東京大学大学院新領域創成科学研究科
環境学研究系自然環境学専攻
海洋生命環境学分野

平成２４年度
修士論文

前肢を欠損したアカウミガメの遊泳能力の評価
Evaluating the swimming ability of forelimbs-lost loggerhead turtles, *Caretta caretta*

2013 年 1 月 24 日提出
2012 年度 3 月修了
指導教員　佐藤克文　准教授

47-106623
鬼塚(林)果林

平成二十四年度修士論文

前肢を欠損したアカウミガメの遊泳能力の評価

鬼塚(林) 果林

Table of contents

1. Introduction

Loggerhead turtle, *Caretta caretta*, is one of seven extant species of sea turtles and spends most of its lifetime underwater. A sufficient swimming ability is essential for survival of sea turtles because they have to swim for foraging, migrating, and avoiding predators. The oldest sea turtle skeleton was found in Brazil in the Early Cretaceous Period of some 110 million years ago, and the morphology of the extant species of sea turtles is similar to that of the 110 million years ago (Hirayama 1998). One reason that sea turtles could have flourished for such a long time is their great swimming ability to migrate for long distances to avoid dangers of extinction from sudden environmental change (Kamezaki 2012a). However, sea turtle's population has been decreasing due to human exploitations, such as bycatch, excessive hunting, and decline in spawning grounds exacerbated by shore embankment (Matsuzawa and Kamezaki 2012). As of 2012, five out of seven species were listed as either critically endangered or endangered species in the IUCN Red List of Threatened Species (IUCN 2012), and have been increasing concerns regarding the conservation of sea turtles worldwide.

A female loggerhead turtle that lost half of left forelimb and one third of right forelimb probably due to shark attack was found in a set net in Kii Channel, Japan, in June 2008 (Fig. 1). The functions of forelimbs are important for sea turtle locomotion because sea turtles, including loggerhead turtles, use their forelimbs to generate thrust underwater (Wyneken 1997; Kamezaki 2012b), and also because female sea turtles use their forelimbs to move on land for nesting. Thus, reduced size of forelimbs would negatively affect sea turtle's survival in the wild. There was a controversy to whether releasing the forelimb injured turtle, named 'Yu', back in to the ocean or continue keeping it under protection. After the controversy, movements to protect 'Yu' until it recovers its own swimming ability became stronger among people around Kobe City. Being incited by this movement, the Sea Turtle Association of Japan established a project to improve 'Yu's' swimming ability by attaching artificial fins. To understand the swimming ability of an injured turtle under natural conditions, right forelimb-lost turtle, named 'Hikari', and healthy turtles under natural conditions were also studied.

In the present study, the swimming behaviors of limb-handicapped 'Yu', those of healthy turtles in captivity as controls, and those of sea turtles under natural conditions were monitored by using animal-borne recorders. The purpose of this monitoring was to compare the swimming ability of 'Yu' with a smaller forelimb area than that of healthy turtles, the swimming ability of 'Yu' with an artificial fins compared to that of healthy turtles, and the swimming ability of the right forelimb-lost sea turtle under natural conditions.

Fig. 1 The forelimb injured sea turtle 'Yu'

2. Materials and Methods

2. 1 Swimming of sea turtles

Sea turtles including loggerhead turtles generate thrust forward direction by moving their forelimbs like wings of birds, which is called powerstroke (Wyneken 1997). Therefore, forelimbs are critical for sea turtle locomotion. Sea turtles swim forward in water by stroking their forelimbs up and down. As they swim, four kinds of forces act on their body: "thrust" (forward), "drag" (backward and parallel to thrust), "buoyancy" (upward and equal to the weight of sea water displaced), and "gravity" (downward) (Fig. 2).

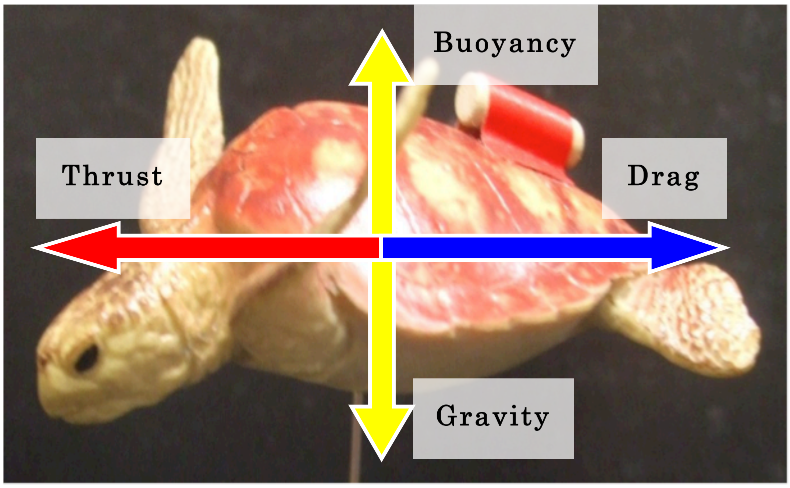

Fig. 2 Forces that act on a swimming sea turtle.

When a sea turtle swims horizontally at constant speed, the thrust and drag, horizontal forces and the buoyancy and gravity, vertical forces are balanced. Sea turtles produce thrust to swim forward by generating lift forces by up-and-down movement of forelimbs. The strength of thrust (lift) depends on water density (ρ_w), lift coefficient of forelimbs (C_{Lf}), area of forelimbs (S_f), and stroke speed (U_f). The strength of drag that works opposite to thrust, however, depends on water density, drag coefficient of body (C_{Db}), frontal projected area (S_b), and swim speed (U_b). At a quasi-steady state, thrust and drag are balanced, which can be expressed as Equation 1.

$$\frac{1}{2}\rho_w C_{Lf} S_f {U_f}^2 = \frac{1}{2}\rho_w C_{Db} S_b {U_b}^2 \quad \text{Eq. 1}$$

It is assumed that water density, drag coefficient, and frontal projected area in Equation 1 would not change before or after application of the artificial fins. However, lift coefficient, area of forelimbs, stroke speed, and swim speed would likely differ after application of the artificial fins. Thus, by focusing on those four forces, Equation 1 can be turned into an equation that signifies the square of lift coefficient; area of forelimbs and stroke speed are proportional to the square of swimming speed (Eq. 2).

$$C_{Lf} S_f {U_f}^2 \propto {U_b}^2 \quad \text{Eq. 2}$$

The stroke speed (U_f) in Eq. 2 can be expressed as the product of stroke frequency (F) that represents how many times sea turtles stroke their forelimbs up and down per second, and the curved distance from the highest point to the lowest point of one stroke (A) (Eq. 3).

$$U_f = FA \quad \text{Eq. 3}$$

In this study, it was assumed that the curved distance from the highest point to the lowest point of one stroke would not change (the distance could differ if the length and area of forelimbs changed), so it is possible to say stroke speed is always proportional to stroke frequency. Therefore, instead of stroke speed, stroke frequency was applied to Equation 2 (Eq. 4).

$$C_{Lf} S_f F^2 \propto {U_b}^2 \quad \text{Eq. 4}$$

Then, Equation 5 evolved from Equation 4.

$$U_b \propto F\sqrt{C_{Lf} S_f} \quad \text{Eq. 5}$$

From Equation 5, it is expected that swim speed would be faster if stroke frequency or lift coefficient becomes higher, or area of forelimbs becomes larger. The swimming ability was evaluated based on Equation 5, which shows three factors that influence on sea turtle swim speed:

stroke frequency, lift coefficient, and area of forelimbs.

As Equation 5 shows, swim speed is proportional to stroke frequency and to the square root of lift coefficient and area of forelimbs. Focusing on stroke frequency that is directly proportional to swim speed, the relationship between swim speed and dominant stroke frequency was used to examine swimming ability, in terms of swim speed at certain stroke frequency calculated from linear regression lines. If two sea turtles stroke their forelimbs at the same frequency, the one that achieved higher swim speed was deemed to have better swimming ability than the other. Since 'Yu' has smaller area of forelimbs due to injury, it can be expected that 'Yu' could not achieve the same swim speed as healthy turtles at same frequency; that is 'Yu's' swimming ability would be lower than that of healthy turtles. Then, the swimming ability of 'Yu' using artificial fins similar to the size of healthy turtles was expected to become more like to healthy turtles (Fig. 3). The swimming ability was evaluated by swim speed at a certain stroke frequency as previously stated, relative lift coefficient and the distance covered per stroke.

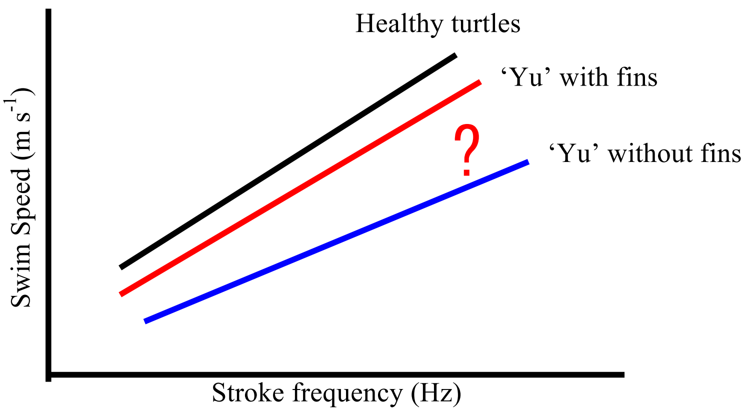

Fig. 3 Expected relationship between swim speed and stroke frequency of healthy turtles and 'Yu' with and without artificial fin.

2. 2 Studied animals and field study procedures

2. 2. 1 'Yu' and healthy turtles in captivity

Forelimb-injured sea turtle 'Yu' is a female loggerhead turtle *Caretta caretta* with 77.6 cm in average standard carapace length (SCL) and 82.2 kg in average body mass (BM). SCL and BM were averaged because 'Yu' grew during the experiment, causing SCL and BM to vary. Healthy similar-sized loggerhead turtles (71.8 - 85.0 cm in SCL and 53.5 - 85.3 kg in BM, n = 4) were also used in this study as controls (Fig. 4, Table 1). Morphological measurements such as SCL and BM were taken with a calliper and a scale. Our next step was to obtain behavioral data such as swim speed, dive depth, and 2 or 3-axis accelerations. To achieve this, a data logger was either attached directly on a turtle's carapace using epoxy resin (Fig. 5), or attached with automatic time-scheduled release system (Narazaki et al. 2009). When a data logger was attached directly to a turtle's carapace, recapturing the animal in order to obtain the data was necessary. On the other hand, when a data logger was attached with an automatic time-scheduled release system, the data logger was programmed to detach from the animal at 5 to 168 hours after deployment. Once the logger was released from turtles, a directional antenna was used to search for VHF signals transmitted from the automatic time-scheduled release system in order to retrieve the logger. All experiments were conducted from September 2009 to December 2012 either in an artificial lagoon (34°38'06" N, 135°12'37" E, perimeter about 500 m and max. depth 3 - 5 m) located on the western side of the Kobe Airport Island off the coast of Kobe City in Japan's Inland Sea, or in a wave tank (quantity of water 1200 m^3) of Suma Aqualife Park (34°38'38" N, 135°07'39" E) Kobe City (Fig. 8).

Table 1 Morphological data and experiment period of 'Yu' and healthy turtles.

ID	Sex	SCL (ave.±s.d., cm)	BM (ave.±s.d., kg)	Experiment period
Yu	Female	77.6±3.30	82.2±14.4	31 May 2009 – 9 Dec. 2012※
Sho	Male	76.1	57.5	31 May 2009 – 13 Sep 2009
Inoki	Male	71.8	54.0±0.71	11 Sep. 2010 – 24 Oct. 2010
Shoko	Female	77.1±0.46	57.7±1.23	4 Dec. 2010 – 28 Nov. 2011
Teruo	Male	84.7±0.21	84.5±1.03	28 Apr. 2012 – 9 Dec. 2012

ID (filled with gray color) were not used in the analysis due to data loss in the giant tsunami of Tohoku in March 2011 or due to troubles in obtaining data concerning swimming behavior because the sea turtles did not swim during the experiment.

※Data of 2009 was provided by Katsufumi Sato lab.

Fig. 4 Pictures of forelimbs of 'Yu' (top) and healthy turtle Shoko (bottom) with a scale.

Fig. 5 Data logger deployed on center of carapace of 'Yu'

2. 2. 2 Sea turtles under natural conditions

All sea turtles under natural conditions used in this study were loggerhead turtles, *Caretta caretta*. They were captured by set nets at coastal area of Otsuchi Town, Iwate Prefecture, and transferred to and kept in tanks at the International Coastal Research Center, Atmosphere and Ocean Research Institute, The University of Tokyo (39°21'05" N, 141°54'05" E) (Fig. 8) located in the same general area. Morphological measurements such as SCL and BM were taken with a calliper and a hanging scale (Table 2). Each turtle was kept in a tank from one day to up to 90 days until they were released in the middle of Otsuchi Bay, Iwate Prefecture, Japan (39°20'30" N, 141°56'00" E). Seventeen sea turtles were released after data logger deployment from 2006 to 2010. Out of seventeen sea turtles, the data from 2006 to 2009 (n=14) and data of right forelimb-lost individual ('Hikari') were provided by T. Narazaki (2009b). The behavioral data of three sea turtles (L1002, L1004, and L1005) from 2010 were taken by the author. The three sea turtles were released in the middle of Otsuchi Bay after positioning a data logger and a SRDL (satellite relay data-logger) on 21 and 23 July 2010. The SRDL transmitted the location of the sea turtle via Argos satellite system (Argos 1996; Boehme et al. 2009). The SRDL was attached directly on the carapace of the sea turtles using epoxy resin (Fig. 7). The data logger was deployed on carapace of the sea turtles with automatic time-scheduled release system (Narazaki et al. 2009) as described in the previous section, and it was programmed to detach from the turtle at five or seven days after the release of each turtle. Because sea turtles could swim away outside of the VHF signal coverage area during the experiment period, we needed to follow them with the research vessel *Tanseimaru* based on location information transmitted from SRDL. Thus, we could receive VHF signal transmitted from the release system, once the data logger was detached. The data loggers of L1002 and L1005 were successfully retrieved on 26 and 28 July 2010, respectively. However, the data logger of L1004 was unretrievable due to rough weather on 30 July 2010, which prevented searching for the data logger. Data from all sea turtles were used to determine the relationship between SCL and average swim speed. The behavioral data of 'Hikari', L0601, and L0602 were used to evaluate swimming ability, especially the relationship between swim speed and stroke frequency (Table 2).

Table 2 Morphological data and experiment periods of sea turtles under natural conditions.

ID	Sex	SCL (cm)	BM (kg)	Period of experiment
'Hikari'	Unknown	76.0	53.0	1 Sep. 2010※[a]
L0601	Male	72.8	61.6	4 Aug. 2006※[a]
L0602	Male	78.8	65.5	27 - 28 Aug. 2006※[a]
L1002※[b]	Unknown	63.8	39.0	21 - 26 Jul. 2010
L1004	Male	82.5	59.0	23 - 30 Jul. 2010
L1005※[b]	Male	82.5	77.7	23 – 28 Jul. 2010

L1004 (filled with grey color) was excluded from analysis due to failure of retrieving data logger.

※[a] Data was provided by T. Narazaki.

※[b] Data was only used to analyze the relationship between SCL (cm) and average swim speed (ms^{-1}).

