

RESEARCH ARTICLE

Swimming strategies and energetics of endothermic white sharks during foraging

Yuuki Y. Watanabe^{1,2,*}, Nicholas L. Payne^{3,4}, Jayson M. Semmens⁵, Andrew Fox⁶ and Charlie Huvneers⁷

ABSTRACT

Some fishes and sea turtles are distinct from ectotherms by having elevated core body temperatures and metabolic rates. Quantifying the energetics and activity of the regionally endothermic species will help us understand how a fundamental biophysical process (i.e. temperature-dependent metabolism) shapes animal ecology; however, such information is limited owing to difficulties in studying these large, highly active animals. White sharks, *Carcharodon carcharias*, are the largest fish with regional endothermy, and potentially among the most energy-demanding fishes. Here, we deployed multi-sensor loggers on eight white sharks aggregating near colonies of long-nosed fur seals, *Arctocephalus forsteri*, off the Neptune Islands, Australia. Simultaneous measurements of depth, swim speed (a proxy for swimming metabolic rate) and body acceleration (indicating when sharks exhibited energy-efficient gliding behaviour) revealed their fine-scale swimming behaviour and allowed us to estimate their energy expenditure. Sharks repeatedly dived (mean swimming depth, 29 m) and swam at the surface between deep dives (maximum depth, 108 m). Modal swim speeds ($0.80\text{--}1.35\text{ m s}^{-1}$) were slower than the estimated speeds that minimize cost of transport ($1.3\text{--}1.9\text{ m s}^{-1}$), a pattern analogous to a 'sit-and-wait' strategy for a perpetually swimming species. All but one shark employed unpowered gliding during descents, rendering deep (>50 m) dives 29% less costly than surface swimming, which may incur additional wave drag. We suggest that these behavioural strategies may help sharks to maximize net energy gains by reducing swimming cost while increasing encounter rates with fast-swimming seals.

KEY WORDS: Biologging, Swim speed, Cost of transport, Optimal behaviour

INTRODUCTION

The metabolic rate of organisms plays fundamental roles in physiological ecology by setting the 'pace of life' (Brown et al., 2004). Ectotherms (invertebrates, fishes, amphibians and reptiles) generally have lower body temperatures and, hence, lower metabolic rates than similar-sized endotherms (birds and mammals). Consequently, ectotherms are considered to 'live life

in the slow lane' (e.g. move slower, eat less and grow slower), whereas endotherms have more active lifestyles, eat more food and grow more rapidly. The dichotomy of ectotherms and endotherms has long been a basis for understanding the lifestyles of diverse animals and their broad-scale ecological implications (Buckley et al., 2012); however, remarkable intermediate forms exist. Some fishes (tunas, opah and some sharks) and leatherback sea turtles have elevated core body temperatures and metabolic rates (Dickson and Graham, 2004; Paladino et al., 1990; Wegner et al., 2015), and exhibit highly active lifestyles (e.g. swim faster and migrate longer distances) (Watanabe et al., 2015) with elevated growth rates (Grady et al., 2014) compared with their ectothermic counterparts. The thermal physiology of these animals, referred to as regional endothermy (Dickson and Graham, 2004), is distinct from the true endothermy of birds and mammals owing to their confined warmed organs and incomplete abilities of regulating body temperature (Clarke and Portner, 2010). To stress their intermediate thermal physiology between true ectotherms and endotherms, some authors proposed the term 'mesothermy' (Grady et al., 2014). Quantifying the energetics and activity of regionally endothermic species in the wild will lead to a better understanding of how a fundamental biophysical process (i.e. temperature-dependent metabolism) shapes the ecology of diverse animals. However, such information is still limited, primarily because of difficulties in studying these large, highly active animals.

White sharks, *Carcharodon carcharias* (Linnaeus 1758), the largest fish with regional endothermy (typical adult body mass, 300–800 kg), are likely to have unusually high energy expenditure for a fish. Although they eat a variety of foods, including teleosts, other sharks and cephalopods (Estrada et al., 2006; Hussey et al., 2012), they seasonally aggregate near pinniped colonies in temperate waters to hunt weaned pups or adult seals. Once caught, a seal will become a disproportionately energy-rich food, equivalent to hundreds of teleosts or cephalopods, owing to its large body size and high fat content. However, seals, especially otariids (fur seals and sea lions), are fast swimmers with remarkable manoeuvrability (Fish et al., 2003; Watanabe et al., 2011). To maximize net energy gains, white sharks are expected to employ behavioural strategies that increase prey encounter rates while reducing the energetic cost of swimming. Despite previous studies on the movement patterns of white sharks near seal colonies (recorded by acoustic telemetry) (Goldman and Anderson, 1999; Huvneers et al., 2013; Jewell et al., 2014; Klimley et al., 2001; Towner et al., 2016), spatiotemporal distributions of seal-predation attempts (directly observed from a boat) (Martin et al., 2005, 2009) and the estimates of daily energy expenditure (Carey et al., 1982; Semmens et al., 2013), the potential behavioural strategies and their consequence on energetics in white sharks have not been sufficiently addressed.

In this study, we attached a package of recording devices, consisting of an accelerometer (with a speed, depth and temperature sensor) and video camera, to white sharks aggregating near the

¹National Institute of Polar Research, Tachikawa, Tokyo 190-8518, Japan.

²SOKENDAI (The Graduate University for Advanced Studies), Tachikawa, Tokyo 190-8518, Japan. ³University of Roehampton, Holybourne Avenue, London SW15 4JD, UK. ⁴Trinity College Dublin, Dublin 2, Ireland. ⁵Fisheries and Aquaculture Centre, Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 49, Hobart, Tasmania 7001, Australia. ⁶Fox Shark Research Foundation, Adelaide, South Australia 5070, Australia. ⁷College of Science and Engineering, Flinders University, Bedford Park, South Australia 5042, Australia.

*Author for correspondence (watanabe.yuuki@nipr.ac.jp)

 Y.Y.W., 0000-0001-9731-1769

colonies of long-nosed fur seals, *Arctocephalus forsteri* (formally New Zealand fur seals), off the Neptune Islands, Australia. The direct measurements of swim speed (a proxy for swimming metabolic rate) and body acceleration (indicating when sharks exhibited energy-efficient gliding behaviour) not only revealed their fine-scale swimming behaviour, but also allowed us to estimate their instantaneous field metabolic rates (FMR). Based on this information, we tested two hypotheses regarding shark swimming strategies. First, we hypothesized that white sharks swim slower than the speed that minimizes the cost of transport (hereafter, $U_{COT-min}$, where COT is the energy needed to move a unit body mass over a unit distance). According to a theoretical model (Papastamatiou et al., 2018), sharks should do so to maximize net energy gain when the average speed of prey is comparable to that of the sharks (such as our white shark and seal system). This is because, in such systems, the probability of prey arriving at the predator's location without the predator moving is relatively high, and predators do not need to find prey through active searching at the cost of increased metabolic rates. In other words, $U_{COT-min}$, which minimizes energy expenditure per unit distance rather than per unit time, is not optimal when predators can 'sit and wait'. Second, we hypothesized that cost-efficient gliding behaviour with negative buoyancy, exhibited by white sharks during descending phases of dives (Gleiss et al., 2011a), has substantial effects on their overall swimming costs. More specifically, we would expect that a series of deep dives (passive descents followed by active ascents) shown by white sharks is associated with decreased FMR compared with surface swimming shown by sharks between deep dives. By testing these two hypotheses, we aim to better understand the energy management strategies of this evolutionarily interesting, regionally endothermic species.

