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A miniaturized threshold-triggered acceleration data-logger for recording burst movements of aquatic animals

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ABSTRACT

Although animal-borne accelerometers are effective tools for quantifying the kinematics of animal behaviors, quantifying the burst movements of small and agile aquatic animals remains challenging. To capture the details of burst movements, accelerometers need to sample at a very high frequency, which will inevitably shorten the recording duration or increase the device size. To overcome this problem, we developed a high-frequency acceleration data-logger that can be triggered by a manually defined acceleration threshold, thus allowing the selective measurement of burst movements. We conducted experiments under laboratory and field conditions to examine the performance of the logger. The laboratory experiment using red seabream (*Pagrus major*) showed that the new logger could measure the kinematics of their escape behaviors. The field experiment using free-swimming yellowtail kingfish (*Seriola lalandi*) showed that the loggers trigger correctly. We suggest that this new logger can be applied to measure the burst movements of various small and agile animals.

KEY WORDS: Accelerometer, Bio-logging, Escape, Fast start, Feeding strike, Telemetry

INTRODUCTION

Animal-borne accelerometers have been used to estimate energy expenditure (Murchie et al., 2011; Payne et al., 2011), activity patterns (Kawabe et al., 2004; Payne et al., 2016; Sato et al., 2007), and specific behaviors such as porpoising, feeding, mating and spawning (Føre et al., 2011; Tsuda et al., 2006; Watanabe and Takahashi, 2013; Whitney et al., 2010; Yoda et al., 1999) of aquatic animals. In general, accelerometers record acceleration in a continuous manner at a defined frequency (e.g. 1–100 Hz) or record a defined time-average of the acceleration, either digitally stored or transmitted (Cooke et al., 2016). Subsequently, these acceleration data are often transformed into various components (e.g. dynamic and static accelerations) to estimate energy budgets and activity, or to carry out classification into more detailed behaviors (Gleiss et al., 2011; Shepard and Wilson, 2008; Tanaka et al., 2001; Wilson et al., 2006).

Most previous studies have used accelerometers with sampling frequencies below 32 Hz and recorded routine behaviors such as cruising, gliding and resting (Kawabe et al., 2004; Murchie et al., 2011; O'Toole et al., 2010; Tsuda et al., 2006). However, such low sampling frequencies cannot be used to measure the detailed burst movement dynamics of small and agile animals (e.g. teleost fish), which occur over short time scales (i.e. of the order of 100 ms), despite the fact that these burst movements include ecologically important behaviors such as escape responses and feeding strikes. The *in situ* measurement of such behaviors would provide novel insights into the movement performance, energy expenditure and survival strategies of animals in complex natural habitats.

Recently, Broell et al. (2013) demonstrated that an accelerometer with a sampling frequency of at least 30 Hz (ideally, 100 Hz) is required to identify the escape responses and feeding strikes of the sit-and-wait predator *Myoxocephalus polyacanthocephalus*. Moreover, accelerometers with a sampling frequency of 200 Hz have been demonstrated as useful in distinguishing the feeding behavior of trophic generalist fish on different prey types (Horie et al., 2017; Kawabata et al., 2014). These studies clearly show that high-frequency accelerometers are useful in measuring the burst movements of agile animals; however, such high-frequency sampling rapidly consumes electricity and memory, which inevitably shortens the duration of the recording (e.g. 100 h recording duration at 20 Hz sampling frequency, 10 h recording duration at 100 Hz sampling frequency for ORI400-D3GT, Little Leonardo Co., Tokyo, Japan), or increases its size [e.g. the recording duration of a 37 g (in air) data logger is two times longer than that of a 23 g (in air) data logger; Takuji Noda, Institute of Statistical Mathematics, Japan, personal communication]. Thus, applying high-frequency accelerometers to field studies remains a challenging task.

To overcome this problem, we developed a data-logger that selectively records acceleration signals based on a manually defined threshold (event logger), which reduces electricity and memory requirements and thus enables us to measure the burst movements of animals for a relatively long period (e.g. 5 day battery life with a sampling frequency of 500 Hz and 10 burst movements per day) despite its small size (7.7 g in air). Similar selective recording systems were used to measure the predatory behaviors of the piscivorous fish *Esox lucius* in a laboratory setting (Van Deurs et al., 2017) and the terrestrial carnivore *Acinonyx jubatus* in the wild (Wilson et al., 2013). However, the details of the logger system, the measurement performance of the logger and its practicality for aquatic field measurements were not provided. In the present study, we describe the selective recording system of the event logger, present results

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from a laboratory performance test conducted on the escape response of the red seabream, *Pagrus major* (Temminck and Schlegel 1843), and show the results of the field performance test conducted on the yellowtail kingfish, *Seriola lalandi* Valenciennes 1833.

MATERIALS AND METHODS

Ethical approval

Animal care and experimental procedures were approved by the Animal Care and Use Committee of the Institute for East China Sea Research, Nagasaki University (permit no. ECSER15-13), in accordance with the Regulations of the Animal Care and Use Committee of Nagasaki University, and the Animal Care and Ethics Committee of the University of New South Wales (permit no. 15/126B). The field work was carried out under the guidelines of the Department of the Environment, Water and Natural Resources (DEWNR) scientific research (permit no. M26292), and Marine Parks (permit no. MR00047).