Fig. 6 Right forelimb-lost turtle, “Hikari”

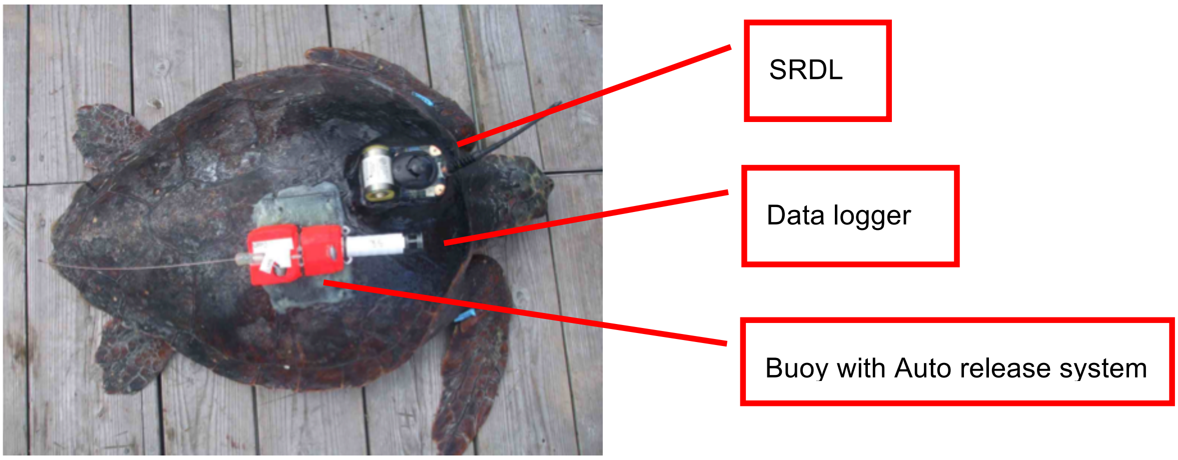

Fig. 7 Turtle deployed with a data logger and SRDL on its carapace.

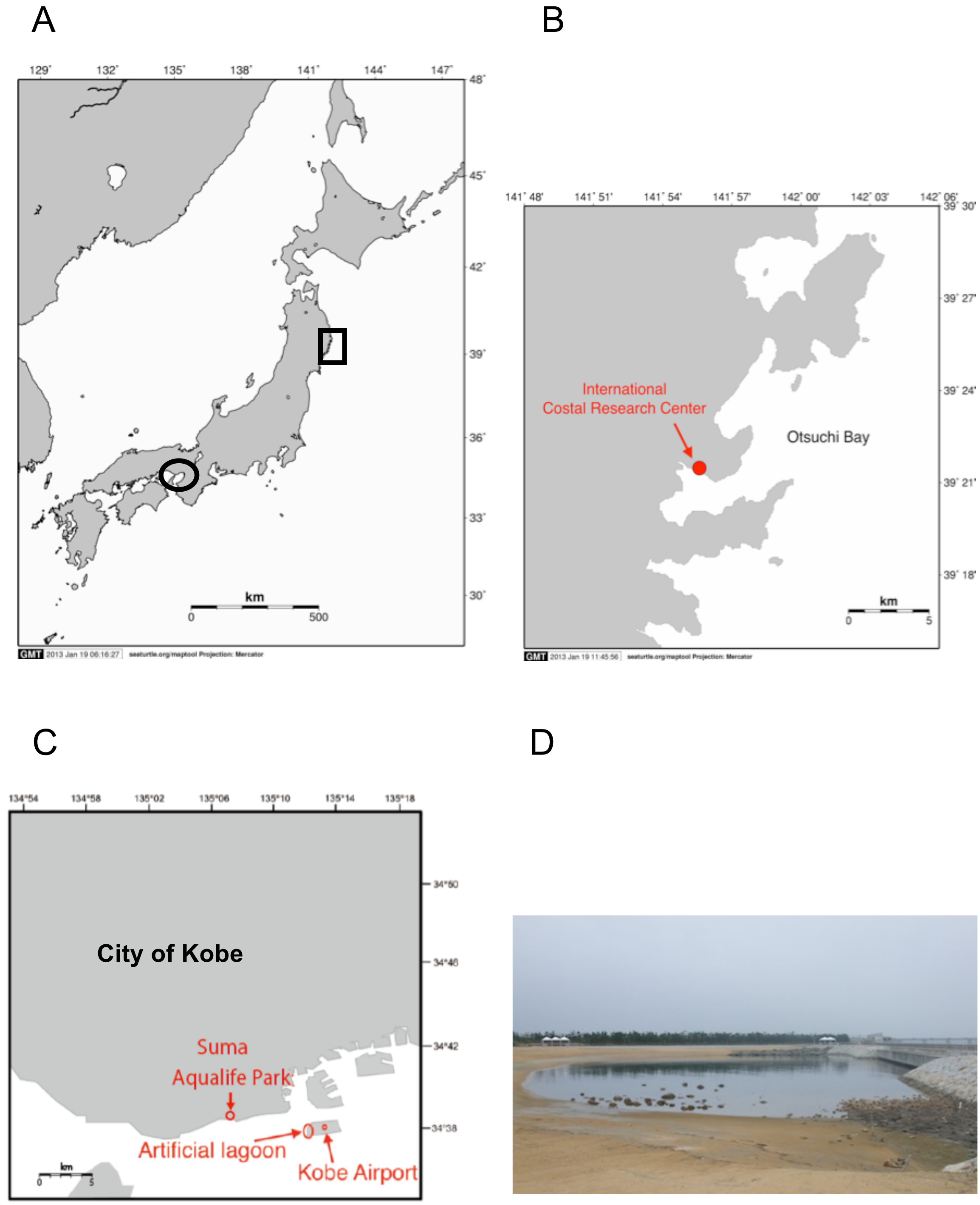

Fig. 8 Maps and a picture of study sites

(A) Area overlaid in the rectangle indicates study site for sea turtles under natural conditions. Area encircled indicates study site of 'Yu' and healthy turtles in the artificial lagoon.

(B) Magnified map of rectangle area of Fig. 8 (A)

(C) Magnified map of encircled area of Fig. 8 (A)

(D) Artificial lagoon located on the westen side of Kobe Airport Island.

2. 3 Animal-borne recorder (Data logger)

Four types of multi-sensor animal-borne recorders (data loggers) developed by Little Leonard Corp., Tokyo, Japan were used; W1000-PD2GT (23 mm in diameter, 123 mm in length, 90 g in air), W1000L-PD2GT (27 mm in diameter, 127 mm in length, 125 g in air), W1000-3MPD3GT (26 mm in diameter, 175 mm in length, 140 g in air), and W1000-PD3GT (22mm in diameter, 123mm in length, 72g in air, Fig. 9). Mass of data loggers used in this experiment were less than 140 g in air so that it is assumed that attaching the data logger would not affect drastically on natural behaviors of a sea turtle, which weighs about 60 kg or over. Each data logger was programmed to record swim speed (at 1 sec or 2 sec intervals), depth (at 1 sec interval), 2-axis or 3-axis accelerations (at 1/32 sec or 1/16 sec intervals) for calculating stroke frequency, and temperature (at 1 sec or 2 sec intervals). Swim speed was recorded as rotation numbers of an external propeller. In order to obtain equations to convert propeller's rotation numbers into swim speed, preliminary experiment was conducted. Each data logger was pulled from 40 m deep to the surface in the ocean or pulled from one end to another in 25 m pool at different speeds by an electric reel to count the rotation numbers of propeller at each speed. Conversion equations were calculated from a regression line between rotation numbers and speeds. As a result, the stall speed, which the propeller starts rotating properly, was estimated as between 0.2 m s^{-1} and 0.3 m s^{-1}. Thus, behavioral data of swim speed below the stall speed was eliminated from analysis. Each logger was deployed on 'Yu', the healthy sea turtles in captivity, and sea turtles under natural conditions to record swimming behaviors (see Table 3 and 4 for deployment summary).

Satellite Relay Data Loggers (SRDL, 7.2 cm in width, 12.0 cm in length, 6.0 cm in height, 545 g in air), developed by NERC Sea Mammal Research Unit (SMRU), St Andrews, UK, were deployed on the center of carapace of three sea turtles under natural conditions, L1002, L1004, and L1005. SRDL recorded dive profile, conductivity, temperature, and pressure to a maximum depth of around 2000 m. These data as well as location information were transmitted at the surface via the Argos satellite system (Boehme et al. 2009, Argos 1996). It enabled us to access the data through web site of SMRU (http://www.smru.st-and.ac.uk/protected/tu59/tu59.html) or Argos web (http://www.argos- system .org/?nocache=0.20438026538039045).

Fig. 7 Data loggers that were used in the experiment: W1000L-PD2GT (top) and W1000-3MPD3GT (bottom)

Table 3 Summary of data logger deployment in the artificial lagoon or the tank of Suma Aqualife Park.

Deployment Number	Turtle ID	Date of deployment	Deployment duration (h)	Ver. of artificial fins (Short or Long term※)	Study site
1[a]	Healthy (Sho)	31 May 2009	44.8	N/A	lagoon
2[a]	Healthy (Sho)	20 Jun. 2009	21.0	N/A	lagoon
3[a]	Healthy (Sho)	25 Jul. 2009	19.5	N/A	lagoon
4[a]	Healthy (Sho)	10 Sep. 2009	69.8	N/A	lagoon
5[b]	Healthy (Inoki)	11 Sep. 2010	0.6	N/A	lagoon
6[b]	Healthy (Inoki)	17 Oct. 2010	167.2	N/A	lagoon
7[b]	Healthy (Shoko)	4 Dec. 2010	188.4	N/A	pool
8[b]	Healthy (Shoko)	12 Dec. 2010	69.5	N/A	pool
9[b]	Healthy (Shoko)	2 Jul, 2011	177.0	N/A	lagoon
10	Healthy (Shoko)	7 Aug.2011	140.5	N/A	lagoon
11	Healthy (Shoko)	23 Nov.2011	127.7	N/A	lagoon
12[b]	Healthy (Teruo)	28 Apr. 2012	170.0	N/A	pool
13[b]	Healthy (Teruo)	2 Jun. 2012	173.0	N/A	pool
14	Healthy (Teruo)	16 Jul.2012	84.6	N/A	lagoon
15	Healthy (Teruo)	5 Aug.2012	102.0	N/A	lagoon
16	Healthy (Teruo)	4 Nov.2012	99.7	N/A	lagoon
17[b]	Healthy (Teruo)	9 Dec.2012	0.9	Jacket※※	pool
18[b]	Healthy (Teruo)	9 Dec.2012	0.6	N/A	pool
19[a]	Yu	31 May 2009	44.8	N/A	lagoon
20[a]	Yu	20 Jun. 2009	0.2	Type1	lagoon
21[a]	Yu	20 Jun. 2009	19.8	N/A	lagoon
22[a]	Yu	25 Jul. 2009	0.5	Type 3	lagoon
23[a]	Yu	25 Ju. 2009	0.3	Type 4	lagoon
24[a]	Yu	25 Jul. 2009	19.0	N/A	lagoon
25	Yu	10 Sep.2009	69.6	Ver. 5 (Short)	lagoon

26	Yu	1 Nov.2009	210.0	Ver. 5 (Long)	lagoon
27	Yu	13 Nov.2009	186.2	Ver. 5 (Long)	lagoon
28	Yu	25 Nov.2009	238.6	Ver. 5 (Long)	lagoon
29 [c]	Yu	20 Jun.2010	0.9	Ver. 6	lagoon
30	Yu	20 Jun.2010	0.4	N/A	lagoon
31 [c]	Yu	11 Sep. 2010	0.8	Ver. 8	lagoon
32 [c]	Yu	17 Oct.2010	0.6	Ver. 9	lagoon
33	Yu	17 Oct.2010	179.6	N/A	lagoon
34 [b]	Yu	4 Dec. 2010	138.6	Ver. 10	pool
35 [b]	Yu	10 Dec. 2010	36.5	N/A	pool
36 [b]	Yu	12 Dec. 2010	69.5	Ver. 11	pool
37	Yu	2 Jul.2011	1.1	Ver.12 (Short)	lagoon
38 [c]		7 Aug.2011	139.5	Type13	lagoon
39	Yu	7 Aug.2011	0.45	N/A	lagoon
40 [c]	Yu	18 Sep. 2011	167.8	Ver. 14	lagoon
41 [c]	Yu	23 Nov. 2011	0.5	Ver. 16	lagoon
42 [b]	Yu	2 Feb, 2012	172.7	Ver. 19	pool
43 [b]	Yu	28 Apr. 2012	164.9	Ver. 20	pool
44 [b]	Yu	19 May.2012	100.1	Ver. 21	pool
45 [b]	Yu	2 Jun. 2012	174.5	Ver. 22	pool
46	Yu	16 Jul.2012	83.0	Ver. 23 (Short)	lagoon
47	Yu	5 Aug.2012	103.0	Ver. 24 (Short)	lagoon
48	Yu	8 Oct.2012	1.2	Ver. 24 (Long)	lagoon
49	Yu	10 Oct.2012	82.7	Ver. 25 (Short)	lagoon
50	Yu	4 Nov.2012	101.0	Ver. 26 (Short)	lagoon
51	Yu	9 Dec.2012	0.37	Ver. 26 (Long)	lagoon
52 [b]	Yu	9 Dec.2012	0.7	Ver. 26	pool
53 [b]	Yu	9 Dec.2012	0.9	N/A	pool

Deployments filled with grey color were excluded from analysis due to trouble(s) as stated as follow:

[a] Data loss in the giant tsunami of Tohoku in March 2011.

[b] Troubles in obtaining data concerning swimming behavior because sea turtles did not constantly swim.

[c] Failure to attach the artificial fins to 'Yu' properly.

※It was stated "Short" if the behavioral data was only taken at beginning of the artificial fins application, and stated "Long" if the behavioral data was taken after long-term application of artificial fins.

※※Effect of wearing a jacket was tested on 'Teruo' in a pool.

Table 4 Summary of data-logger deployment under natural conditions.

Deployment Number	Turtle ID	Date of deployment	Deployment duration (h)
54※	Hikari (Lost right limb)	1 Sep. 2010	5.7
55※	L0601 (Healthy)	4 Aug. 2006	6.0
56※	L0602 (Healthy)	27 Aug. 2006	14.5
57	L1002 (Healthy)	21 Jul. 2010	110.2
58	L1004 (Healthy)	23 Jul. 2010	N/A
59	L1005 (Healthy)	23 Jul. 2010	110.7

Deployment 58 (filled with grey color) was excluded from analysis due to failure of retrieving data logger.

※Data was provided by T. Narazaki.

2. 4 Artificial fins

In total, 26 versions of artificial fins have been developed by Kawamura Gishi Co., Ltd. Out of all the developed artificial fins, ver. 5, 12, 23, 24, 25 and 26 were successfully attached to 'Yu' for some periods, and the others were excluded form the analysis due to failure of keeping the artificial fins on 'Yu'. Fin ver. 5, which was tested on 'Yu' from 10 Sep. 2009 to 25 Nov. 2009, was attached by tightening on the base of forelimbs. The shape of fins was symmetrical and similar to natural forelimbs of a healthy turtle (Fig. 10, Table 5). The rest of artificial fins were attached to 'Yu' with a jacket like suit (Jacket type; Fig. 10, Table 5). The fins were suspended from the jacket so that it would not compress the base of forelimbs from tightening. Fin ver. 12 was tested on 'Yu' from 2 Jul. 2012 to 11 Jul. 2012. The shape of fins was similar on both sides, but the area of left fin was larger than that of the right fin. Fin ver. 23, which was tested on 16 Jul. 2012, was asymmetry. The left fin had a paddle like structure at the rear of the fin, and the shape of the right fin was close to natural forelimb (Fig. 10, Table 5). Fin ver. 24, which was tested from 5 Aug. 2012 to 8 Oct. 2012, was symmetry (Fig. 10, Table 5). Fin ver. 25, which was tested on 10 Oct. 2012, had the same fin as ver. 24, but only applied on the left forelimb (Fig. 10, Table 5). Fin ver. 26, which was tested from 4 Nov. 2012 to 9 Dec. 2012, was longer than the other fins (Fig. 10, Table 5). Fin ver. 13, 23, and 25 were only tested at the beginning of the artificial fins deployment (stated as "short-term"). Fin ver. 5, 24, and 26 were tested not only at the beginning of application, but also after long-term application of artificial fin (one to two months after the application, stated as "long-term") to see long-term effects. In order to see effects on swim speed from wearing a jacket, experiment was conducted on 'Teruo' in the pool of Suma Aqualife Park on 9 Dec. 2012. 'Teruo' was released in a pool with a jacket for

50 min, and it was released in a pool again without wearing a jacket for 50 min. Then, the average swim speeds were compared. Mann-Whitney exact test was used for statistics to determine if there was a significant difference in the average swim speeds. The value for statistical significance was set at $p < 0.05$.