MATERIALS AND METHODS

Fieldwork and instrumentation

The fieldwork was conducted at the Neptune Islands Group (Ron and Valerie Taylor) Marine Park in Australia (35°14'S, 136°04'E) during August–September 2014, October–November 2015 and January 2016. The island system is composed of two groups of small, rocky islands (the North and South Neptune Islands), which are approximately 10 km apart. In this area, commercial cage-diving tours are operated, in which customers can watch white sharks underwater from cages (Huvneers et al., 2017). Off the North Neptune Islands, sharks were attracted to a boat using bait and chum. When sharks swam past the boat, a metal clamp (to which an electronic biologging package was attached) was placed on the first dorsal fin of the sharks using a deployment pole (Customized Animal Tracking Solutions) (Chapple et al., 2015) (Fig. 1A). This remote attachment method has a great advantage over the conventional method of hooking and catching sharks, where, owing to stress, animals can exhibit unusual behaviour after being released (Sundström and Gruber, 2002; Whitney et al., 2016b). The package was programmed to detach from the clamp 1–2 days later by a time-scheduled release mechanism (Little Leonardo), float to the surface, and be located and recovered using signals from a satellite transmitter (Wildlife Computers) and VHF transmitter (Advanced Telemetry Systems) (Watanabe et al., 2004, 2008). The clamp had a corrodible section, and was designed to come off the dorsal fin after approximately 1 week (that is, nothing would remain attached to the sharks after the research was finished). For each shark tagged, sex was determined by underwater observation, and total length (TL, in m) was visually estimated in relation to the length of several parts of the boat (Table 1). The estimated TL was

converted to precaudal length (PCL, in m; $PCL = -0.09 + 0.85 \times TL$) and then body mass [M_b , in kg; $\ln(M_b) = 2.83 + 2.95 \times \ln(PCL)$] using published relationships for this species (Mollet and Cailliet, 1996). However, our estimates of body size may be inaccurate, and sensitivities were tested in the energetic modelling (see below).

The package included a PD3GT accelerometer (21 mm diameter, 115 mm length, 60 g; Little Leonardo), which recorded depth, swim speed (measured by a propeller sensor) and temperature at 1-s intervals, and triaxial acceleration (along longitudinal, lateral and dorso-ventral axes) at 1/16- or 1/32-s intervals throughout the deployment periods (1–2 days). The package on three individuals also included a DVL400M camera (21 mm width, 22 mm height, 68 mm length, 47 g; Little Leonardo), which recorded video (1440×1080 pixels at 30 frames s⁻¹) for approximately 6 h. The camera was programmed with a 3–12 h delay start to target daytime periods when cage-diving operators were not present.

All necessary permits were obtained from the Department of Environment, Water and Natural Resources (DEWNR) (M26292), Marine Parks (MR00047), PIRSA Exemption (9902693 and 9902777) and the Flinders University ethics committee (E398).

Swim speed measurement

Relative swim speed, measured by the number of rotations per second of the propeller sensor, was converted to actual swim speed (m s⁻¹) using equations obtained from a flow tank calibration experiment. In the experiment, a PD3GT accelerometer was set in the tank and flow speed was increased from 0.3 to 1.1 m s⁻¹ at intervals of 0.1 m s⁻¹. The relationship obtained was linear ($R^2 > 0.99$, $N = 9$ data points). Although the upper speed range was limited to 1.1 m s⁻¹ by the capacity of the tank, a linear relationship between propeller rotation and swim speed has been validated for up to approximately 3.8 m s⁻¹ (Aoki et al., 2012). Inevitable differences between the pitch angles of the sharks and those of the accelerometers (calculated from low-pass filtered longitudinal accelerations) were estimated for each shark using the within-data calibration method (Kawatsu et al., 2010). This 'attachment angle' was accounted for in the conversion of swim speed by dividing the raw speed estimate by the cosine of the attachment angle. To validate this correction method, another set of flow tank experiments was conducted. A PD3GT accelerometer was set in the tank at angles of 15, 30 and 45 deg relative to flow, and the flow speed was increased from 0.4 to 1.0 m s⁻¹ at intervals of 0.2 m s⁻¹ for each angle. Using the correction method, errors in the speed estimates (i.e. difference between the true and estimated speeds, expressed as percentages of the true speeds) were reduced (average error across the four different speeds was 1%, 8% and 9% for angles of 15, 30 and 45 deg, respectively). Therefore, the correction method was considered valid, as long as the attachment angle was moderate (<45 deg). By contrast, the differences between the yaw angles of the sharks and those of the accelerometers were assumed to be zero, because the packages were firmly attached to the side of the dorsal fins (Fig. 1A). The package was accidentally set vertically on the dorsal fin for shark 8, and the propeller sensor did not rotate properly. Swim speed and field metabolic rate (FMR) were not estimated for this individual.

Depth and acceleration data analyses

Behavioural data were analysed using the software Igor Pro (WaveMetrics) with the Ethographer extension (Sakamoto et al., 2009). The periods during which sharks interacted with the boat, representing unnatural behaviour (Huvneers et al., 2018), were excluded from the analyses. Based on the depth profiles, shark

