thus, the metabolic rate generated different cADLs in the western North Pacific and the Mediterranean Sea populations (Fig. 8), which should explain why the dive durations differed between populations. Our study confirmed that juvenile loggerhead turtles in the western North Pacific maintained higher RMR than those in the Mediterranean Sea.

Effect of T_w on metabolic rate (Q_{10})

Temperature is the most important factor regulating metabolic rate in sea turtles. As previously reported (Hochscheid et al., 2004; Lutz et al., 1989), the metabolic rate of juvenile loggerhead turtles is positively correlated with T_w . Our results indicated that the degree to which temperature affected metabolic rate differed between populations. The metabolic rate of juvenile turtles originating from the western North Pacific slightly declined ($Q_{10}=1.8$) from 25.0 to 15.0°C. In comparison, Hochscheid et al. (2004) reported a distinct decline in the metabolic rate of loggerhead turtles in the

Mediterranean Sea ($Q_{10}=5.4$) from 27.1 to 15.3°C. Based on the different Q_{10} values, the thermal response in metabolic rate differed between the western North Pacific and the Mediterranean Sea populations. The typical Q_{10} value for the metabolic rate of reptiles ranges from 2 to 3 (Bennett and Dawson, 1976). The leatherback turtle is a remarkable exception, whereby the metabolism of muscle tissue allows them to tolerate low T_w at high latitudes, giving them thermal independence ($Q_{10}=1.0$) (Penick et al., 1998). Green turtles appear to be capable of maintaining activity year round, with low Q_{10} (=1.5) values for metabolic rate when T_w decreases from 26°C to 17°C (Southwood et al., 2003). The Q_{10} of juvenile loggerhead turtles in the western North Pacific indicates that they have a greater tolerance of thermal fluctuations than juvenile loggerhead turtles in the Mediterranean Sea. In winter, the juvenile loggerheads in the Mediterranean Sea made prolonged inactive dives, whereas the juveniles in the western North Pacific conducted only slightly longer dives in winter than in summer. Such differences in the seasonal pattern of dive duration between the two populations are consistent with Q_{10} trends between summer and winter.

Ecological implications of differences in RMR

In this study, we found that the RMR of juvenile loggerhead turtles in the western North Pacific is higher than that of juvenile loggerhead turtles in the Mediterranean Sea. Such differences in RMR between individuals or populations have been reported in