Table 5 Versions of artificial fins

Ver. of artificial fins	Characteristics	Deployment period
Ver. 5※	Tightened, Symmetry	10 Sep. 2009 – 5 Dec. 2009
Ver. 12	Jacket, Asymmetry (larger left fin)	2 Jul. 2012 – 11 Jul. 2012
Ver. 23	Jacket, Asymmetry (left fin with paddle)	16 July. 2012
Ver. 24※	Jacket, Symmetry	5 Aug. 2012 – 8 Oct. 2012
Ver. 25	Jacket, Left limb only	10 Oct. 2012
Ver. 26※	Jacket, Long (high aspect ratio)	4 Nov. 2012 – 9 Dec. 2012

※Artificial fins were tested for a long-term.

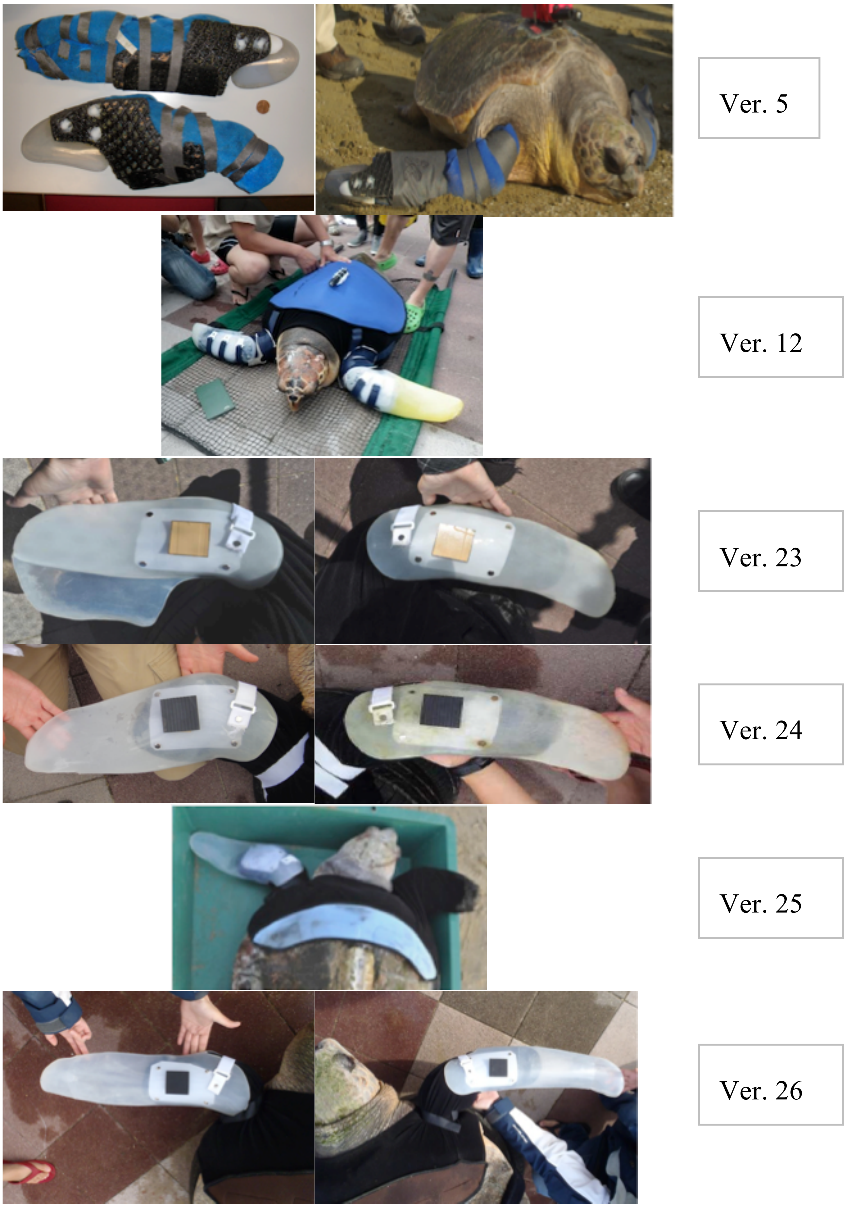

Fig. 10 Artificial fins applied on 'Yu'. Fin ver. 5 was applied to 'Yu' by tightening at the base of forelimbs. The others were applied to a jacket slipped over head of 'Yu'.

2. 5 Data analysis

2. 5. 1 Area of forelimbs

Area of the artificial fins, the healthy sea turtles (n = 27), and forelimbs of 'Yu' were calculated from the photo taken with a scale, using PHOTOSHOP (Adobe System, Inc., San Jose, CA, USA) by the following procedures. Length of forelimbs from the tip to base was measured by converting the number of pixels into cm using the scale. Then, outline of forelimbs was traced, and the traced area was extracted. The narrowest part of the base of forelimbs was defined as the end of forelimbs

(Fig. 11). With IGOR PRO (WaveMetrics, Inc., Lake Oswego, OR, USA), number of pixels of the traced area was converted into cm^2, by multiplying the square of forelimb length (cm / pixel).

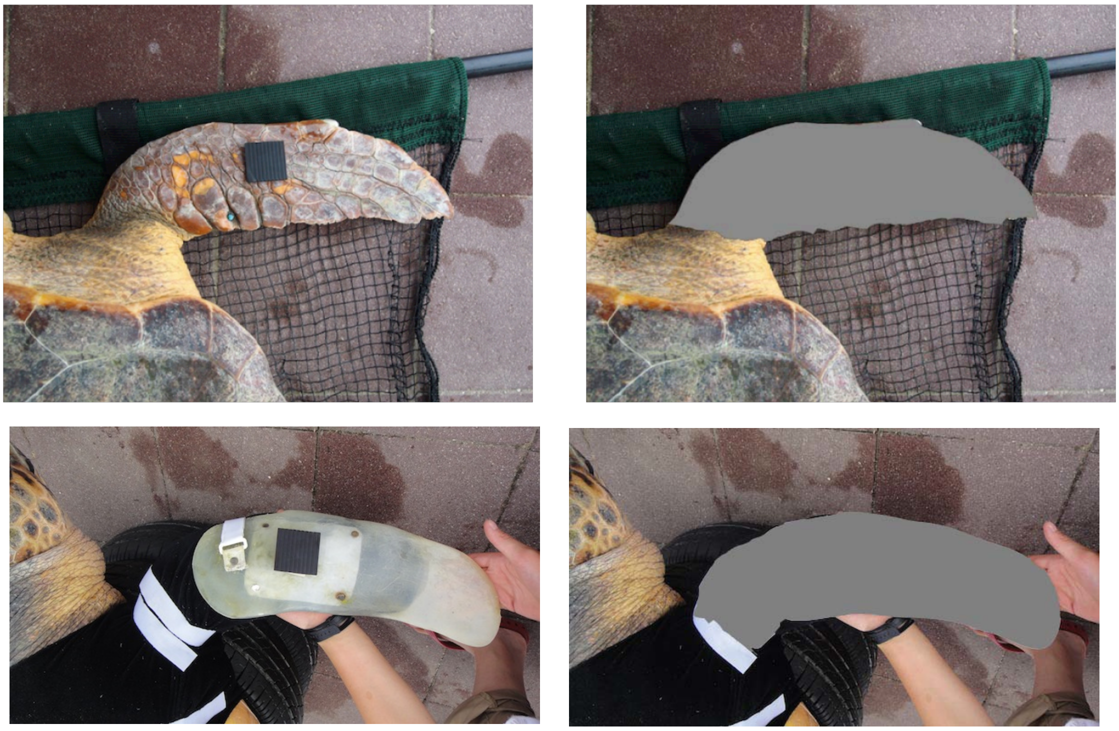

Fig. 11 Pictures of forelimbs and a scale that were used for calculating areas of forelimbs and artificial fins (Top: 'Teruo', Bottom: 'Yu' with fin ver 24). The grey colored area was calculated as area of forelimb (top and bottom right). Photos by the Sea Turtle Association of Japan

2. 5. 2 Analysis of swim speed

The time-series data obtained from multi-sensor data loggers were analyzed with IGOR PRO (WaveMetrics, Inc., Lake Oswego, OR, USA). "Swim" was defined as the period when turtles constantly moved faster than stall speeds of a propeller for more than 10 seconds. Also, to avoid effects of buoyancy, behaviors when turtles constantly moved toward surface and bottom for longer than 3 seconds were excluded from the analysis of "Swim". Generally, swim speed of 'Yu' in the artificial lagoon is low; thus, a propeller of a logger did not rotate properly most of the time (i.e. below the stall speed). Therefore, the data of first 30 min from release of the sea turtles in captivity when swim speed was comparatively high due to handling stress was used for analysis. The data of dorso-ventral acceleration were used to calculate stroke frequency (Fig. 12). Dominant stroke frequency of each sea turtle was determined by calculating the power spectral density (PSD) of the acceleration data (data of 30 min after release for 'Yu' and healthy turtles in captivity, and entire dataset for turtles under natural conditions) from each individual using a Fast Fourier Transformation. The dominant stroke frequency was considered as the peak of PSD (Sato et al.

2007). Distinguished from the dominant stroke frequency, which signifies the most prominent frequency of entire dataset, stroke frequency per second was also determined. In order to select the frequency of a stroke per second where amplitude of signal was the strongest, acceleration spectrogram was generated by converting time series dorso-ventral acceleration data into a spectrum, using continuous wavelet transformation. The dominant frequency was traced with peak tracer of "Ethographer", developed by Sakamoto et al. (2009). Linear regression lines of swim speed and stroke frequency were obtained. Swim speed was compared at dominant stroke frequency and also at higher stroke frequency. Relative lift coefficient was also calculated by substituting swim speed, area of forelimbs and dominant stroke frequency in Equation 5. The distance travelled over body length per each stroke was calculated from the linear regression line obtained as the swim speed ($m\ s^{-1}$) multiplied by stroke cycle (sec) divided by the SCL (cm) of each sea turtle (Bainbridge 1957). The relationship between average swim speed and SCL was examined with time-series data of sixteen turtles under natural conditions. Average swim speed was calculated from swim speed during dives defined as submergences deeper than 1 m for more than 5 sec with the maximum depth of > 4 m. The regression line was obtained in a relation of average swim speed and SCL.

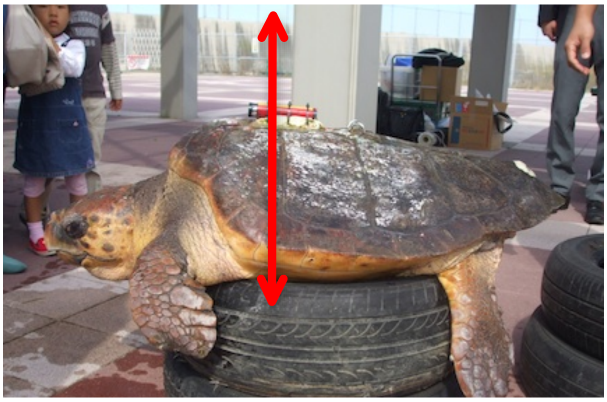

Fig. 12 'Yu' equipped with data logger. The arrow indicates axis of dorso-ventral acceleration.

2. 5. 3 Diving behavior

In order to evaluate whether 'Yu' could have natural behaviors, such as diving and surfacing, those behaviors were examined. "Dive" was determined as any submergence to a depth deeper than 1 m for more than 5 sec. The average dive duration, maximum dive duration, average dive depth, maximum dive depth, and number of dives were compared among 'Yu' with and without fins, the healthy turtles in captivity, and sea turtles under natural conditions. To avoid environmental influences, such as water temperature, visibility of water and weather condition, the behaviors were compared among the datasets that were taken at the same time.

2. 5. 4 Statistical analysis

All of the statistical analysis in this study was processed in R 2.11.0 (R Development Core Team 2010). Before obtaining a linear regression line for the relationship between area of forelimbs and SCL, I examined if the relationship exhibits isometric scaling or allometric scaling. The equation was selected on the basis of Akaike Information Criterion (AIC).

In order to examine what variables influence the swim speed, generalized linear model (GLM) was used. Explanatory variables were frequency, type of forelimbs (injured forelimbs, artificial fins, or healthy limbs), and interactions of frequency and type of forelimbs. Dependent variable was swim speed. Link function was identity. The most parsimonious model was selected on the basis of AIC. Then regression lines of swim speed and explanatory variables chosen by GLM were obtained. Similarly, model for relationship between SCL, the dominant stroke frequency, and average swim speed was selected, by having SCL and PSD as explanatory variables and average swim speed as dependent variable. Link function was identity.

3. Results

3. 1 Area of forelimbs

3. 1. 1 'Yu' and the healthy turtles in captivity

Total forelimbs area of 'Yu' was 520.6 cm^2, which was about 60% compared with 'Shoko' that had a similar SCL with 'Yu' (Table 6). Fin ver. 5, ver. 12, ver. 24 gave 'Yu' similar forelimbs areas with healthy turtles with similar SCL (Table 6). When fin ver. 23, which was asymmetrical, was applied, left forelimb was 140% larger than the right forelimb. As a result, the total area of fin ver. 23 (1034.4 cm^2) was larger than the healthy turtle. Area of forelimbs with fin ver. 25 was smaller (727.3 cm^2) than the healthy turtles because the fin was applied on the left limb only. Fin ver. 26 gave a larger area of forelimbs (1154.7 cm^2) than the healthy turtle, especially in right limb that was 124% larger than the left limb (Table 6).

Table 6 Areas of forelimbs of 'Yu' without fins, 'Yu' with artificial fins, and healthy turtles

ID (Ver. of fin)	SCL (cm)	Area of left forelimb (cm^2)	Area of right forelimb (cm^2)	Total area of forelimbs (cm^2)
Shoko	77.1	437.1	450.6	887.6
Teruo	84.7	461.4	465.78	927.2
Yu (no fins)	77.6	214.8	305.8	520.6
Yu (ver. 5)	77.6	428.7	491.5	920.2
Yu (ver. 12)	77.6	495.0	421.5	916.5
Yu (ver. 23)	77.6	601.2	433.2	1034.4
Yu (ver. 24)	77.6	421.5	433.2	854.7
Yu (ver. 25)	77.6	421.5	305.8	727.3
Yu (ver. 26)	77.6	513.7	641.0	1154.7

3. 1. 2 Sea turtles under natural conditions

A total of 30 sea turtles were used to measure the area of forelimbs (range = 52.2 - 84.7 cm in SCL). The areas of left and right limbs of each sea turtle were similar to each other (Fig. 13). The equation that showed allometric relationship between area of forelimbs and SCL was selected based on AIC (Appendix 1). The regression lines of SCL and forelimbs were as followings: total forelimbs area $y = 1.6980x^{1.4394}$, right forelimb area $y = 0.3674x^{1.6361}$, and left forelimb area $y = 1.9597x^{1.2429}$ (Fig. 13). The forelimb of 'Hikari' was not measured because of failure of taking pictures of a forelimb due to technical problems. Thus, it was estimated from the regression line for the relationship between total area of forelimbs and SCL. The forelimbs area of 'Hikari' was estimated as 426.5 cm^2, which was about 47% of forelimbs of healthy turtles with similar SCL as 'Hikari' (Table 7).