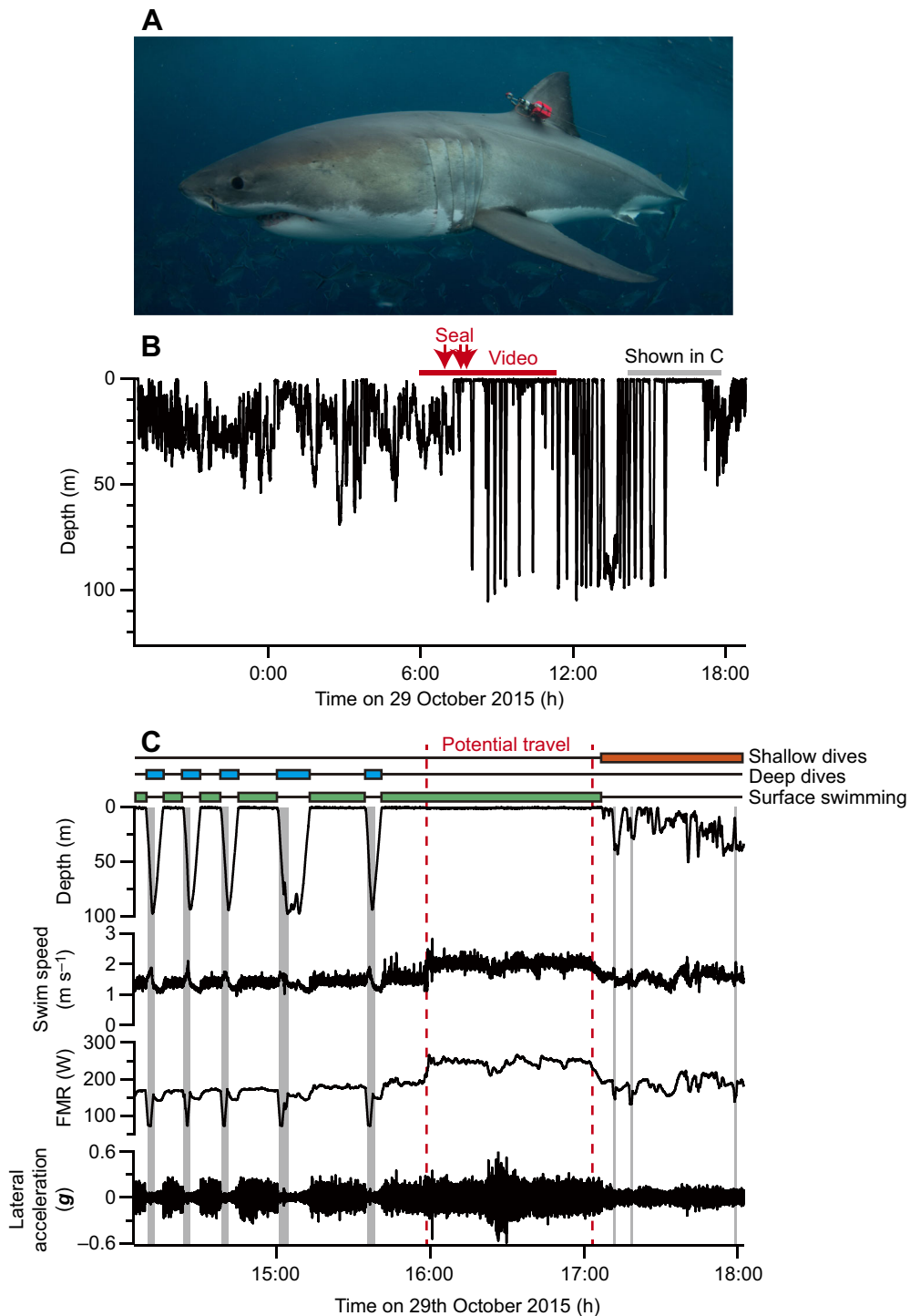


Fig. 1. White shark swimming behaviour. (A) A shark with a biologging package attached. Photo credit: A. Fox. (B) The entire 24 h record of swimming depth for shark 5. This shark interacted with the boat during the initial 48 min and the last 30 min of the data. The red horizontal bar represents the period of simultaneous video recording, and red arrows represent the times when a seal was seen. The grey horizontal bar represents the period shown in detail in C. (C) An enlarged view of the swimming pattern, composed of shallow dives, deep dives and surface swimming (top horizontal bars), showing depth, swim speed, estimated field metabolic rate (FMR) and high-pass filtered lateral acceleration. Red vertical dashed lines denote the period of surface swimming with an elevated speed (2 m s^{-1}), which may represent travel from the North to the South Neptune Islands (see Results). Grey vertical bars represent gliding periods.

behaviour was categorized into three groups: (i) shallow dives, when the sharks undertook repeated up-and-down movements at $<50 \text{ m}$ depth without extended surfacing periods; (ii) deep dives, when the sharks dived from the surface to $>50 \text{ m}$ depth and returned to the surface within 1 h; and (iii) surface swimming, when the shark kept swimming at the surface ($0\text{--}2 \text{ m}$ depth) for $>5 \text{ min}$ (Fig. 1C). Although some intermediate patterns (e.g. continuous deep dives without surfacing) were also observed, 80% of our 150-h records was covered by the three categories (Table 2).

Gliding periods during descending phases of dives were determined by the lateral acceleration records as the periods

showing no cyclic changes. This method was confirmed to be valid by the simultaneously recorded video footage (Movie 1). Overall dynamic body acceleration (ODBA) (Wilson et al., 2006), a proxy for energy expenditure of the animals, was calculated as the sum of the absolute values of high-pass filtered acceleration over three axes.

Field metabolic rate

Instantaneous FMR of individual sharks was estimated based on swim speed, water temperature and whether the shark was actively swimming versus passively gliding. A previous experiment with

Table 1. Descriptive information, swimming behaviour and energetics of white sharks

Shark no.	Sex	Total length (m)	Body mass (kg) ^a	Deployment month/year	Duration (h) ^b		Swimming depth (m)		Experienced temperature (°C)		Mean field metabolic rate (W)
					Accelerometer	Video	Mean	Range	Mean	Range	
1	M	3.3	323	8/2014	12.7	–	11.5	0–45.9	15.5	15.3–16.1	93
2	M	3.2	294	8/2014	15.6	–	23.8	0–68.1	15.4	15.1–15.4	85
3	F	4.2	671	9/2014	14.3	–	38.9	0–85.8	15.1	15.0–15.3	144
4	M	4.3	721	9/2014	27.0	–	22.4	0–72.8	15.2	15.0–15.3	146
5	M	3.8	496	10/2015	22.6	6.0	21.2	0–105.4	15.5	15.0–15.9	163
6	M	3.7	457	10/2015	11.3	1.8	41.5	0–108.3	15.4	15.0–15.9	124
7	M	2.9	218	10/2015	9.2	–	36.4	0–95.9	15.5	15.0–15.9	69
8	M	3.5	386	1/2016	37.3	–	37.9	0–96.1	16.3	12.4–20.6	–

^aEstimated from total length.

^bPeriods during which sharks interacted with the boat were excluded from the duration calculation.

swim-tunnel respirometry for short-fin mako sharks, *Isurus oxyrinchus* (6.1 kg body mass; 18°C water temperature), a species with regional endothermy closely related to white sharks, showed that their FMR (in mg O₂ kg⁻¹ h⁻¹) during active swimming is approximated by:

$$\log_{10}(\text{FMR}) = \log_{10}(\text{SMR}) + 0.97U, \quad (1)$$

where SMR is standard (or resting) metabolic rate in mg O₂ kg⁻¹ h⁻¹ and U is swim speed in TL s⁻¹ (Sepulveda et al., 2007). Although this equation was obtained from sharks smaller than the white sharks tagged in the present study, the effects of body size on swimming metabolic rates in fishes can be removed by using swim speed relative to body length (Beamish, 1978). More specifically, log swimming metabolic rates plotted against swim speed relative to body length produce similar straight lines independently of body size of the fish (Beamish, 1978). Owing to the lack of direct measurements of swimming metabolic rates for larger fishes with regional endothermy, Eqn 1 was regarded as the best available information.