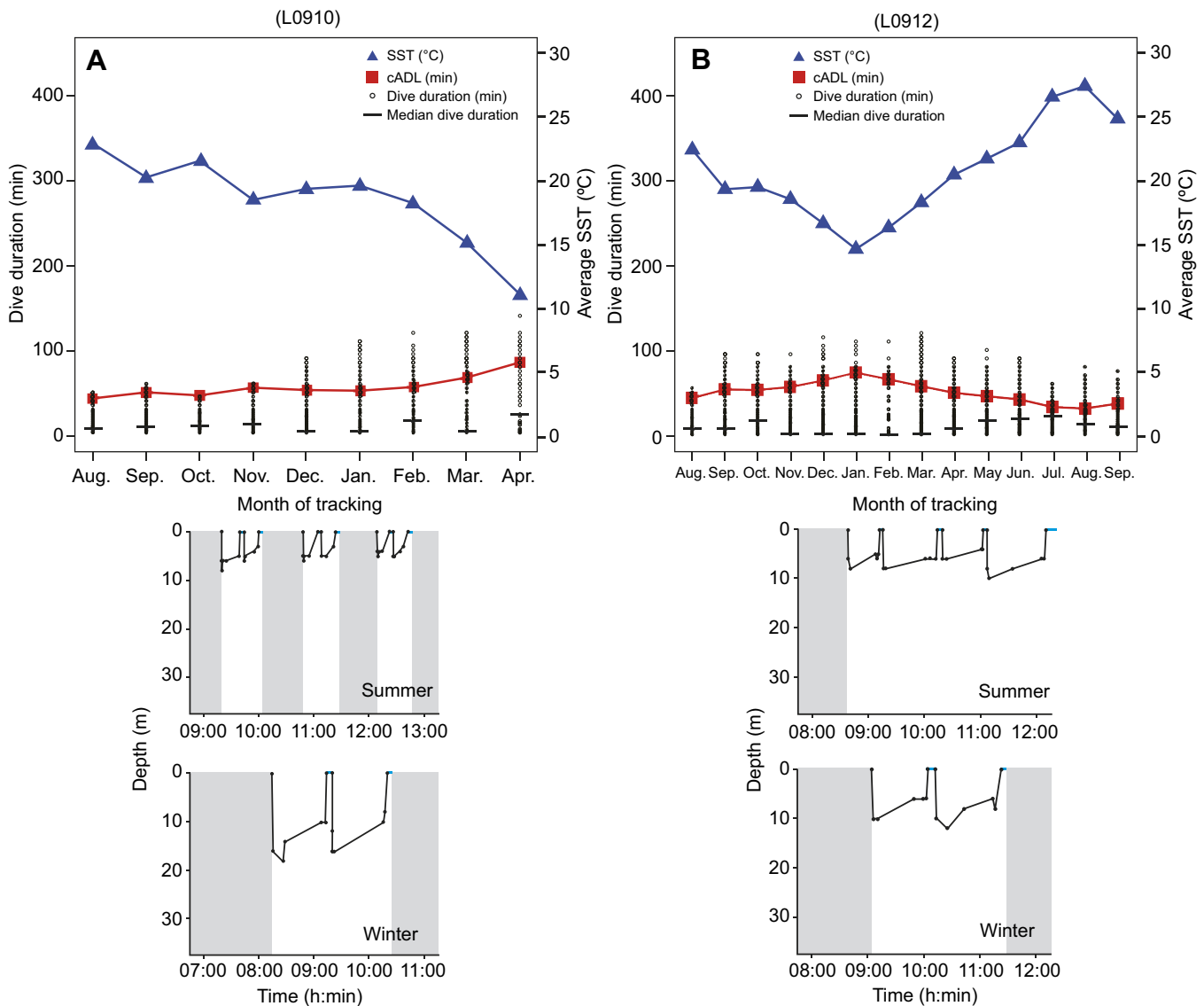


Fig. 7. Typical example of the relationship among dive duration, SST and calculated aerobic dive limit (cADL). Dive duration of each turtle (A: L0910, B: L0912) for different months during the tracking period. The monthly average cADL and monthly average SST are also shown. Solid bars indicate the median dive duration in each month. The lower panels show examples of the diving profile of the two individuals (L0910, L0912) in summer and winter. The SST was 20.8 and 11.5°C (summer and winter, respectively) for L0910 and 18.5 and 13.8°C (summer and winter, respectively) for L0912. The post-dive surface time is indicated by blue lines. No dive profile data were transmitted during the shaded periods.

different animal taxa (Burton et al., 2011; Biro and Stamps, 2010; Arnott et al., 2006). In some fish and mammalian species, individuals with relatively high RMR are more active or aggressive than those with lower RMR (Biro and Stamps, 2010). In the case of the Atlantic silverside, *Menidia menidia*, which is a broadly distributed species of marine fish, high-latitude populations tend to have higher RMR and growth rates than low-latitude populations (Arnott et al., 2006). It has also been hypothesized that RMR affects fitness. The ‘context dependence’ hypothesis states that high RMR individuals are likely to have higher fitness when environmental conditions are favourable and lower fitness when foraging conditions are poor (Burton et al., 2011). Thus, if food abundance is satisfied, individuals with high RMR would profit, while those with low RMR would have higher fitness when food conditions are poor because they have lower self-maintenance costs and can devote more energy to growth and reproduction. The western North Pacific is an area of high productivity because of the