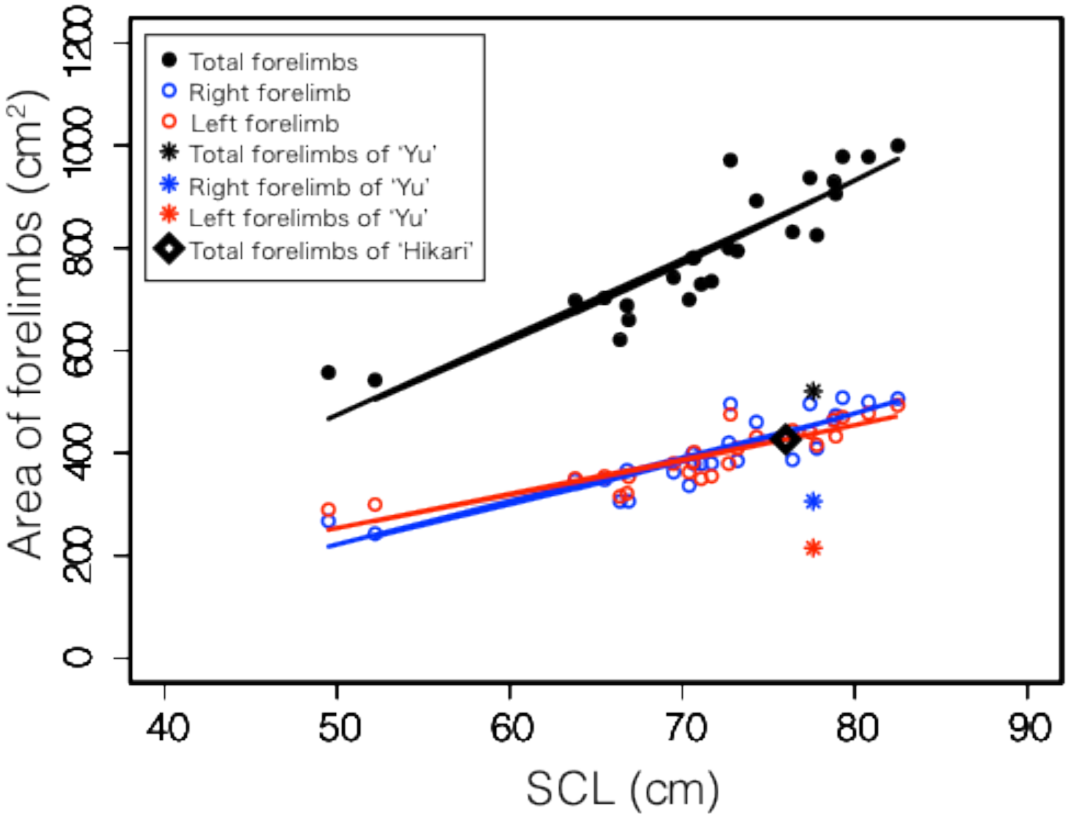

Fig. 13 The relationship between standard carapace length (cm) and area of forelimbs (cm^2). Solid lines indicate regression lines.

Table 7 Area of forelimbs of sea turtles under natural conditions.

ID	SCL (cm)	Area of left forelimb (cm^2)	Area of right forelimb (cm^2)	Total area of forelimbs (cm^2)
L0601	72.8	475.6	495.8	971.4
L0602	78.8	465.1	465.1	930.1
Hikari	76.0	432.7※	N/A	432.7※

※The area was expected from the regression line of the relationship between SCL and total area of forelimbs.

3. 2 Swimming Ability

The GLM for swim speed showed frequency and types of forelimbs (injured forelimbs, artificial fins, or healthy limbs) and interactions of frequency and type of forelimbs were related to swim speed (Appendix 2). Thus, the regression lines were obtained based on the model selected.

3. 2. 1 'Yu' and the healthy turtles in captivity

A total of fourteen deployments were conducted to obtain data from the forelimb injured sea turtle 'Yu', and five deployments were conducted using healthy turtles in captivity 'Shoko' and 'Teruo' (Table 8). The average dominant stroke frequency of 'Yu' and the healthy turtles was 0.43 Hz. Thus, in order to evaluate swimming ability of 'Yu', swim speed and distances travelled over body length per stroke at 0.43 Hz and 0.86 Hz (i.e. twice of the average dominant stroke frequency) were compared. Considering lift coefficient of 'Shoko' as the standard (i.e. relative coefficient of 'Shoko' is 1), relative lift coefficient of each forelimb type was calculated by using swim speed obtained at stroke frequency of 0.43 Hz.

'Yu' without artificial fins and the healthy turtles

The maximum swim speeds of the two healthy turtles were 1.5 m s^{-1} for 'Teruo' and 1.7 m s^{-1} for 'Shoko', respectively. 'Yu' was able to swim at maximum speed of 1.9 m s^{-1}, which was higher than that of the healthy turtles (Table 8). However, swim speeds of 'Yu' was 71% of the healthy turtles at 0.43 Hz and 58% at 0.86 Hz, respectively. The dominant stroke frequency of 'Yu' was 0.43 Hz (Fig. 15, Table 8). Relative lift coefficient of 'Yu' was 1.12, which was higher than that of 'Shoko' and lower than that of 'Teruo' (1.41, Table 8). The distance travelled per stroke of 'Yu' ranged from 0.9 – 1.5 of the body length, which was 65 – 79% of the healthy turtles (Table 10). The histogram of swim speed from the entire data set of 'Yu' (17 Oct. 2010) and 'Teruo' (4 Nov. 2012) showed a peak at 0.35 m s^{-1} (Fig. 23).

'Yu' with the artificial fins (from overall data)

When artificial fins were applied for a short-term, the maximum swim speed of 'Yu' was 1.1 m s^{-1}, but it increased to 1.4 m s^{-1} after a long-term application (Table 8). Swim speeds at 0.43 Hz and 0.86 Hz during short-term applications were lower (0.4 m s^{-1} and 0.6 m s^{-1}, respectively) than that of 'Yu' without fins (0.5 m s^{-1}, 0.7 m s^{-1}, respectively, Table 8). After the long-term application of artificial fins, swim speed increased to 0.9 m s^{-1} at 0.86 Hz, which was higher than that of 'Yu' without fins. However, it was not as high as the swim speed of the healthy turtles (1.2 m s^{-1}, Fig. 15, Table 8). At the beginning of artificial fins application, the distance travelled per stroke at 0.43 Hz and 0.86 Hz were 1.3 BL and 0.9 BL, respectively (Table 10). After the long-term application, it increased to 1.3 BL at 0.86 Hz, which was higher than 'Yu' without fins but lower than the healthy turtles (1.6 – 1.7 BL, Table 10).

Tightened type artificial fins (Fin ver. 5)

Swimming ability of 'Yu' with the tightened type artificial fins, ver. 5, was tested at the beginning and after the long-term application. At the beginning of the application, the maximum swim speed was 0.8 m s^{-1}. Swim speed at 0.43 Hz and 0.86 Hz were lower (0.4 m s^{-1} and 0.8 m s^{-1}, respectively) than those of the healthy turtles (Fig. 16, Table 8). After the long-term application, swim speed increased at both stroke frequencies (0.6 m s^{-1} and 1.3 m s^{-1} for 0.43 Hz and 0.86 Hz, respectively), which were higher than 'Yu' without fins. At stroke frequency of 0.86 Hz, swim speed of 'Yu' with fin ver. 5 was even higher than those of healthy turtles (Table 8). Distance travelled per stroke at 0.43 Hz and 0.86 Hz was 1.2 BL, which was lower than the healthy turtles (Table 10). However, after the long-term application, it increased to 2.1 BL at 0.86 Hz, which was larger than the healthy turtles (Table 10). Relative lift coefficient of 'Yu' with fin ver. 5 was 0.35 for the short-term application, but it improved to 0.77 after the long-term application of fins. However, after the long-term application of fin ver. 5, it was found that the base of forelimbs where the artificial fins were tightened became necrotic. Thus, another method to attach artificial fins to 'Yu' without injuring the limbs was developed, which was the jacket type artificial fins.

<u>Jacket type artificial fins (Fin ver. 12, 23, 24, 25 and 26)</u>

Dominant stroke frequency of 'Yu' with the jacket type artificial fins ranged from 0.34 (ver. 26) to 0.53 Hz (ver. 23, Table8). Among the 5 different jacket type artificial fins tested, the maximum swim speed recorded during the deployment was 1.1 m s^{-1} (ver. 23, Table 8). None of the jacket type artificial fins provided higher swim speeds than those of the healthy turtles. However, in comparisons with 'Yu' without fins, swim speeds of 'Yu' were higher with ver. 12, 23 and 24 at 0.86 Hz, and with ver. 23 at 0.43 Hz. Relative lift coefficient was the highest in fin ver. 23, although it was lower than those of the healthy turtles. The distance travelled per stroke over body length was largest in fin ver. 23 (1.7 BL at 0.43 Hz) and smallest in fin ver. 25 (0.4 BL at 0.86 Hz, Table 10). The swim speed, relative lift coefficient, and the distance travelled per stroke were not improved after the long-term application in ver. 24 and ver. 26 (Table 10). The effect of wearing a jacket on swim speed was examined with 'Teruo'. When 'Teruo' was released without a jacket, average swim speed was 0.4 m s^{-1} (Fig. 24, Table 12). However, the average swim speed decreased to 0.3 m s^{-1} when a jacket was deployed (Fig. 24, Table 12). There was a significant difference in average swim speed before and after wearing a jacket (Mann-Whitney exact test, $\boldsymbol{U}$ = 245080.5, $\boldsymbol{P} < 0.001$).

3. 2. 2 Sea turtles under natural conditions

Behavioral data under natural conditions were obtained from two healthy turtles (L0601, L0602), and 'Hikari', which lost its right forelimb completely from its base. All of them had the same dominant stroke frequency of 0.31 Hz (Table 9). Thus, swim speed and distance travelled over body length per each stroke at 0.31 Hz was used to evaluate swimming ability of them. Swim speed at the high stroke frequency was not used since turtles stroked at a narrow range. The dominant stroke frequency of 0.31 Hz was also used to calculate relative lift coefficient. The maximum swim speed of ‘Hikari’ was lower (0.7 m s^{-1}) than that of the healthy turtles (0.9 m s^{-1}, Table 9). The swim speed at 0.31 Hz was also lower for ‘Hikari’ (0.5 m s^{-1}) than that for the healthy turtles (0.7 m s^{-1}, Fig. 22, Table 9). The distance travelled per stroke over body length was small for ‘Hikari’ (2.0 BL) than that of the healthy turtle (2.9 BL for L0601, and 2.7 BL for L0602, respectively, Table 11). Considering L0602 as the standard, relative lift coefficients were 0.93 for L0601 and 1.04 for ‘Hikari’. The histograms of swim speed showed an unimodal distribution with a peak around 0.67 m s^{-1} for L0601 and 0.48 m s^{-1} for ‘Hikari’ (Fig. 23). The GLM for average swim speed showed SCL was related to average swim speed. Thus, the regression lines were obtained based on the model selected (Ave. swim speed = 0.007090*SCL) (Fig. 25, See Appendix 3). The average swim speed of ‘Hikari’, shown as red closed dot in Fig. 25, was not much lower than the regression line.

Table 8 Summary of swimming ability of 'Yu' and healthy turtles in captivity

Deployment number	Turtle ID	Ver. of artificial fins (Short or Long term※)	Relative forelimbs area	Max. swim speed (m s^{-1})	Swim speed at 0.43 & 0.86Hz (m s^{-1})	Dominant Stroke frequency (Hz)	Lift Coefficient	Linear regression equations for swim speed vs. stroke frequency
10,11,14,15,16	Healthy※※	N/A			0.7 , 1.2			y = 0.26 + 1.08x
10,11	Healthy (Shoko)	N/A	1	1.7	0.6 , 1.1	0.44	1	y = 0.15 + 1.09x
14,15,16	Halthy (Teruo)	N/A	1.04	1.5	0.8 , 1.2	0.50	1.41	y = 0.28 + 1.09x
30,33,39	Yu (w/o fins)	N/A	0.59	1.9	0.5 , 0.7	0.43	1.12	y = 0.26 + 0.55x
25,37,46,47,49,50	Yu※※	Short		1.1	0.4 , 0.6			y = 0.25 + 0.44x
26,27,28,48,51	Yu※※	Long		1.4	0.5 , 0.9			y = 0.08 + 0.91x
25	Yu	Ver. 5 (Short)	1.04	0.8	0.4 , 0.8	0.38	0.35	y = -0.002 + 0.88x
26,27,28	Yu	Ver. 5 (Long)	1.04	1.4	0.6 , 1.3	0.31	0.77	y = -0.21 + 1.77x
37	Yu	Ver. 12 (Short)	1.03	0.8	0.5 , 0.8	0.44	0.57	y = 0.18 + 0.69x
46	Yu	Ver. 23 (Short)	1.17	1.1	0.6 , 0.8	0.53	0.80	y = 0.36 + 0.56x
47	Yu	Ver. 24 (Short)	0.96	0.8	0.5 , 0.8	0.50	0.67	y = 0.23 + 0.63x
48	Yu	Ver. 24 (Long)	0.96	0.9	0.4 , 0.7	0.50	0.33	y = 0.01 + 0.79x
49	Yu	Ver. 25 (Short)	0.82	0.4	0.3 , 0.3	0.44	0.23	y = 0.24 + 0.06x
50	Yu	Ver. 26 (Short)	1.30	0.5	0.3 , 0.6	0.34	0.19	y = -0.004 + 0.72x
51	Yu	Ver. 26 (Long)	1.30	0.6	0.3 , 0.6	0.34	0.20	y = 0.06 + 0.60x

※It was stated "Short" if the behavioral data was only taken at begging of the artificial fins application, and stated "Long" if the behavioral data was taken after long-term application of artificial fins.

※※Data of more than two deployments were treated as one data.

Table 9 Summary of swimming ability of sea turtles under natural conditions

Deployment number	Turtle ID	Relative forelimbs area	Max. swim speed ($m\ s^{-1}$)	Swim speed at 0.31Hz ($m\ s^{-1}$)	Dominant Stroke frequency (Hz)	Lift coefficient	Linear regression equations for swim speed vs. stroke frequency
54	Hikari (right limb-lost)	0.47	0.7	0.5	0.31	1.04	$y = -0.004 + 1.51x$
55	L0601 (healthy)	1.04	0.9	0.7	0.31	0.93	$y = 0.24 + 1.34\ x$
56	L0602 (healthy)	1	0.9	0.7	0.31	1	$y = -0.35 + 3.27x$

Table 10 Distance travelled per stroke over body length at 0.43 Hz of 'Yu' and the healthy turtles in captivity

Deployment Number	Turtle ID	Ver. of artificial fins (Short or Long term※)	Distance travelled per stroke over body length at 0.43 & 0.86 Hz (BL)
1,2,3,4,5	Shoko (healthy)	N/A	1.9 , 1.6
	Teruo (healthy)	N/A	2.1 , 1.7
10,11,13	Yu (nofin)	N/A	1.5 , 1.1
6,12,14,15,17,18	Yu (combined)※※	Short	1.3 , 0.9
7,8,9,16,19	Yu (combined)※※	Long	1.4 , 1.3
6	Yu	Ver. 5 (Short)	1.2 , 1.2
7,8,9	Yu	Ver. 5 (Long)	1.7 , 2.1
12	Yu	Ver. 12(Short)	1.4 , 1.1
14	Yu	Ver. 23 (Short)	1.7 , 1.2
15	Yu	Ver. 24 (Short)	1.4 , 1.1
16	Yu	Ver. 24 (Long)	1.0 , 1.0
17	Yu	Ver. 25 (Short)	0.8 , 0.4
18	Yu	Ver. 26 (Short)	0.9 , 0.9
19	Yu	Ver. 26 (Long)	0.9 , 0.8

※It was stated "Short" if the behavioral data was only taken at begging of the artificial fins application, and stated "Long" if the behavioral data was taken after long-term application of artificial fins.
※※Data of more than two deployments were treated as one data.