The SMR of short-fin mako sharks, estimated by an extrapolation of the relationship between swim speed and metabolic rate to zero speed, is 124 mg O₂ kg⁻¹ h⁻¹ (Sepulveda et al., 2007). The SMR of white sharks was estimated by scaling up the short-fin mako shark value to the body mass of white sharks using a scaling exponent of 0.79 (Payne et al., 2015), and adjusted for the water temperature experienced by the sharks using a Q_{10} value of 2.42, a typical value reported for sharks (Whitney et al., 2016a) (see below for sensitivity analyses). Instantaneous FMR during active swimming periods was estimated based on swim speed and total length of the sharks using Eqn 1. All but one shark exhibited gliding behaviour during descending phases of dives, and FMR during gliding periods was set at SMR. FMR was smoothed using a 1-min running average to obtain a physiologically appropriate time scale for changes in

metabolic rate (Williams et al., 2014). The units of FMR were converted from mg O₂ kg⁻¹ h⁻¹ to W by assuming that 1 mol O₂ equates to the utilization of 434 kJ.

We are aware of the limitations of scaling up a 6 kg short-fin mako shark to model 200–700 kg white sharks (see Payne et al., 2015); therefore, our focus in this study was to compare FMR among different behavioural categories and to estimate $U_{\text{COT-min}}$ for individual sharks, rather than compare FMR of white sharks with that of other species.

Hypothesis testing

To test the hypothesis that white sharks swim slower than $U_{\text{COT-min}}$, the relationship between swim speed and COT was constructed for individual sharks based on Eqn 1 and the estimates of SMR as explained above (Fig. 2). COT (J m⁻¹ kg⁻¹) was calculated by dividing FMR (W) by swim speed (m s⁻¹) and body mass (kg). The mean water temperature experienced by individual sharks was used in the calculation of FMR (Table 1). However, FMR and COT are sensitive to several parameters, especially body mass (estimated from visually determined body length), the scaling exponent of metabolic rates (set at 0.79) and Q_{10} values. To address these uncertainties, four additional scenarios were considered. In the first and second scenarios, the TL of each shark was assumed to be 0.3 m shorter and longer, respectively, than our estimate. A recent study conducted at the same site (C. May, unpublished data) showed that the mean difference between white shark TL visually estimated by scientists and that measured by stereo-video cameras is approximately 0.2 m. Our choice of 0.3 m, therefore, represents a conservative case, encompassing likely biases in size estimates. In the third scenario, the scaling exponent of metabolic rates was set at 0.84 (Sims, 2000). In the fourth scenario, the Q_{10} value was set at 1.67, which was reported for endothermic tunas (Dewar and Graham, 1994).

To test the hypothesis that deep diving behaviour (passive descents followed by active ascent) is cost-efficient, mean FMR and ODBA was calculated for each behavioural event, including shallow dives, deep dives and surface swimming. Because shallow dive events continued for hours without clear breaks, these events were split into 15-min segments to calculate mean FMR and ODBA. Then, the effects of behavioural categories on FMR and ODBA were examined with linear mixed-effect models with shark ID as a random factor, using the software R with the lme4 extension (Bates et al., 2014). Statistical significance was tested by comparing the full models and the models without behavioural categories using the likelihood ratio test.

High ODBA values for surface swimming events (0–2 m depth; Fig. 3B) may overestimate the swimming costs, because dorsal fins of the sharks (and the accelerometers attached) may oscillate while

Table 2. Proportion of time spent in each behavioural category

Shark no.	Recording duration (h)	Shallow dives (%)	Deep dives (%)	Surface swim (%)	Others (%)
1	12.7	94	0	5	1
2	15.6	58	0	16	26
3	14.3	49	0	1	50
4	27.0	96	0	0	4
5	22.6	53	13	24	9
6	11.3	9	44	22	24
7	9.2	79	0	1	20
8	37.3	42	23	6	29
Total	150.0	60	11	9	20