confluence of three currents (Kawai, 1972; Sugimoto and Tameishi, 1992). The juvenile loggerheads in the western North Pacific overwinter offshore at 28–40°N (Narazaki et al., 2015). In this area, the surface water converges as a result of the Ekman Transport generated by westerly winds and trade winds (Roden, 1980). A chlorophyll front is generated by phytoplankton, with many zooplankton and free-floating gelatinous prey converging (Olson et al., 1994). Despite their low caloric value (Doyle et al., 2007), dense aggregations of gelatinous prey might offer sufficient food resources for juvenile turtles during summer (Narazaki et al., 2013). Because the juvenile turtles conducted active dives in offshore areas during winter, they would eat gelatinous prey as the main food resource. In contrast, the productivity in the sea surface layer is much lower in the Mediterranean Sea, because of the sedimentation of nutrients beneath the euphotic zone (Pinet, 2006). It is possible that there is not enough food for active overwintering by juvenile loggerheads in the Mediterranean Sea. Therefore, conditions in the

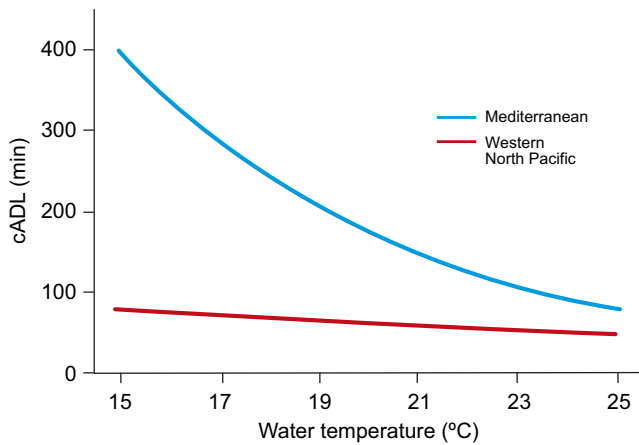


Fig. 8. Effect of water temperature on cADL estimated for two populations. The blue line indicates the cADL of a turtle in the Mediterranean Sea (M_b 50 kg) from \dot{V}_{O_2} data in Hochscheid et al. (2004) and the red line indicates the cADL of a turtle in the western North Pacific (M_b 50 kg; present study).

western North Pacific might favour juvenile turtles with high metabolic rates, facilitating their survival and growth. In comparison, conditions in the Mediterranean Sea might favour juvenile turtles with low metabolic rates. Juvenile turtles might respond flexibly to contrasting food environments by adjusting their RMR, supporting the context dependence hypothesis. As a result, the flexibility of RMR might facilitate different overwintering strategies, such as the ‘sit-and-wait’ strategy in the Mediterranean Sea (Hochscheid et al., 2005) and the ‘spend more, gain more’ strategy in the western North Pacific (Narazaki et al., 2015). Thus, we suspect that the high RMR with low thermal dependence of juvenile loggerheads in the western North Pacific induces active dives during the overwintering period.

This study presents the first evidence of intraspecific differences in RMR in sea turtles across temperature ranges. Researchers are interested in why RMR varies across species. However, there are many complex factors, with both intrinsic and extrinsic influences; thus, it is difficult to clarify the mechanism causing variation in RMR within the same species (Burton et al., 2011). Loggerhead turtles have the widest geographical range of any member of the Cheloniidae (Wallace et al., 2010). The physiological state of turtles might vary across populations in response to the different environments they inhabit. Therefore, it is important to conduct comparative studies of RMR, because RMR must be an ecological and evolutionary trait. The present study only compared juvenile loggerhead turtles from two populations. Juveniles originating from the western Atlantic exhibit a dichotomous migratory strategy, with residents versus non-residents (Mansfield et al., 2009). Such migratory variation could be induced by differences in their physiological state. Thus, further studies on how RMR varies among other populations and life stages would be important to understand how it affects their fitness.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

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

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