Table 11 Distance travelled per stroke over body length at 0.31 Hz of turtles under natural conditions

Deployment Number	Turtle ID	Distance travelled per stroke over body length
20	Hikari (lost right limb)	2.0
21	L0601 (healthy)	2.9
22	L0602 (healthy)	2.7

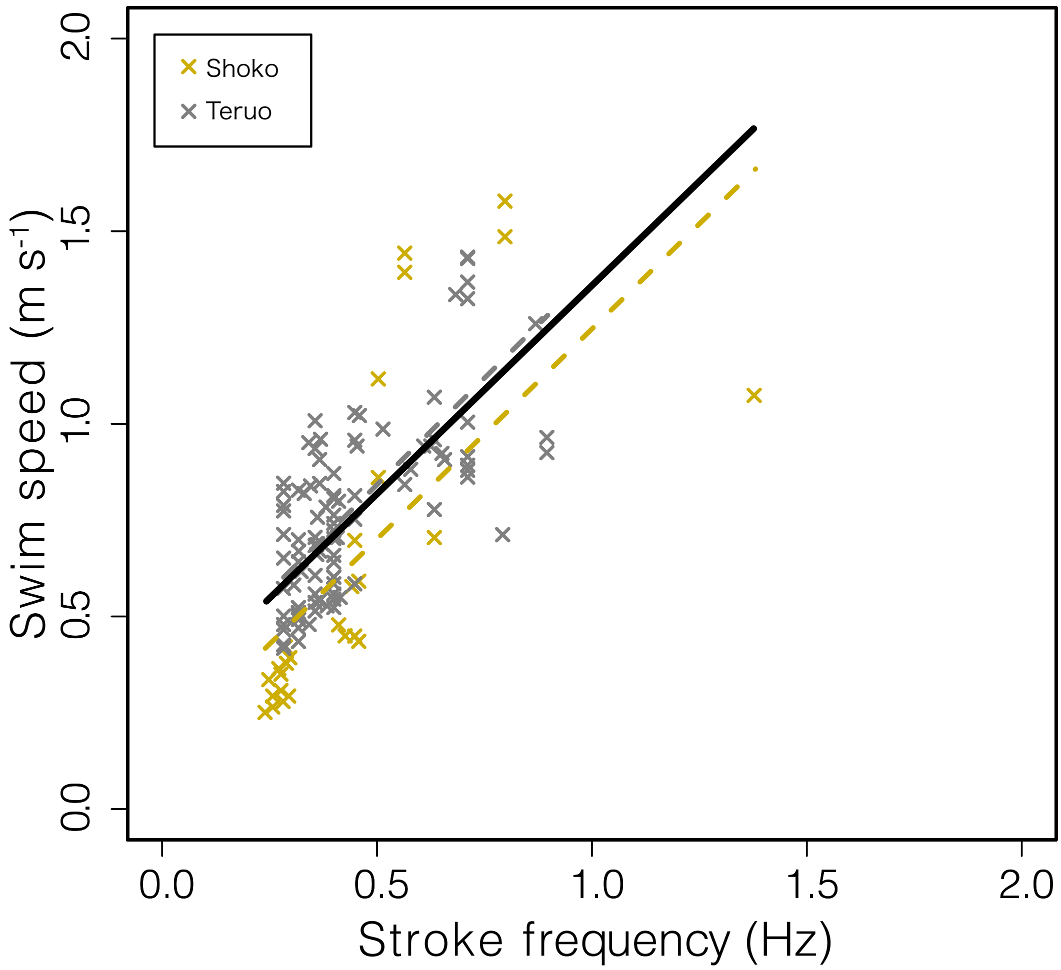

Fig. 14 Regression lines of swim speed and stroke frequency of the healthy turtles in captivity. The dashed lines indicate regression line of ‘Shoko’ and ‘Teruo’. The solid line indicates the regression line where data of ‘Shoko’ and ‘Teruo’ were combined.

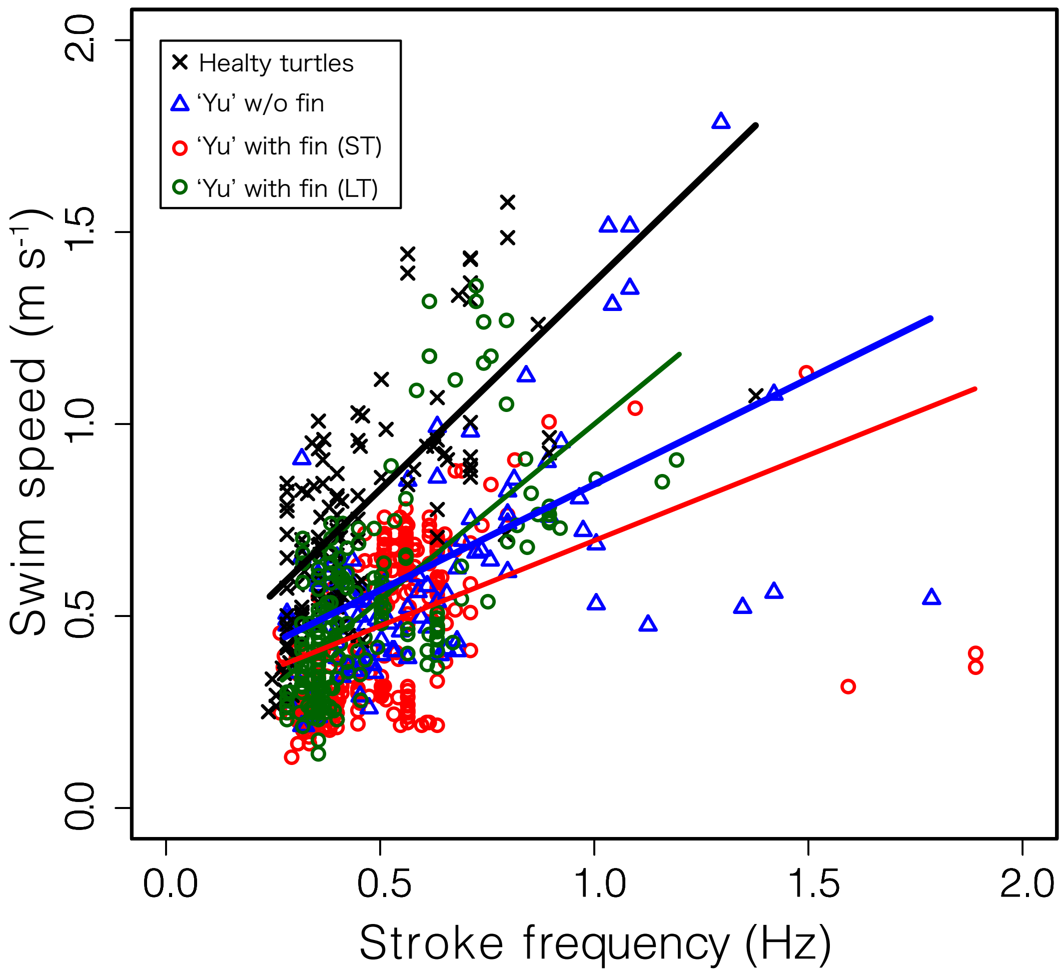

Fig. 15 Regression lines of swim speed and stroke frequency of the healthy turtles in captivity and 'Yu' without fin and with fin (short-term deployment, ST and long-term deployment, LT). The solid lines indicate regression lines of swim speed and stroke frequency.

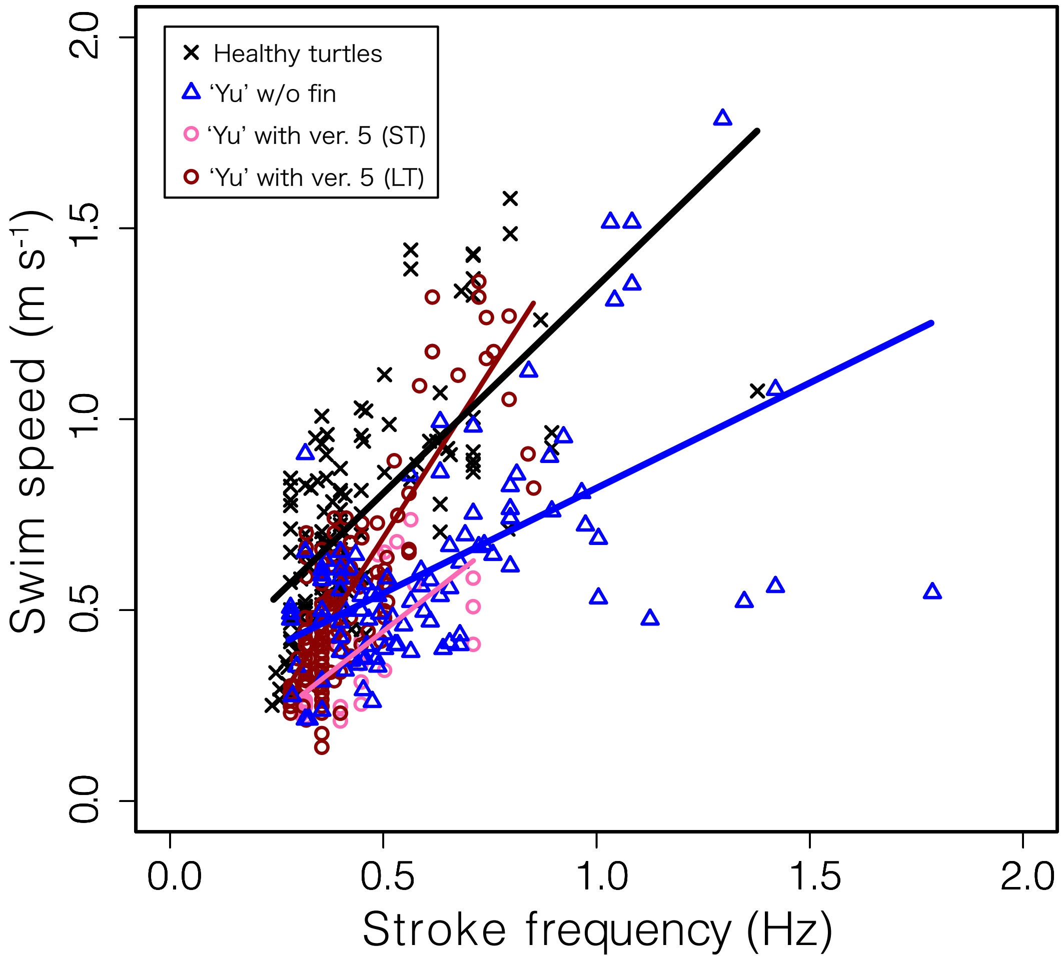

Fig. 16 Regression lines of swim speed and stroke frequency of the healthy turtles in captivity and 'Yu' without fin and with fin ver.5 (short-term deployment, ST and long-term deployment, LT). The solid lines indicate regression lines of swim speed and stroke frequency.

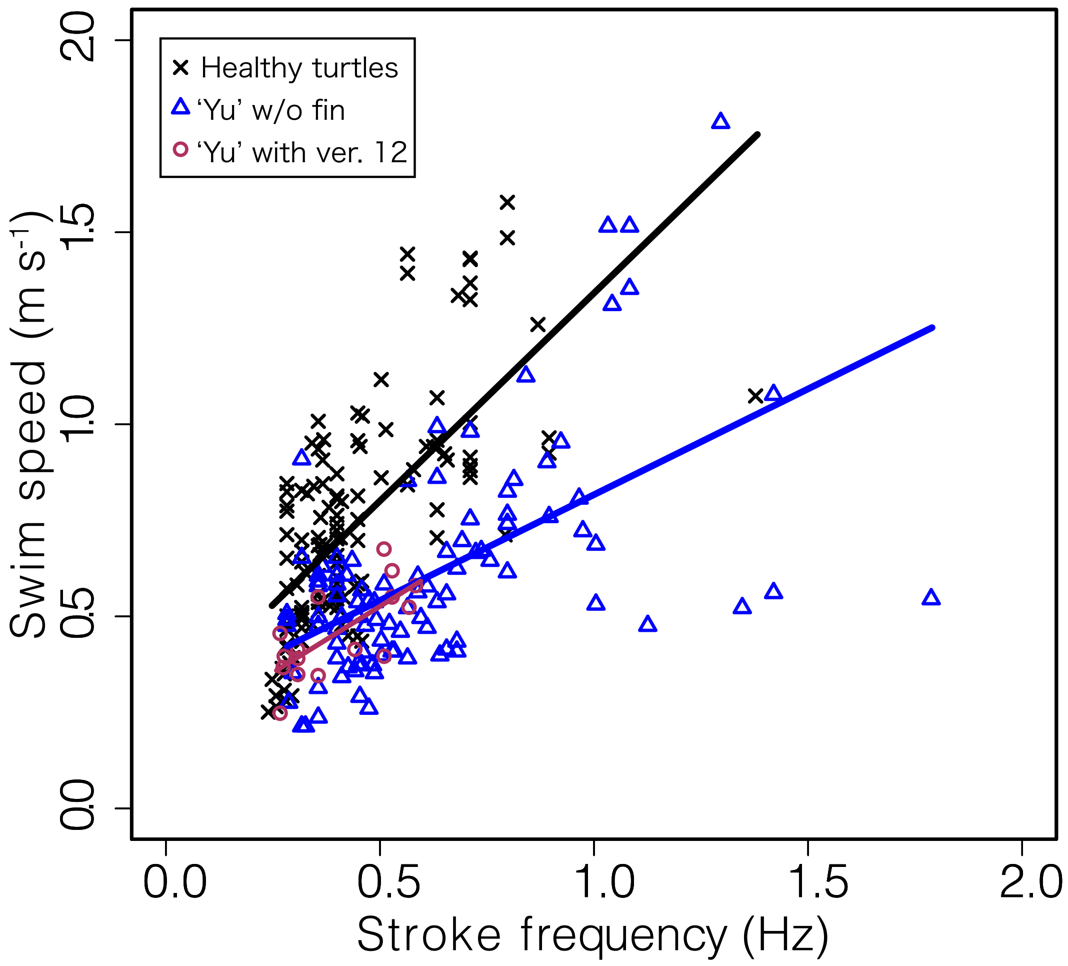

Fig. 17 Regression lines of swim speed and stroke frequency of the healthy turtles in captivity and 'Yu' without fin and with fin ver. 12. The solid lines indicate regression lines of swim speed and stroke frequency.