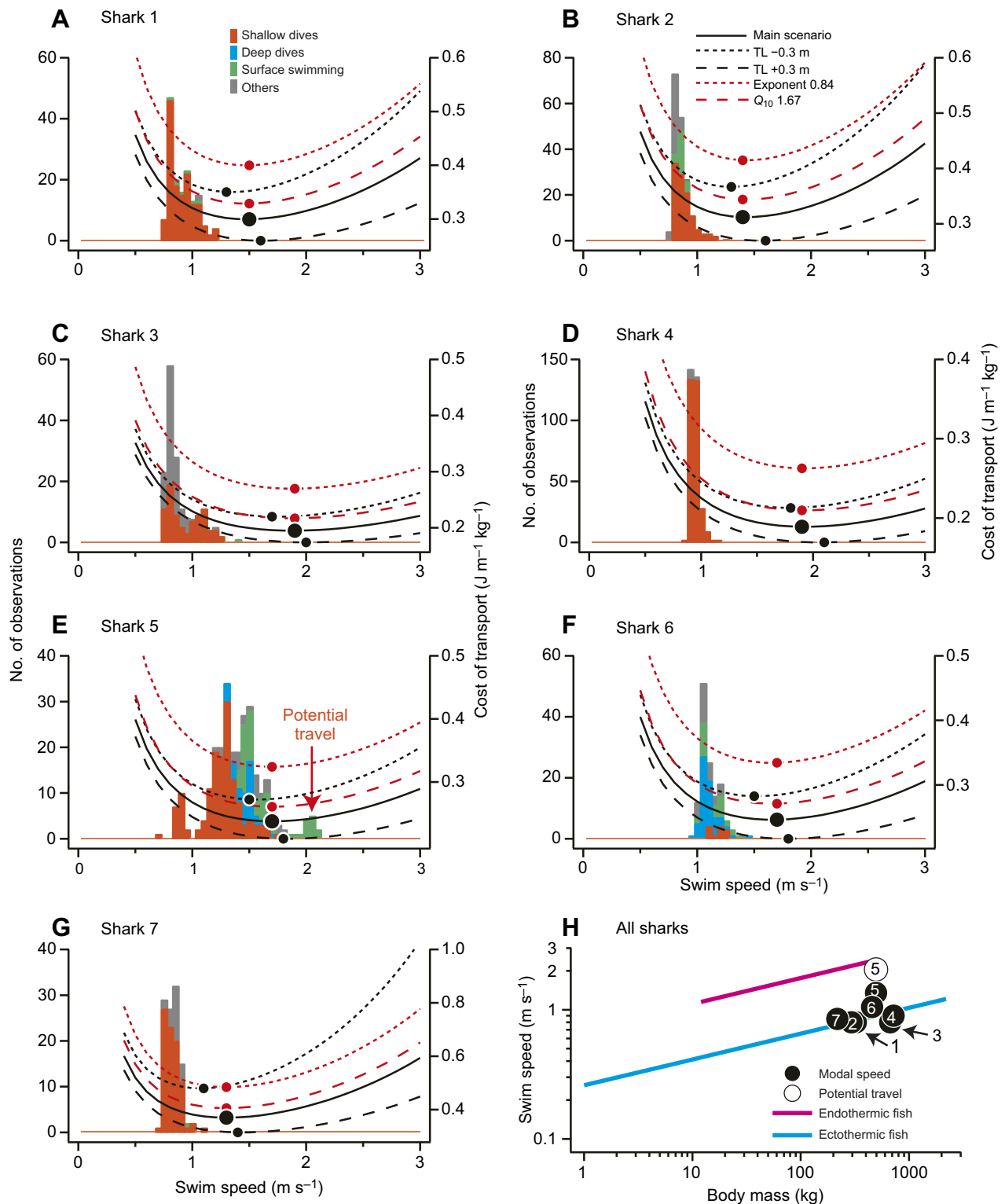


Fig. 2. Sustained swim speed of white sharks (A–G) Frequency distributions of sustained (i.e. 5-min average) swim speed (bars) and the estimated cost of transport (curves) with its minimum value (circles) for individual sharks. As in Figs 1 and 3, different colours of the bars represent different behavioural categories (shallow dives, deep dives, surface swim and others). At each speed, different behavioural categories are accumulated (i.e. not superimposed), so that all data can be seen. Dotted and dashed curves represent the cost of transport under different scenarios [black dotted curve, total length (TL) of the shark is 0.3 m shorter than our estimate; black dashed curve, TL of the shark is 0.3 m longer than our estimate; red dotted curve, the scaling exponent of metabolic rates is 0.84; red dashed curve, Q_{10} value is 1.67]. Shark 5 showed a high sub-peak (denoted by red arrow), which may represent the period when this shark travelled from the North to the South Neptune Islands. (H) Modal swim speeds for individual sharks (filled circles, with shark ID numbers) and swim speed during the putative travel between the islands recorded for shark 5 (open circle), plotted against body mass in log scales. For comparison, the allometric relationships of sustained swim speed for regionally endothermic fishes (pink line) and ectothermic fishes (light blue line) (Watanabe et al., 2015) are also shown.

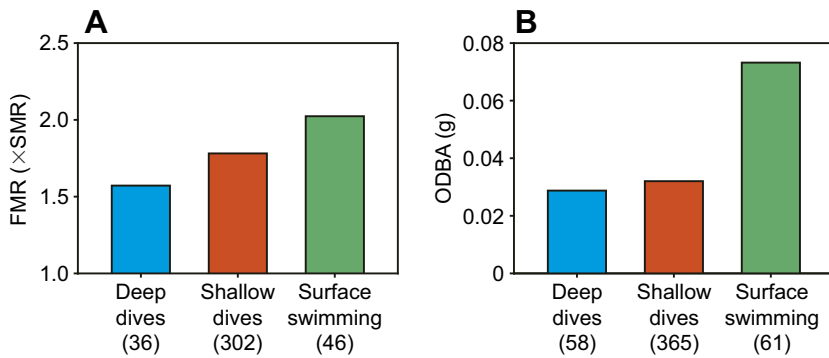


Fig. 3. White shark energetics. (A) Field metabolic rates (FMR) as multiples of standard metabolic rates (SMR), and (B) overall dynamic body acceleration (ODBA) for different behavioural categories, based on linear mixed-effects model analyses of data for all seven (FMR) or eight (ODBA) sharks. Numbers in parentheses are the number of behavioural events used in the analyses.

breaking the surface. To test this possibility, deeper portions of surface swimming events (1–2 m depth for >10 s) were subsampled, in which dorsal fins (approximately 0.5 m length) are unlikely to break the surface. The depth sensors had a sufficient resolution (0.097 m) and accuracy (calibrated to zero when they were floating at the surface) for this subsampling. Statistical analysis was repeated with the subsamples.

RESULTS

We attached the biologging packages to 10 sharks over three research cruises; however, in two individuals, the clamp came off prematurely and the recording durations were <2.5 h. Excluding these individuals and all periods during which sharks interacted with the boat (0–13 h), the effective sample size was eight, with recording durations of 9–37 h (total duration, 150 h) (Table 1). Despite considerable variation among individuals, the behaviour of all eight sharks was composed of shallow dives (60%), deep dives (11%), surface swimming (9%) and other behaviours (20%) (Table 2). Surface swimming mostly occurred between deep dives (Fig. 1C), but some surface swimming was observed between shallow dives. Based on the acceleration data, all but one (shark 3) shark exhibited gliding behaviour during descending phases of dives (Fig. 1C, Movie 1). Deep dives had more consistent dive profiles and proportionally longer gliding periods (20% of total durations) than shallow dives (8% of total durations). Video footage was obtained for three of the eight sharks, but one shark interacted with the boat throughout the footage. In the video footage obtained from shark 5, a seal was seen three times, once on the sea floor during shallow dives, and twice during surface swimming (Fig. 1B).

The modal, sustained swim speed (calculated as the 5-min average of swim speed) for individual sharks ranged from 0.80 to 1.35 m s⁻¹ (overall average, 0.94 m s⁻¹), which was slower than the estimated $U_{\text{COT-min}}$ (range 1.3–1.9 m s⁻¹; Fig. 2A–G). Under the scenarios that the TL of each shark is 0.3 m shorter and longer than our estimates, respectively, $U_{\text{COT-min}}$ shifted to a lower range (1.1–1.8 m s⁻¹) and a higher range (1.4–2.1 m s⁻¹), respectively (black dotted and dashed curves in Fig. 2A–G). Nevertheless, the recorded modal swim speeds were still slower than the $U_{\text{COT-min}}$ values. Under the additional two scenarios that (i) the scaling exponent is 0.84 rather than 0.79, and (ii) Q_{10} is 1.67 rather than 2.42, the COT curves shifted upward without affecting $U_{\text{COT-min}}$ (red dotted and dashed curves in Fig. 2A–G). In addition, the recorded speeds were slower than the predicted speeds for the body mass and regionally endothermic physiology of white sharks, based on a published allometric relationship (Watanabe et al., 2015) (Fig. 2H). However, shark 5 had a higher subpeak at 2.05 m s⁻¹, which was close to its $U_{\text{COT-min}}$ (Fig. 2E) and the predicted speed from allometry (Fig. 2H). This subpeak corresponded to the period when the

shark exhibited surface swimming with elevated speeds for 1 h (Fig. 1C). We know that this shark moved from the North Neptune Islands (where it was tagged) to the South Neptune Islands (where it was re-observed the next day and the tag was manually recovered, approximately 10 km away from the North Neptune Islands) during the deployment period. As such, the fast surface swimming period might represent travel between the islands.

Linear mixed-effects models based on the data for seven (for FMR, expressed as multiples of SMR) and eight sharks (for ODBA) showed that behavioural categories (shallow dives, deep dives and surface swim) affected both FMR ($\chi^2=157.1$, $P<0.0001$) and ODBA ($\chi^2=564.4$, $P<0.0001$), with deep dives being the least energetically expensive (Fig. 3). Based on FMR and ODBA, shallow dives were 13% and 11% more costly, respectively, whereas surface swimming was 29% and 155% more costly, respectively, than deep dives. Interestingly, surface swimming was 19% and 146% more costly (based on FMR and ODBA, respectively) than the non-gliding, ascending phase of deep dives (FMR, $\chi^2_1=54.0$, $P<0.0001$; ODBA, $\chi^2_1=153.0$, $P<0.0001$). When surface swimming events were replaced by deeper subsamples of the events (1–2 m depth), the estimate of ODBA for surface swimming decreased by 28% (in the model including shallow dives, deep dives and surface swimming) and 37% (in the model including surface swimming and the ascending phase of deep dives), but remained significantly higher than that of deep and shallow dives ($\chi^2_2=84.7$, $P<0.0001$) and the ascending phase of deep dives ($\chi^2_1=19.4$, $P<0.0001$). The results for FMR changed little.