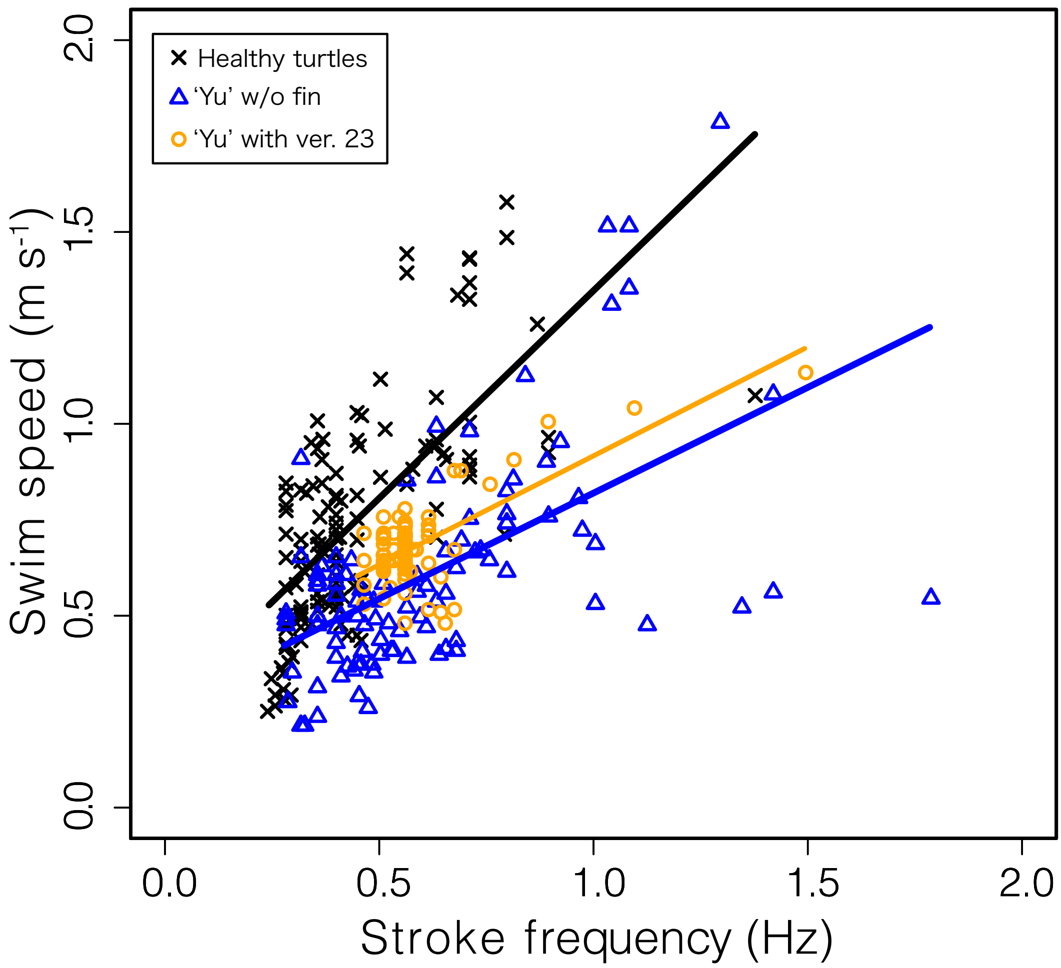

Fig. 18 Regression lines of swim speed and stroke frequency of the healthy turtles in captivity and 'Yu' without fin and with fin ver.23. The solid lines indicate regression lines of swim speed and stroke frequency.

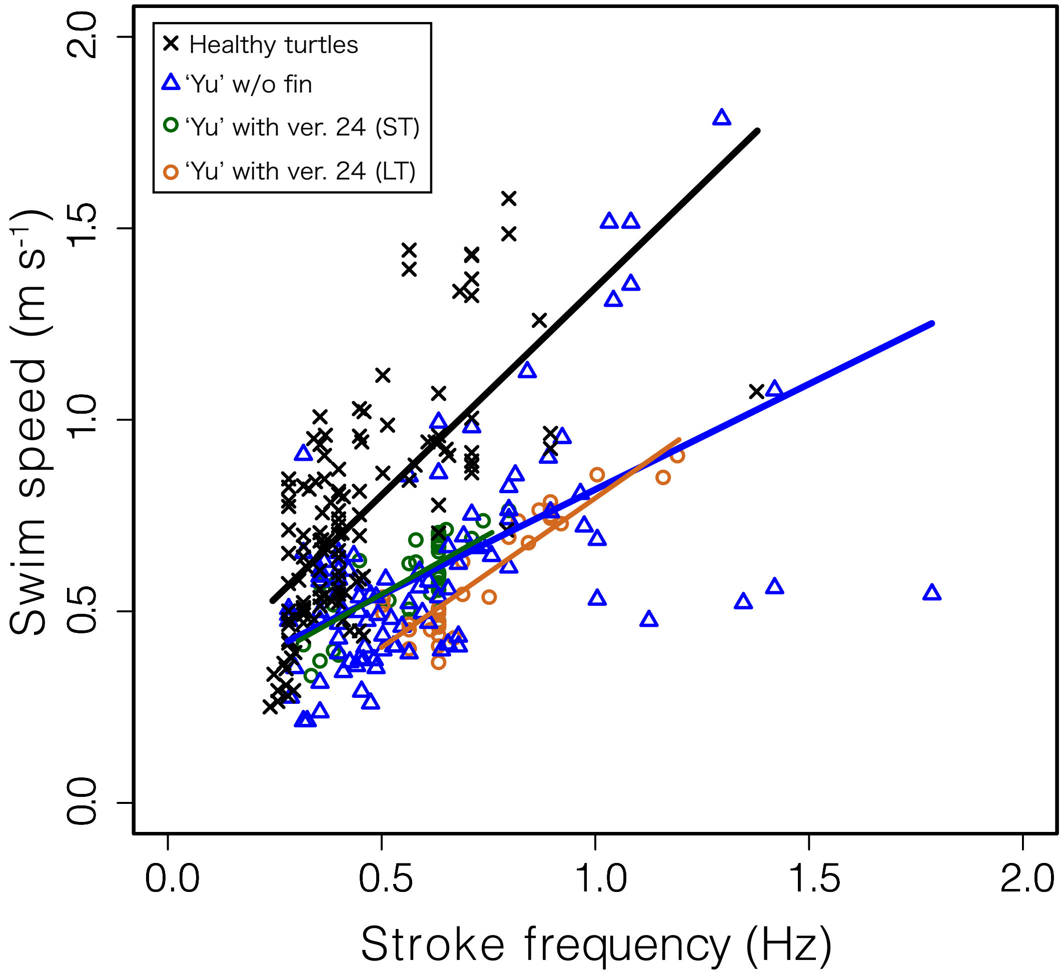

Fig. 19 Regression lines of swim speed and stroke frequency of the healthy turtles in captivity and 'Yu' without fin and with fin ver. 24 (short-term deployment, ST and long-term deployment, LT). The solid lines indicate regression lines of swim speed and stroke frequency.

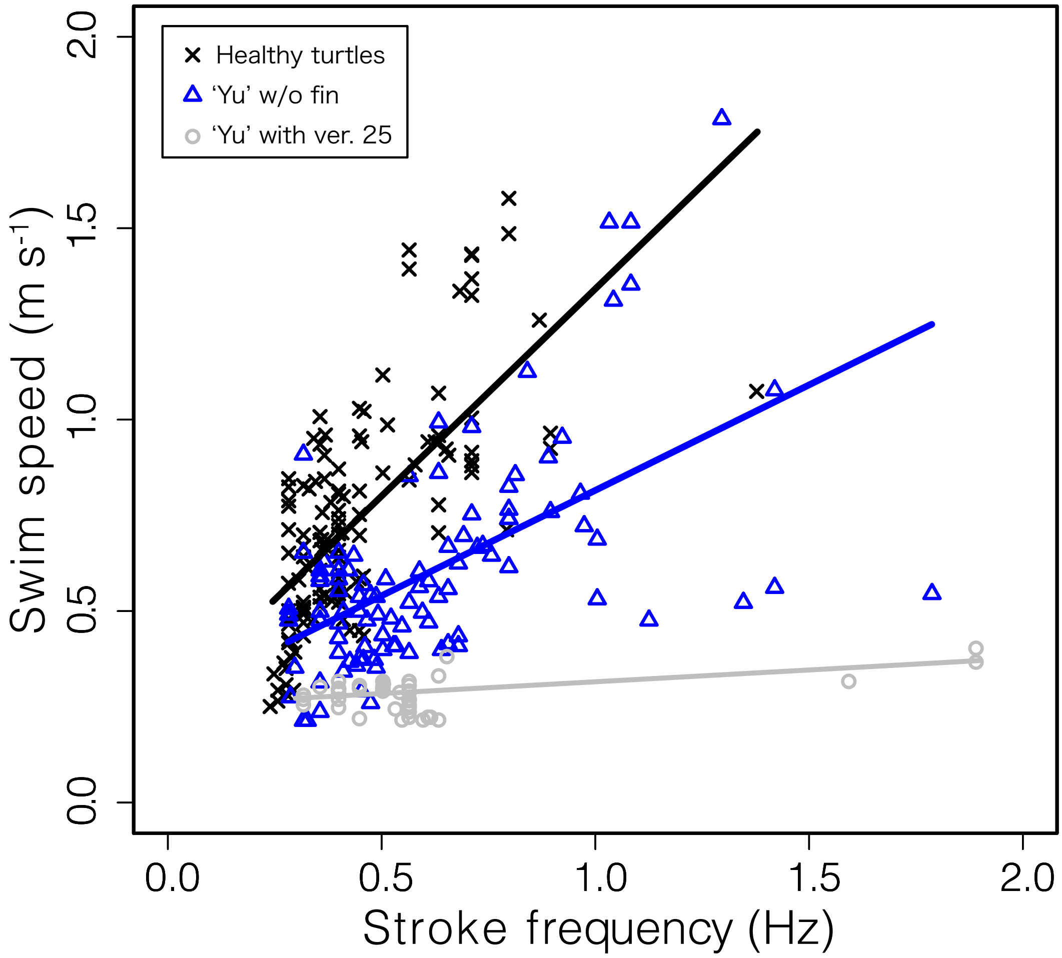

Fig. 20 Regression lines of swim speed and stroke frequency of the healthy turtles in captivity and 'Yu' without fin and with fin ver. 25. The solid lines indicate regression lines of swim speed and stroke frequency.

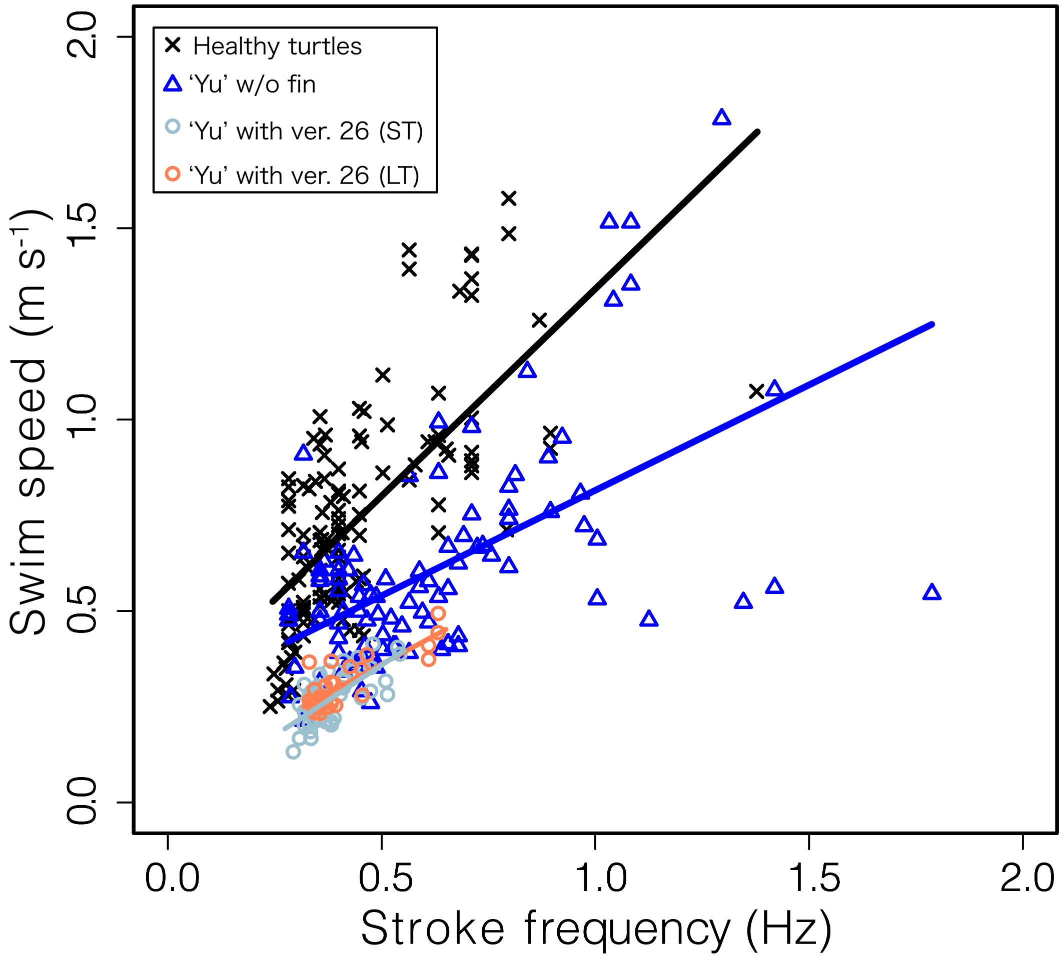

Fig. 21 Regression lines of swim speed and stroke frequency of the healthy turtles in captivity and 'Yu' without fin and with fin ver.26 (short-term deployment, ST and long-term deployment, LT). The solid lines indicate regression lines of swim speed and stroke frequency.

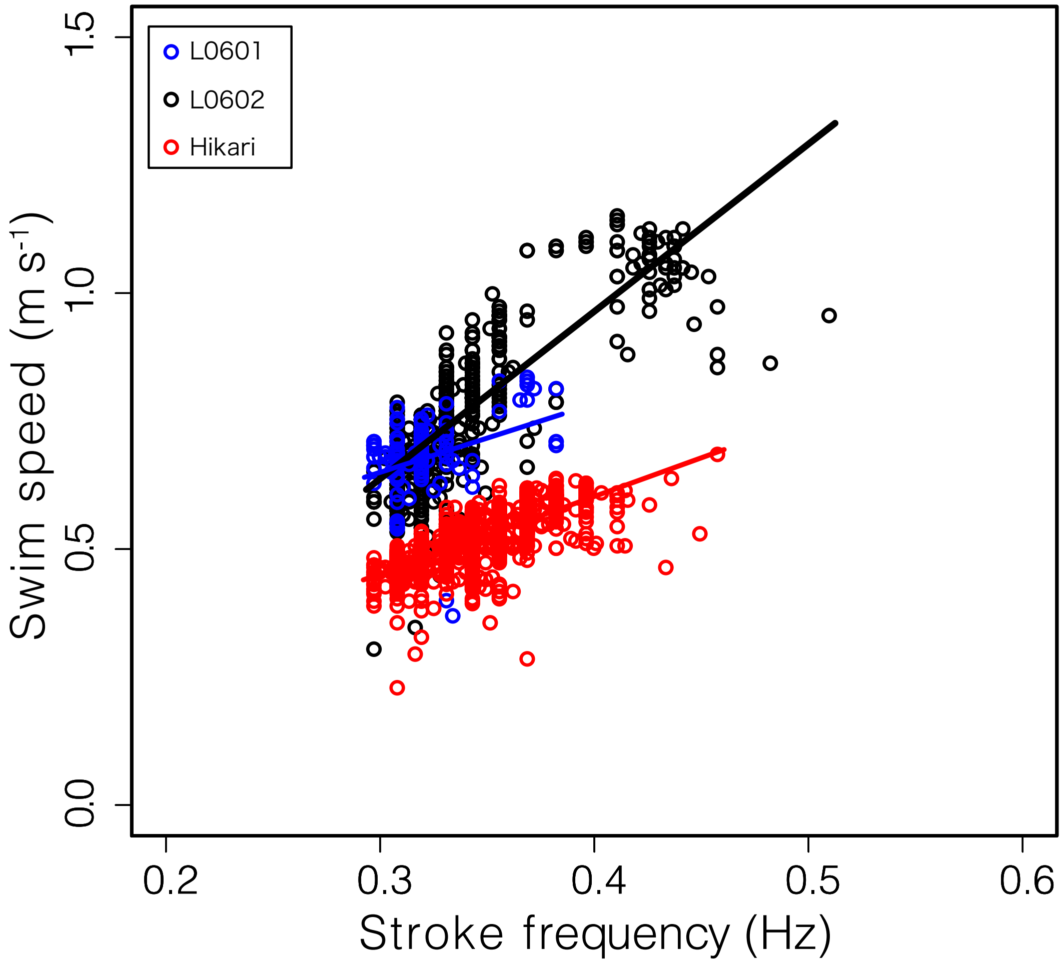

Fig. 22 Regression lines of swim speed and stroke frequency of sea turtles under natural conditions. The solid lines indicate regression lines of swim speed and stroke frequency.