DISCUSSION

Slow swim speed

Using propeller speed sensors, we showed that white sharks sustain swim speeds of 0.80–1.35 m s⁻¹, which are slower than the estimated $U_{\text{COT-min}}$ values. Our results were robust to some uncertainties in shark body size, the scaling exponent of metabolic rates and Q_{10} values, as shown by the sensitivity analyses (Fig. 2A–G). In addition, the recorded swim speeds were slower than the predicted speeds for the body mass and regionally endothermic physiology of white sharks (Fig. 2H). Our swim speed records are lower than the previous estimates based on acoustic telemetry [median 1.34 m s⁻¹ (Klimley et al., 2001); median 2.25 m s⁻¹, mean 2.91 m s⁻¹ (Semmens et al., 2013)]; however, swim speed may have been overestimated in those studies, which relied on a positioning system with significant error. Our findings agree with a theoretical model (Papastamatiou et al., 2018) that states that sharks should swim slower than their $U_{\text{COT-min}}$ to maximize net energy gain when the average prey speed is comparable to the average predator speed (such as our white shark and seal system). Largemouth bass in the wild also swim

slower than its $U_{\text{COT-min}}$, presumably to increase foraging efficiency rather than maximize travel efficiency (Han et al., 2017). Another, but not mutually exclusive, interpretation is that white sharks might reduce energy expenditure by swimming at the minimum speed at which the forces acting on them, including hydrodynamic lift and negative buoyancy, are balanced (Gleiss et al., 2015; Iosilevskii and Papastamatiou, 2016). This interpretation is supported by our observation that shark 3, which swam the slowest compared with its $U_{\text{COT-min}}$ (Fig. 2C), is the only individual that did not exhibit gliding behaviour during descents. That is, shark 3, which is a female, might have a buoyancy close to neutral owing to its high fat content, and could balance forces at slower swim speeds compared with other individuals. Overall, our results support our hypothesis that white sharks aggregating near seal colonies adopt slow speeds that may be optimized to increase encounter rates with fast-swimming seals while reducing swimming costs. This strategy is as close to a 'sit-and-wait' strategy as is possible for perpetual swimmers such as white sharks.

Interestingly, however, we also showed that a shark (shark 5) swam at a high speed (2 m s^{-1}) at the surface for 1 h, presumably when it travelled from the North Neptune Islands to the South Neptune Islands. This sustained speed is among the highest values recorded for fishes (Watanabe et al., 2015), and close to the predicted speed for their body mass and regionally endothermic physiology. Moreover, the speed is close to $U_{\text{COT-min}}$ of the shark, indicating that this shark adopted a different, faster optimal speed when travelling rather than foraging. Although we need more data to confirm our observations, this finding suggests that white sharks may use different swim speeds depending on the context to optimize their energy use, as previously reported for flight speeds of a bat (Grodzinski et al., 2009).

Cost-efficient gliding behaviour

Gliding behaviour during descending phases of dives was previously reported for white sharks (Gleiss et al., 2011a), but quantitative assessments of the energetic benefit based on field data have never been made. In theory, passive gliding descents followed by active ascents with negative buoyancy could lead to substantial energy savings compared with continuous horizontal swimming, because animals incur decreased drag during passive gliding for a given swim speed (Weihs, 1973). Moreover, cost-efficient intermittent swimming was experimentally validated using a pitching foil operated in a water tunnel at variable duty cycles (Floryan et al., 2017). In accordance with the previous studies, we showed that deep dives (which had proportionally longer gliding periods than shallow dives) were the least expensive, followed by shallow dives, with surface swimming the most expensive, based on our FMR estimates (Fig. 3A). One may argue that sharks are expected to work harder for a given swim speed during ascending phases of deep dives compared with horizontal swimming, and that the costs of deep dives are underestimated. Although this possibility cannot be fully assessed by our FMR estimates, ODBA, a proxy for energy expenditure that quantifies the relative body movements of the animals, showed a trend similar to that of FMR (Fig. 3B), supporting our argument that deep dives are the least expensive. Unexpectedly, even ascending phases of deep dives had lower FMR and ODBA than surface swimming. Therefore, the absence of gliding behaviour is not the only factor that explains the higher costs of surface swimming. Another factor is the relatively high speed during surface swimming, especially in shark 5 (Fig. 2). Additionally, when moving at the surface, animals inevitably create waves and incur increased drag (called wave drag, which may increase body movements and ODBA), even when they are fully submerged (Alexander, 2003). To avoid wave drag, animals may

need to swim deeper than approximately 2.5 body diameters (Alexander, 2003), which is approximately 2 m for white sharks. Particularly high ODBA during surface swimming (Fig. 3B) could be due to the dorsal fins breaking the surface rather than high activities of the whole bodies. In fact, ODBA decreased by 28–37% when surface swimming events were replaced by deeper subsamples, in which dorsal fins are unlikely to break the surface. However, the subsamples still had higher ODBA than deep dives, shallow dives and ascending phases of deep dives, indicating that high energetic cost of surface swimming is a robust result.

The main function of deep-diving behaviour might be foraging rather than energy saving, as suggested by some burst swimming events observed during deep dives (Y. Y. Watanabe, unpublished data). In addition, five of the eight sharks did not exhibit deep diving behaviour during our limited recording periods (Table 2). Nevertheless, a large difference in FMR between deep dives and surface swimming, as well as the commonness of deep diving behaviour in both coastal and offshore habitats reported for this species from longer-term satellite telemetry data (Domeier and Nasby-Lucas, 2008; Sims et al., 2012; Weng et al., 2007), suggests that gliding behaviour has substantial effects on the overall swimming costs of white sharks. Among large-bodied sharks, prolonged gliding during descents has also been reported for whale sharks (Gleiss et al., 2011b), but not for tiger or Greenland sharks (Nakamura et al., 2011; Watanabe et al., 2012), despite their negative buoyancy. As apparently rare cases, prolonged gliding during ascents with positive buoyancy was reported for bluntnose sixgill and prickly sharks (Nakamura et al., 2015). How the interspecific variation in gliding behaviour is linked to species-specific foraging strategies would be an interesting question for future research. In addition, it is intriguing that surface swimming is costly for white sharks, given that they have a strong preference for surface swimming during oceanic migrations (Bonfil et al., 2005; Domeier and Nasby-Lucas, 2008; Sims et al., 2012). If surface swimming during long travels is for navigation purposes (e.g. using celestial cues) (Bonfil et al., 2005), it would mean a trade-off between navigation and energy saving, a topic that would merit further investigations.

In conclusion, by using modern biologging technologies, we provided support for the two hypotheses regarding behavioural strategies of white sharks aggregating near seal colonies. First, they swim slower than $U_{\text{COT-min}}$, presumably to increase encounter rates with fast-swimming seals while reducing swimming costs, as predicted by theoretical models. White sharks can be considered 'sit-and-wait' predators in this sense, although they are continuous swimmers. Second, sharks exhibit gliding behaviour during descending phases of dives, rendering diving behaviour less costly than horizontal surface swimming, which presumably incurs additional wave drag. This study highlights some new aspects of energy management strategies for white sharks, a species with unique eco-physiology among vertebrates.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: Y.Y.W., N.P., J.S., A.F., C.H.; Methodology: Y.Y.W., N.L.P., J.M.S., A.F., C.H.; Formal analysis: Y.Y.W.; Investigation: Y.Y.W., N.L.P., J.M.S., A.F., C.H.; Writing - original draft: Y.Y.W.; Writing - review & editing: N.L.P., J.M.S., C.H.

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Data availability

Data used in the linear mixed-effect model analyses are available from the figshare repository: 10.6084/m9.figshare.7671836

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.185603.supplemental>

References

- Alexander, R. M. (2003). *Principles of Animal Locomotion*. Princeton University Press.
- Aoki, K., Amano, M., Mori, K., Kourogi, A., Kubodera, T. and Miyazaki, N. (2012). Active hunting by deep-diving sperm whales: 3D dive profiles and maneuvers during bursts of speed. *Mar. Ecol. Prog. Ser.* **444**, 289-301.
- Bates, D., Mächler, M., Bolker, B. and Walker, S. (2014). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1-48.
- Beamish, F. (1978). Swimming capacity. In *Fish Physiology Vol. 7. Locomotion* (ed. D. J. R. William and S. Hoar), pp. 101-187. London: Academic Press.
- Bonfil, R., Mejer, M., Scholl, M. C., Johnson, R., O'brien, S., Oosthuizen, H., Swanson, S., Kotze, D. and Paterson, M. (2005). Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* **310**, 100-103.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* **85**, 1771-1789.
- Buckley, L. B., Hurlbert, A. H. and Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Glob. Ecol. Biogeogr.* **21**, 873-885.
- Carey, F. G., Kanwisher, J. W., Brazier, O., Gabrielson, G., Casey, J. G. and Pratt, H. L., Jr (1982). Temperature and activities of a white shark, *Carcharodon carcharias*. *Copeia* **1982**, 254-260.
- Chapple, T. K., Gleiss, A. C., Jewell, O. J. D., Wikelski, M. and Block, B. A. (2015). Tracking sharks without teeth: a non-invasive rigid tag attachment for large predatory sharks. *Anim. Biotelem.* **3**, 14.
- Clarke, A. and Portner, H.-O. (2010). Temperature, metabolic power and the evolution of endothermy. *Biol. Rev.* **85**, 703-727.
- Dewar, H. and Graham, J. (1994). Studies of tropical tuna swimming performance in a large water tunnel – I. Energetics. *J. Exp. Biol.* **192**, 13-31.
- Dickson, K. A. and Graham, J. B. (2004). Evolution and consequences of endothermy in fishes. *Physiol. Biochem. Zool.* **77**, 998-1018.
- Domeier, M. L. and Nasby-Lucas, N. (2008). Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Mar. Ecol. Prog. Ser.* **370**, 221-237.
- Estrada, J. A., Rice, A. N., Natanson, L. J. and Skomal, G. B. (2006). Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. *Ecology* **87**, 829-834.
- Fish, F. E., Hurlley, J. and Costa, D. P. (2003). Maneuverability by the sea lion *Zalophus californianus*: turning performance of an unstable body design. *J. Exp. Biol.* **206**, 667-674.
- Floryan, D., Van Buren, T. and Smits, A. J. (2017). Forces and energetics of intermittent swimming. *Acta Mech. Sin.* **33**, 725-732.
- Gleiss, A. C., Jorgensen, S. J., Liebsch, N., Sala, J. E., Norman, B., Hays, G. C., Quintana, F., Grundy, E., Campagna, C. and Trites, A. W. (2011a). Convergent evolution in locomotory patterns of flying and swimming animals. *Nat. Commun.* **2**, 352.
- Gleiss, A. C., Norman, B. and Wilson, R. P. (2011b). Moved by that sinking feeling: variable diving geometry underlies movement strategies in whale sharks. *Funct. Ecol.* **25**, 595-607.
- Gleiss, A. C., Potvin, J., Keleher, J. J., Whitty, J. M., Morgan, D. L. and Goldbogen, J. A. (2015). Mechanical challenges to freshwater residency in sharks and rays. *J. Exp. Biol.* **218**, 1099-1110.
- Goldman, K. J. and Anderson, S. D. (1999). Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, central California. *Environ. Biol. Fishes* **56**, 351-364.
- Grady, J. M., Enquist, B. J., Dettweiler-Robinson, E., Wright, N. A. and Smith, F. A. (2014). Evidence for mesothermy in dinosaurs. *Science* **344**, 1268-1272.
- Grodzinski, U., Spiegel, O., Korine, C. and Holderied, M. W. (2009). Context-dependent flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus kuhlii*? *J. Anim. Ecol.* **78**, 540-548.
- Han, A. X., Berlin, C. and Ellerby, D. J. (2017). Field swimming behavior in largemouth bass deviates from predictions based on economy and propulsive efficiency. *J. Exp. Biol.* **220**, 3204-3208.
- Hussey, N. E., McCann, H. M., Cliff, G., Dudley, S. F., Wintner, S. P. and Fisk, A. T. (2012). Size-based analysis of diet and trophic position of the white shark (*Carcharodon carcharias*) in South African waters. In *Global Perspectives on the Biology and Life History of the White Shark* (ed. M. L. Domeier), pp. 27-49. CRC Press.
- Huveneers, C., Rogers, P. J., Beckmann, C., Semmens, J. M., Bruce, B. D. and Seuront, L. (2013). The effects of cage-diving activities on the fine-scale swimming behaviour and space use of white sharks. *Mar. Biol.* **160**, 2863-2875.
- Huveneers, C., Meekan, M. G., Apps, K., Ferreira, L. C., Pannell, D. and Vianna, G. M. S. (2017). The economic value of shark-diving tourism in Australia. *Rev. Fish Biol. Fish.* **27**, 1-16.
- Huveneers, C., Watanabe, Y. Y., Payne, N. L. and Semmens, J. M. (2018). Interacting with wildlife tourism increases activity of white sharks. *Conserv. Physiol.* **6**, coy019.
- Iosilevskii, G. and Papastamatiou, Y. P. (2016). Relations between morphology, buoyancy and energetics of requiem sharks. *R. Soc. Open Sci.* **3**, 160406.
- Jewell, O. J. D., Wcisel, M. A., Towner, A. V., Chivell, W., van der Merwe, L. and Bester, M. N. (2014). Core habitat use of an apex predator in a complex marine landscape. *Mar. Ecol. Prog. Ser.* **506**, 231-242.
- Kawatsu, S., Sato, K., Watanabe, Y., Hyodo, S., Breves, J. P., Fox, B. K., Grau, E. G. and Miyazaki, N. (2010). A new method to calibrate attachment angles of data loggers in swimming sharks. *Eurasip J. Adv. Signal Process.* **2010**, 732586.
- Klimley, A. P., Le Boeuf, B. J., Cantara, K. M., Richert, J. E., Davis, S. F., Van Sommeran, S. and Kelly, J. T. (2001). The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Mar. Biol.* **138**, 617-636.
- Martin, R. A., Hammerschlag, N., Collier, R. S. and Fallows, C. (2005). Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *J. Mar. Biol. Assoc. U.K.* **85**, 1121-1135.
- Martin, R. A., Rossmo, D. K. and Hammerschlag, N. (2009). Hunting patterns and geographic profiling of white shark predation. *J. Zool.* **279**, 111-118.
- Mollet, H. F. and Cailliet, G. M. (1996). Using allometry to predict body mass from linear measurements of the white shark. In *Great White Sharks: The Biology of Carcharodon carcharias* (ed. P. A. Klimley and D. G. Ainley), pp. 81-89. Academic Press.
- Nakamura, I., Watanabe, Y. Y., Papastamatiou, Y. P., Sato, K. and Meyer, C. G. (2011). Yo-yo vertical movements suggest a foraging strategy for tiger sharks *Galeocerdo cuvier*. *Mar. Ecol. Prog. Ser.* **424**, 237-246.
- Nakamura, I., Meyer, C. G. and Sato, K. (2015). Unexpected positive buoyancy in deep sea sharks, *Hexanchus griseus*, and a *Echinorhinus cookei*. *PLoS ONE* **10**, e0127667.
- Paladino, F. V., O'Connor, M. P. and Spotila, J. R. (1990). Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* **344**, 858.
- Papastamatiou, Y. P., Iosilevskii, G., Leos-Barajas, V., Brooks, E. J., Howey, L. A., Chapman, D. D. and Watanabe, Y. Y. (2018). Optimal swimming strategies and behavioral plasticity of oceanic whitetip sharks. *Sci. Rep.* **8**, 551.
- Payne, N. L., Snelling, E. P., Fitzpatrick, R., Seymour, J., Courtney, R., Barnett, A., Watanabe, Y. Y., Sims, D. W., Squire, L. and Semmens, J. M. (2015). A new method for resolving uncertainty of energy requirements in large water breathers: the 'mega-flume' seagoing swim-tunnel respirometer. *Methods Ecol. Evol.* **6**, 668-677.
- 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* **4**, e5379.
- Semmens, J., Payne, N., Huveneers, C., Sims, D. and Bruce, B. (2013). Feeding requirements of white sharks may be higher than originally thought. *Sci. Rep.* **3**, 1471.
- Sepulveda, C. A., Graham, J. B. and Bernal, D. (2007). Aerobic metabolic rates of swimming juvenile mako sharks, *Isurus oxyrinchus*. *Mar. Biol.* **152**, 1087-1094.
- Sims, D. W. (2000). Can threshold foraging responses of basking sharks be used to estimate their metabolic rate? *Mar. Ecol. Prog. Ser.* **200**, 289-296.
- Sims, D. W., Humphries, N. E., Bradford, R. W. and Bruce, B. D. (2012). Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics. *J. Anim. Ecol.* **81**, 432-442.
- Sundström, L. F. and Gruber, S. H. (2002). Effects of capture and transmitter attachments on the swimming speed of large juvenile lemon sharks in the wild. *J. Fish Biol.* **61**, 834-838.
- Towner, A. V., Leos-Barajas, V., Langrock, R., Schick, R. S., Smale, M. J., Kaschke, T., Jewell, O. J. D. and Papastamatiou, Y. P. (2016). Sex-specific and individual preferences for hunting strategies in white sharks. *Funct. Ecol.* **30**, 1397-1407.
- Watanabe, Y., Baranov, E. A., Sato, K., Naito, Y. and Miyazaki, N. (2004). Foraging tactics of Baikal seals differ between day and night. *Mar. Ecol. Prog. Ser.* **279**, 283-289.
- Watanabe, Y., Wei, Q., Yang, D., Chen, X., Du, H., Yang, J., Sato, K., Naito, Y. and Miyazaki, N. (2008). Swimming behavior in relation to buoyancy in an open swimbladder fish, the Chinese sturgeon. *J. Zool.* **275**, 381-390.