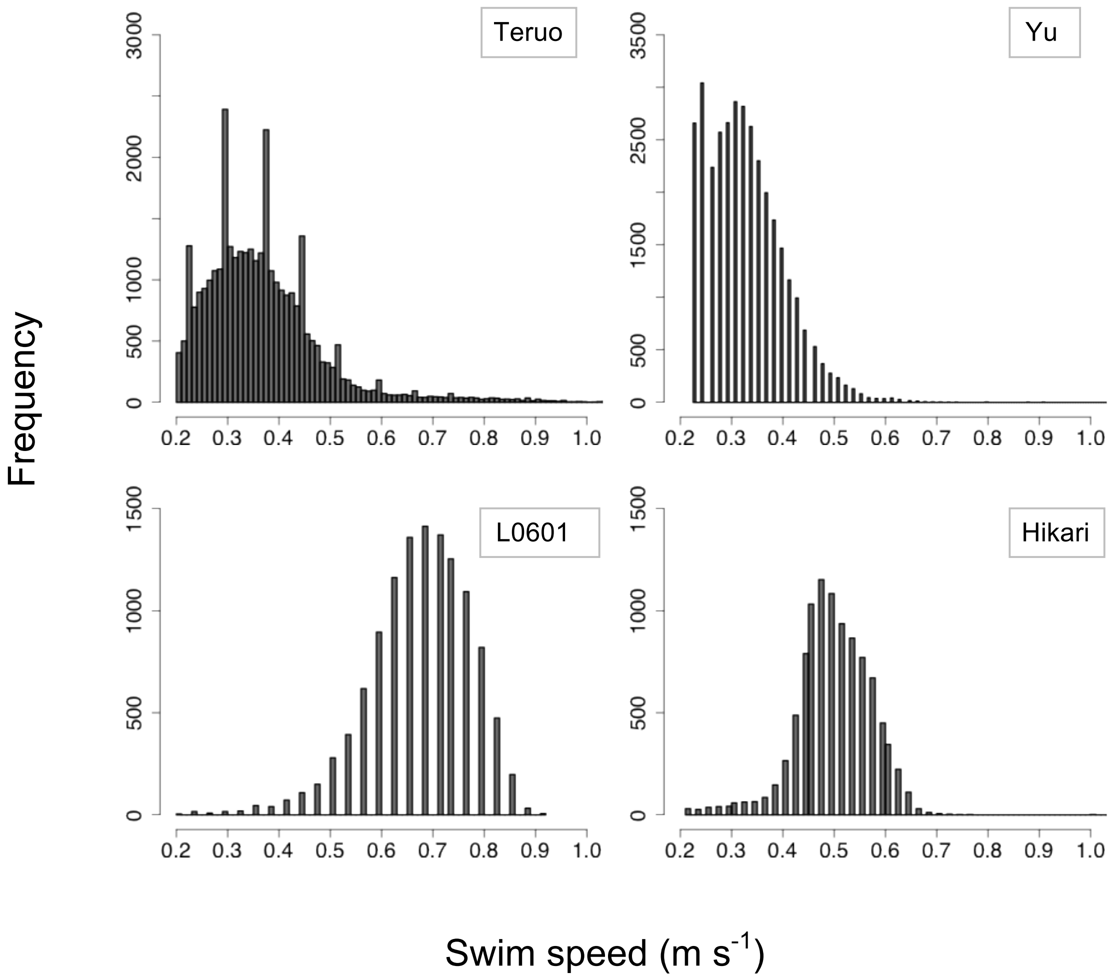

Fig. 23

Histogram of swim speed (Above left: the healthy turtle in captivity 'Teruo', above right: "Yu", bottom left: the healthy turtle under natural conditions L0601, bottom right: "Hikari").

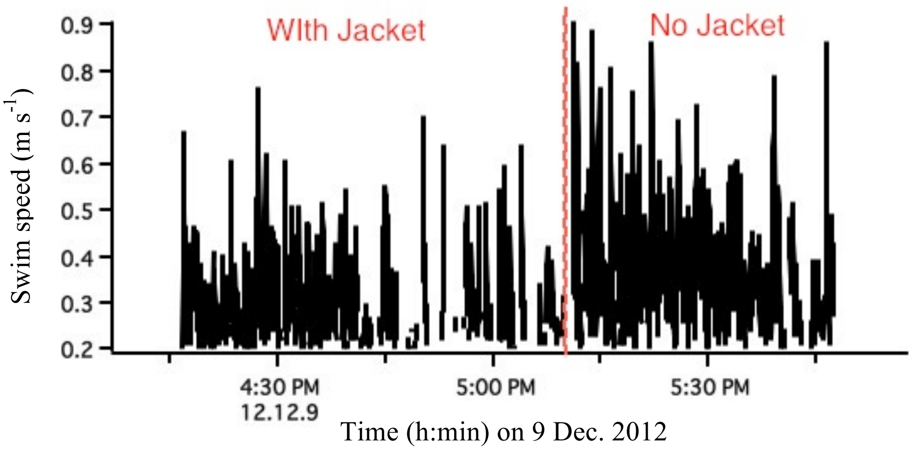

Fig. 24 Swim speed of ‘Teruo’ with and without a jacket. The red line indicates the time when the jacket was taken off from ‘Teruo’.

Table 12 Average and maximum swim speed of ‘Teruo’ with and without a jacket

	Ave. swim speed (ave. ± s.d., m s^{-1})	Max. swim speed (m s^{-1})
Without jacket	0.4 ± 0.1	0.9
With jacket	0.3 ± 0.1	0.8

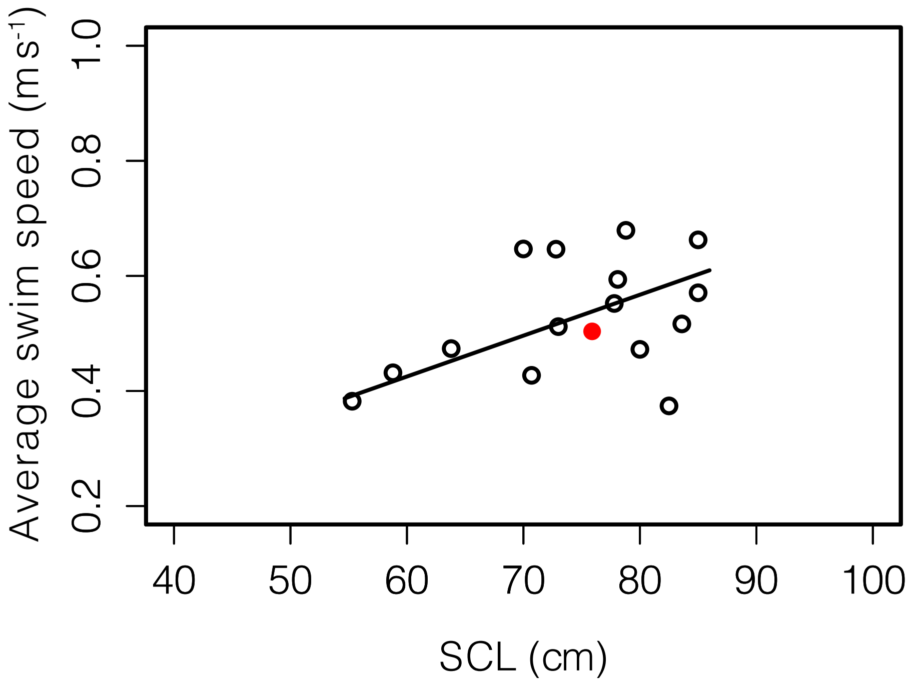

Fig. 25 The relationship between average swim speed and standard carapace length (SCL). The solid line indicates the regression line. The red closed dot indicates ‘Hikari’.

3. 3 Diving behavior

Dive duration and depth ranged from 3.4 to 11.0 min and 1.7 to 2.2 m, respectively, for 'Yu', and from 1.3 to 3.9 min and 1.3 to 1.7 m, respectively, for the healthy turtles (Table 13). The healthy turtles undertook dives more (range: 1329 – 5531) than 'Yu' (range: 524 – 2576, Table 13). Regardless of the application of the artificial fins, 'Yu' was able to perform a number of dives during the experiment.

For the sea turtles under natural conditions, diving data was calculated from each of them. Dive duration and depth of 'Hikari' were 5.0 ± 7.2 min and 13.7 ± 21.7 m (mean ± s.d., n = 66, Table 14), respectively. Mean dive duration and depth of the healthy turtles ranged from 2.8 to 5.1 min and 7.0 to 12.9 m, respectively (Table 14). Among the three sea turtles under natural conditions, it is noteworthy that the maximum dive depth recorded by 'Hikari' (125.8m, Table 14).

Table 13 Summary of dives of 'Yu' and healthy turtles in captivity.

Deployment date	ID	Dive duration (ave. ± s.d., min)	Dive depth (ave. ± s.d., m)	Max. dive depth (m)	Numbers of dives (data length, hr)
17 Oct.2010	Yu (no fin)	3.4 ± 9.3	1.7 ± 0.9	4.8	2576 (179.6)
	Inoki	1.3 ± 5.8	1.3 ± 0.5	4.5	5531 (167.2)
6 Jul.2012	Yu (ver. 23)	4.3 ± 8.1	2.1 ± 0.9	5.3	1072 (83.0)
	Teruo	3.1 ± 8.6	1.6 ± 0.6	4.0	1329 (84.6)
5 Aug.2012	Yu (ver. 26)	4.7 ± 9.8	2.2 ± 1.1	5.8	1190 (103.0)
	Teruo	2.4 ± 7.2	1.7 ± 0.7	4.5	2148 (102.0)
4 Nov.2012	Yu (ver.26)	11.0 ± 28.7	2.0 ± 1.2	5.3	524 (101.0)
	Teruo	3.9 ± 12.8	1.7 ± 0.7	4.0	1351 (99.7)

Table 14 Summary of dives of sea turtles under natural conditions.

ID	Dive duration (ave. ± s.d., min)	Dive depth (ave. ± s.d., m)	Max. dive depth (m)	Numbers of dives (data length, hr)
Hikari	5.0 ± 7.2	13.7 ± 21.7	125.8	66 (5.7)
L0601	5.1 ± 6.2	12.9 ± 11.8	39.0	70 (6.0)
L0602	2.8 ± 4.6	7.0 ± 7.7	48.0	2813 (14.5)

4. Discussions

4. 1 'Yu' and healthy turtles in captivity

According to the dive data, 'Yu' seemed not to have problems to undertake dives. The swimming ability of 'Yu' without fins were lower than that of the healthy turtles because of the low swim speed and the small distance travelled per stroke of 'Yu', which signified that 'Yu' could not produce thrust from each stroke as much as the healthy turtles. It was suggested that swimming abilities of 'Yu' were low due to decreased thrust produced by small forelimbs area. Interestingly, relative lift coefficient of 'Yu' was higher than that of the healthy turtle 'Shoko'. This was against the prediction that relative lift coefficient of 'Yu' would be low because of asymmetrical forelimbs, which could cause difficulties to produce thrust for efficient swimming. As most animals, such as penguins, flying insects, sunfish, eagle rays, and sea lions, have symmetrical wings or fins for lift generations in water or air (Watanabe and Sato 2008), it is also important for sea turtles to have symmetrical forelimbs in order to swim straight by moving their forelimbs synchronously. In the case of 'Yu', on the other hand, the shapes of forelimbs were not symmetrical (Table 6). The high relative lift coefficient suggested that 'Yu' could swim faster than the swim speed expected from its small area of forelimbs. During powerstrokes, the predominant way for sea turtles to swim, the hindlmbs usually do not produce thrust (Wyneken 1997). Kamezaki (2012) stated that sea turtles use their hindlimbs as steering when they swim with their forelimbs, and they use their hindlimbs to produce thrust when their forelimbs are not in use for swimming. The use of hindlimbs while swimming is also known in hatchlings (Wyneken 1997). From visual observations, it was observed that 'Yu' was moving its hindlimbs while swimming. Thus, it was assumed that relative lift coefficient became higher than expected due to thrust produced by hindlimbs. Similarly, usage of the hindlimbs probably caused maximum swim speed of 'Yu' to be higher than that of the healthy turtles (Table 8). High relative lift coefficient of 'Teruo' also might be caused by usages of its hindlimbs. Dominant stroke frequency of 'Yu' without fins was similar or lower than that of the healthy turtles (Table 8), which signifies that 'Yu' did not stroke faster to compensate decreased swim speed caused by decreased forelimbs area.

4. 2 Artificial fins

One of the concerns with applying the artificial fins to 'Yu' was whether 'Yu' could have natural diving behaviors with the fins. The result showed that 'Yu' could perform a number of dives with the artificial fins (Table 13). According to the low swim speed of 'Yu' at the beginning of artificial fins applications, swimming ability of 'Yu' with artificial fins was lower than those of the healthy turtles. The small distance that 'Yu' could travel with the artificial fins during each stroke also supports this result. However, after the long-term application of artificial fins, swim speed was increased at 0.86 Hz, although it was not as fast as the healthy turtles. Distance travelled per stroke at 0.86 Hz also increased after the long-term application. In other words, the application of the artificial fins did not improve swimming ability of 'Yu' at the beginning of the deployment, but the application of the fins might help 'Yu' to improve its swimming ability only when it stroked at a high stroke frequency. The result suggests that 'Yu' might be unfamiliar with the artificial fins, experiencing difficulties to use them in the beginning. During the long-term experiments of artificial fins, 'Yu' might have gained more muscles required to move the artificial fins and adapted to use them. However, the reasons for improved swimming ability only at high stroke frequency remained unknown.

Among the all artificial fins used in the study, ver. 5 fins seemed to be the best artificial fins in terms of swimming ability improvement: swim speed at 0.43 Hz was 58% of the healthy turtles at the beginning of the application, but it increased to 86% after the long-term application (Table 8). Moreover, the distance travelled per stroke at 0.43 Hz and relative lift coefficient became larger after the long-term application than the beginning of the application. Thus, the swimming ability seemed to be improved after the long-term application, but not at the beginning of the application of fins. After the long-term application, distance travelled per stroke, relative lift coefficient and swim speed of 'Yu' at 0.86 Hz was higher than that of the healthy turtles, which suggests that 'Yu' obtained better swimming ability than the healthy turtles when it stroked at high stroke frequency. Therefore, fin ver. 5 seemed to be successful to improve in swimming ability of 'Yu'. Unfortunately, because the base of forelimbs where fin ver. 5 was attached became necrotic from tightening, we could not continue applying the fin ver. 5 to 'Yu'.