- Watanabe, Y. Y., Sato, K., Watanuki, Y., Takahashi, A., Mitani, Y., Amano, M., Aoki, K., Narazaki, T., Iwata, T., Minamikawa, S. et al.** (2011). Scaling of swim speed in breath-hold divers. *J. Anim. Ecol.* **80**, 57-68.
- Watanabe, Y. Y., Lydersen, C., Fisk, A. T. and Kovacs, K. M.** (2012). The slowest fish: Swim speed and tail-beat frequency of Greenland sharks. *J. Exp. Mar. Biol. Ecol.* **426**, 5-11.
- Watanabe, Y. Y., Goldman, K. J., Caselle, J. E., Chapman, D. D. and Papastamatiou, Y. P.** (2015). Comparative analyses of animal-tracking data reveal ecological significance of endothermy in fishes. *Proc. Natl. Acad. Sci. USA* **112**, 6104-6109.
- Wegner, N. C., Snodgrass, O. E., Dewar, H. and Hyde, J. R.** (2015). Whole-body endothermy in a mesopelagic fish, the opah, *Lampris guttatus*. *Science* **348**, 786-789.
- Weih, D.** (1973). Mechanically efficient swimming techniques for fish with negative buoyancy. *J. Mar. Res.* **31**, 194-209.
- Weng, K. C., O'Sullivan, J. B., Lowe, C. G., Winkler, C. E., Dewar, H. and Block, B. A.** (2007). Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Mar. Ecol. Prog. Ser.* **338**, 211-224.
- Whitney, N. M., Lear, K. O., Gaskins, L. C. and Gleiss, A. C.** (2016a). The effects of temperature and swimming speed on the metabolic rate of the nurse shark (*Ginglymostoma cirratum*, Bonaterre). *J. Exp. Mar. Biol. Ecol.* **477**, 40-46.
- Whitney, N. M., White, C. F., Gleiss, A. C., Schwieterman, G. D., Anderson, P., Hueter, R. E. and Skomal, G. B.** (2016b). A novel method for determining post-release mortality, behavior, and recovery period using acceleration data loggers. *Fisheries Research* **183**, 210-221.
- Williams, T. M., Wolfe, L., Davis, T., Kendall, T., Richter, B., Wang, Y., Bryce, C., Elkaim, G. H. and Wilmers, C. C.** (2014). Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science* **346**, 81-85.
- Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. J.** (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J. Anim. Ecol.* **75**, 1081-1090.