Alternatively, the new jacket type fins were developed to prevent necrosis. However, relative lift coefficients of 'Yu' with the jacket type fins were smaller than the healthy turtles and also 'Yu' without fins. The swimming speed and the distance travelled per stroke were only improved with fin ver. 23 (Fig. 18, Table 8). This result was unexpected because shape of the fin ver. 23 was asymmetrical, which seemed to be disadvantageous for efficient swimming. The possible reason for improvement of swimming speed and distance travelled per stroke could be caused by the large area of the fin ver. 23 (Table 6) since the relative lift coefficient of fin ver. 23 was smaller than that of 'Yu' without fin (Table 8). Fin ver. 25 also gave 'Yu' asymmetrical shapes of forelimbs by applying the fins on left forelimb only. Relative lift coefficient of fin ver. 25 was low, and swimming speed and distance travelled per stroke were small as well, suggesting that it is better to apply artificial fins on both sides. Fin ver. 24 and 26 were tested after the long-term applications as well as in the beginning of the applications. However, swimming ability was not improved after long-term application. This result was not consistent with the result of fin ver.5, of which swimming ability was improved after the long-term application. Overall, the jacket type fins did not help 'Yu' to improve the swimming ability like fin ver. 5 (the tightened type). To examine the effect of the jacket itself, swim speed of the healthy turtle, 'Teruo', with and without wearing the jacket was compared. As the swim speed with the jacket was significantly decreased, the increased drag produced by the jacket could explain the failure of improvement in swimming ability of 'Yu' with the jacket type fins. Thus, the result suggested that it is necessary to develop new application method of fin.

4. 3 Swimming ability of 'Yu' and 'Hikari'

During the experiment, 'Hikari' dove to a maximum depth of 125.8 m, which suggests a high diving ability of 'Hikari'. The swimming ability of 'Hikari' was lower than that of the healthy turtles because of the low swim speed and the small distance travelled per stroke. However, the relative lift coefficient was 1.04, which was similar to the healthy turtles. It suggests that swim speed of 'Hikari' was declined because of the reduced area of forelimb. In this study, the relative lift coefficient estimated for 'Yu' was higher than that of 'Hikari' (Table 8 and 9), which could be explained by the length of data used for the analysis. Since "Yu" did not swim most of the time in the artificial lagoon, the data of the first 30 min after the release was used to evaluate swimming ability. During this period, 'Yu' might have been motivated to swim fast using its hindlimbs to escape from underwater observers, which caused relative lift coefficient to be high. On the other hand, the entire data-set was used to evaluate swimming ability of 'Hikari' since it was swimming throughout the experiment. Thus, the effects of handling stress on swim speed of 'Hikari' would be small.

Animals that live underwater are known to swim at optimal swim speed, at which cost of the transport would be the lowest. According to Sato et al. (2010), the theoretical optimal swim speed of a swimming animal can be estimated as a following equation,

$$U_{opt} = \left(\frac{\varepsilon_P \varepsilon_A k}{\rho_w \lambda C_D S} \right)^{1/3}$$

where ε_p is the propeller efficiency with which muscular movements are translated into forward thrust, ε_A is the efficiency with which chemical energy is translated into muscular work, k is basal metabolic rate (W), ρ_w is the density of the seawater, and λ is the ratio of the drag of an active swimmier to that of a passive object, C_D is drag coefficient of gliding animals, and S is wetted surface area (m^2). To estimate the optimal swim speed of sea turtles, the following valued were used: $\varepsilon_p = 0.85$ (Hind and Gurney 1997), $\varepsilon_A = 0.23$ (Prange 1975), $k = 0.21$ (Lutz and Bentley 1985), $\rho_w = 1027$ kg m^{-3}, $\lambda = 1$ (Hind and Gurney 1997), $C_D = 0.34$ (Watson and Granger 1998), and $S = 0.0398$ (Watson and Granger 1998). As a result, the optimal swim speed of a sea turtle was calculated as 0.66 m s^{-1}. The Histogram of swim speed of L0601, the healthy turtle under natural conditions, had a peak at 0.68 m s^{-1} (Fig. 23), which accords with the optimal swim speed calculated based on a theoretical research. Therefore, it is suggested that the healthy turtle under natural conditions was swimming at the optimal swim speed. Although the healthy turtle and 'Hikari' stroked at the same dominant stroke frequency, the histogram of swim speed of 'Hikari' had a peak at 0.48 m s^{-1} (Fig. 23), suggesting that the optimal swim speed of 'Hikari' was lower than that of the healthy turtle.

This result suggests that turtles do not use a swimming strategy that changes their stroke frequencies to achieve a certain swim speed, but they adopt the strategy that maintain a particular stroke frequency to optimize cost of transport. Therefore, the optimal swim speed of 'Hikari' decreased as a consequence of reduced area of forelimbs. In the case of turtles in captivity, the histogram of 'Yu' and the healthy turtles had peaks at 0.35 m s^{-1} (Fig. 23), which were lower than the theoretical optimal swim speed. It can be considered that the turtles in captivity were not motivated to swim optimally in the enclosed lagoon.

In the wild, turtles with injured forelimbs are occasionally found. Some of these turtles adapt to their situation and acquire to swim efficiently. The relationship between average swim speed and SCL showed that the average swim speed of 'Hikari' was not much lower than that of the healthy turtles, which suggests 'Hikari' was adapted to swim efficiently with the left limb alone. 'Yu' was also adapted to swim efficiently by using its hindlimbs. Even though they may not be able to achieve the maximum swim speed as high as the healthy turtles, it may not be a crucial problem for them since turtles in the wild usually swim at optimal swim speed. They are hardly in need of swimming fast unless they are in some emergent occasions such as being chased by predators. 'Yu', similarly, may not have a problem for its survival from its reduced size of forelimbs, except when it needs to move on land for nesting. In the process of developing the artificial fins, we need to consider to create fins that can help 'Yu' to swim efficiently at optimal swim speed and make it possible to move on land.

4.4 Influences 'Yu' gave to people

Unfortunately, the swimming ability of 'Yu' was not improved by applying the artificial fins. However, the artificial fins project offered valuable learning opportunity for public in terms of environmental education. Development of the artificial fins for a sea turtle attracts many people's interests, and the project was introduced in various media, including newspapers, TV and Internet. Many people, including children, could join the artificial fins project so that they could actually touch sea turtles and learn about them. The project also provoked discussions about whether deploying the artificial fins on animals was ethically right or not, which made people to think more about what is good to protect this endangered animals. Protecting an injured individual like 'Yu' may not lead to conservation of the entire population. However, the artificial fins project provided people with opportunities to consider the importance of wildlife and what people could do for the conservation.

5. Acknowledgements

I would like to express my deepest appreciation to my supervisor, Dr. Katsufumi Sato, for his advices and supporting on my research. I would like to express my gratitude to Dr. Shingo Kimura for useful comments. Dr. Tomoko Narazaki always helped me with getting data, analyzing, and writing papers. I appreciate Dr. Naoki Kamezaki, the president of Sea Turtle Association of Japan, for giving an opportunity to join the artificial fins project. I thank members of Kawamura Gishi, especially to Mr. Kei Kawamura, Mr. Yasushi Matsuda, Mr. Kazunori Kanda, Mr. Shigehiro Sakuma, Mr. Katsumi Kobayashi, Mr. Yusuke Kosaka, Ms. Aya Miki, Mr. Ryosuke Nakamura, and Mr. Masaki Misawa for developing the artificial fins and for their useful discussions. Dr. Naomi Kato, professor of Oosaka University, and Dr. Masaaki Sakagami, professor of Kyoto University, gave me helpful advices on my research. Feel grateful to the members of Sea Turtle Association of Japan, especially to Mari Taniguchi and Kanako Mine for their assistance with planning schedule, transporting turtles, morphological measurements, and field works. This study could not be accomplished without supports of divers, staffs of Suma Aqualife Park, staff of Sea turtle museum "Caretta", and volunteers from University of Kobe, and collaborators. The members of Sato laboratory always helped me with analysis. Last, but not least, I would like to express my deepest appreciation to my family for their dearly supports throughout my life.

6. References

Argos (1996): Argos User's manual, Collecte Localisation Satellites (CLS)

Bainbridge, R. (1957): The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat, *The Zoological Laboratory, Cambridge*, pp. 109-133.

Boehme, L., Lovell, P., Biuw, M., Roquet, F., Nicholson, J., Thorpe, S. E., Meredith, M.P. and Fedak, M. (2009): Technical Note: Animal-borne CTD-Satellite Relay Data Loggers for real-time oceanographic data collection. *Ocean Sci*., 5, pp.685-695.

Hind, A. T. & Gurney, W. S. C. (1997): The metabolic cost of swimming in marine homeotherms. *J.Exp. Biol.* vol. 200, pp. 531-542.

Hirayama, R. (2998): Oldest known sea turtle. *Nature*, vol. 392, pp. 705-708.

IUCN. (2012): IUCN Red List of Threatened Species. Version 2012.2. <www.iucnredlist.org>. Downloaded on 22 January 2013.

Kamezaki, N. (2012a): Evolution. In: Kamezaki, N. ed., *Natural history of sea turtles in Japan*, Japan: University of Tokyo Press, pp. 11-34. [In Japanese]

Kamezaki, N. (2012b): Morphology. In: Kamezaki, N. ed., *Natural history of sea turtles in Japan*, Japan: University of Tokyo Press, pp. 37. [In Japanese]

Lutz, P. L. and Bentley T. B. (1985): Respiratory physiology of diving in the sea turtle. Copeia, pp.

671-679.

Matsuzawa, Y. and Kamezaki, N. (2012). Conservation. In: Kamezaki, N. ed., *Natural history of sea turtles in Japan*, Japan: University of Tokyo Press, pp. 227-254. [In Japanese]

Narazaki, T., Sato, K., Abernathy, K. J., Marshall, G. J. and Miyazaki, N. (2009a): Sea turtles compensate deflection of heading at the sea surface during directional travel. *J. Exp. Biol.* vol. 212, pp.4019-4026.

Narazaki, T. (2009b): Diving behavior of loggerhead turtles, *Caretta caretta*, migrating to the northern Pacific coast of Japan. A PhD. Theses. The University of Tokyo.

Prange, H. D. (1975): Energetics of swimming of a sea turtle. *J. Exp. Biol.* vol. 64, pp. 1-12.

R Development Core Team (2010): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org>.

Sakamoto, K.Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F. and Wanless, S. (2009): Can Ethograms Be Automatically Generated Using Body Acceleration Data from Free-Ranging Birds? *PLoS ONE*, vol. 4, no. 4, e5379.

Sato, K., Watanuki, Y., Takahashi, A., Miller, P. O. J., Tanaka, H., Kawabe, R., Ponganis, P. J., Handrich, Y., Akamatsu, T., Watanabe, Y., Mitani, Y., Costa, D.P., Bost, C.A., Aoki, K., Trathan, P., Shapiro, A. and Naito, Y. (2007): Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proc. R. Soc. B*, vol. 274, pp.471-477.

Sato, K., Shiomi, K., Watanabe, Y., Watanuki, Y., Takahashi, A., and Ponganis, P. J. (2009): Scaling of swim speed and stroke frequency in geometrically similar penguins: they swim o ptimally to minimize cost of transport. *Proc. R. Soc. B,* vol. 277, pp. 707-714.

Seaturtle.org Maptool. (2002): Seaturtle.org, Inc. <http://www.seaturtle.org/maptool/> (19 Jan. 2013).

Watanabe, Y. and Sato, K. (2008): Functional Dorsoventral symmetry in relation to lift-based swimming in the ocean sunfish *Mola mola*. PLoS ONE, vol. 3, no. 10, e3446.

Watson, K. P. and Granger R. A. (1998): Hydrodynamic effect of a satellite transmitter on a juvenile green turtle (*Chelonia mydas*). *J. Exp. Biol.* vol. 201. pp. 2497-2505.

Wyneken, J. (1997): Sea turtle locomotion: mechanisms, behavior, and energetics. In: Luts, P.L. and Musick, J.A. eds., *The biology of sea turtles,* Florida: CRC Marine Science Series, CRC Press, pp. 171-183.

7. Appendix

Appendix 1: A list of Akaike Information Criteria (AIC) for selecting equation of forelimbs area and SCL.

	Equations of forelimbs area and SCL	AIC
Total forelimbs area	$y=1.6980x^{1.4394}$	**278.5**
	$y=0.152621x^{2}$	286.2
Right forelimb area	$y=0.3674x^{1.6361}$	**254.2**
	$y= 0.076864x^{2}$	255.3
Left forelimb area	$y=1.9597x^{1.2429}$	**243.2**
	$y= 0.075757x^{2}$	257.2

Appendix 2: A list of Akaike Information Criteria (AIC) for models for swim speed and stroke frequency tested using generalized linear model.

	Models	AIC
Fig. 14	SP~Freq+ID+Freq:ID	-41.1
[Shoko and Teruo]	SP~Freq+ID	**-41.6**
	SP~Freq	-34.6
	SP~ID	41.1
	SP~1	43.0
Fig. 15	SP~Freq+Type+Freq:Type	**-295.3**
[Healthy turtles, 'Yu' without fin,	SP~Freq+Type	-257.8
'Yu' with fin (ST and LT)]	SP~Freq	-80.9
	SP~Type	4.6
	SP~1	104.0
Fig. 16	SP~Freq+Type+Freq:Type	**-190.2**
[Healthy turtles, 'Yu' without fin, 'Yu'	SP~Freq+Type	-123.7
with ver. 5 (ST), 'Yu' with ver. 5 (LT)	SP~Freq	-14.2
	SP~Type	85.0
	SP~1	136.4
Fig. 19	SP~Freq+Type+Freq:Type	**-119.4**
[Healthy turtles, 'Yu' without fin, 'Yu'	SP~Freq+Type	-105.2
with ver. 24 (ST), 'Yu' with ver. 24	SP~Freq	-10.2
(LT)	SP~Type	36.9
	SP~1	52.0

Fig. 21 [Healthy turtles, 'Yu' without fin, 'Yu' with ver. 26 (ST), 'Yu' with ver. 26 (LT)	SP~Freq+Type+Freq:Type	**-139.7**
	SP~Freq+Type	-124.6
	SP~Freq	48.2
	SP~Type	13.7
	SP~1	144.2
Fig. 17, 18, 19 [Healthy turtles, 'Yu' without fin, 'Yu' with Jacket type fin (ST)]	SP~Freq+Type+Freq:Type	**-360.0**
	SP~Freq+Type	-286.6
	SP~Freq	10.6
	SP~Type	-128.2
	SP~1	93.52
Fig.22 [L0601, L0602, Hikari]	SP~Freq+ID+Freq:ID	**-6522**
	SP~Freq+ID	-6143
	SP~Freq	-2693
	SP~ID	-4502
	SP~1	-2398

Appendix 3: A list of Akaike Information Criteria (AIC) for models for average swim speed and SCL tested using generalized linear model.

Models	AIC
SP~SCL+PSD	-22.63
SP~SCL	**-23.95**[※]
SP~PSD	-20.86
SP~1	-22.85

[※]The model was compared with the equation without interception as followed. Then, the equation with no reception was selected.

Equation	**AIC**
SP~SCL	-23.95
SP~SCL (no interception)	**-25.13**

Abbreviations used are as followed: SP, average swim speed; SCL, standard carapace length; PSD, dominant stroke frequency