Event logger system

The event logger consists of two different types of 3-axis accelerometers. One accelerometer detects the threshold excess (detection accelerometer) and the other records data (recording accelerometer), as shown in Fig. S1A. The detection accelerometer is continuously active, while the recording accelerometer is inactive unless the detection accelerometer detects any burst movement signals (i.e. exceeding a set threshold). The detection accelerometer measures accelerations at a rate of 400 Hz. One absolute value is manually set as a threshold (any value from 1.00 to 3.95 ***g***, where 1.00 ***g***=9.81 m s^{-2}) and applied to the absolute values of all 3-axes' accelerations. Once the recording accelerometer becomes active, it records data for a manually set time period (any time period, of the order of 1 s). After the set time period elapses, it reverts to being inactive. If the acceleration exceeds the threshold when the recording accelerometer is still active, the detection accelerometer ignores it. The measurement range of the recording accelerometer is ±16 g with 16-bit resolution, and its sampling frequency can be set manually from 1 to 1000 Hz. The battery life of the event logger depends on the activation frequency and the recording period per activation (e.g. 5 day battery life with 10 activations per day, and a recording of 10 s per activation). The size, mass and discharge capacity of the event logger are 29×11×15 mm, 7.7 g and 8 mAh, respectively (Fig. S1B). For interested users, the logger is available at Sports Sensing Co., Ltd (Fukuoka, Japan; www.sports-sensing.com).

Calibration of the detection accelerometer in the event logger

Inherently, accelerometers have slightly different raw values among units, and the bias level can drift through the process of production, large shock, etc. Therefore, the accelerometers need to be calibrated in advance. We calibrated the recording accelerometer of the event logger by referencing the gravitational acceleration and calibrated the detection accelerometer by the method described below.

To obtain the formula for calibrating the detection accelerometer, we examined the correspondence between actual acceleration values and the occurrence of event logger activation. The event logger was attached to a similar-sized conventional 3-axis acceleration logger, which was continuously active (hereafter termed the reference logger; 29×11×15 mm, 7.2 g, Biologging Solutions Inc.). The sampling frequencies of both loggers were set to 500 Hz. These two loggers were packaged and thrust, by hand, at various intensities (approximately 1–6 ***g***). We set four different threshold values, namely 1.6, 2.4, 3.2 and 3.95 ***g***, in the event logger, and thrust 50 times at each threshold value. Logistic regression analysis was used to obtain the calibration formula. The occurrence of event logger activation was designated, in binary, as 1 (activated) and 0 (not activated); these values were used as the objective variable. The set threshold and maximum acceleration values, recorded by the reference logger, were considered as explanatory variables. In addition, we calculated the time lag between the time when the acceleration exceeded the threshold, and the time when the recording was initiated. Furthermore, to verify the accuracy of the acceleration values recorded by the event logger, maximum acceleration values obtained from the event logger were compared with those obtained from the reference logger.

Experiment 1: laboratory performance test using red seabream

To examine the measurement performance of the logger, we attached the logger package (incorporating the event logger and the reference logger) to *P. major* in a tank and measured its escape response.

Four *P. major* were obtained from a local fish hatchery and transported to the Institute for East China Sea Research at Nagasaki University, Japan. The fish were held in 500 l circular polyethylene tanks (100 cm diameter×75 cm height), with an aeration apparatus and flow-through seawater at a temperature of 19.9–24.2°C. The mean body mass and total length of the fish were 2.50 kg (range: 1.96–3.05 kg) and 52.5 cm (range: 49.9–54.8 cm), respectively.

To attach the logger package, the fish were first anesthetized using 0.1% 2-phenoxyethanol. The logger was then attached using two wiry plastic strings, which were inserted through the package and then through the anterior dorsal musculature, after passing through two syringes, and were anchored in place by two 2 cm round stainless washers. The tagging procedure never exceeded 1 min. The *x*-, *y*- and *z*-axes of the logger were aligned to the lateral (rightward), longitudinal (forward) and vertical (upward) coordinates of the fish body, respectively. The sampling frequencies of both loggers were set to 500 Hz. The threshold value of the event logger was set to 2.0 ***g***, as accelerations in excess of this value rarely occurred during the routine movements of other fish species, namely *Epinephelus ongus* (Kawabata et al., 2014) and *Seriola quinqueradiata* (Noda et al., 2013). The recording period of the event logger was set to 5 s per activation.

The experiment was performed in a 3000 l circular fiber-reinforced plastic tank (193 cm diameter×73 cm height), which was filled with seawater to a depth of 30 cm. The fish were individually introduced into the tank and were allowed to acclimate for approximately 20 h. To induce an escape response, we plunged a hand net into the water, near the fish. For each fish, the escape response was elicited 8–10 times, at 30 min intervals, and a total of 34 trials were carried out with the four fish. To determine the timing at the initiation of the escape response, the fish movements were simultaneously recorded dorsally, by a high-speed video camera (HAS-L1, Detect Co., Tokyo, Japan), at 500 frames s^{-1}. The water temperature was 20.6–22.5°C.

Data analysis

We used 11 of the 34 trials; the remaining 23 trials were omitted because the fish did not show any escape response to the hand net, the response was disturbed by the tank wall or intensive waves, or the hand net obscured the fish's body.

Maximum acceleration values and oscillation cycles are important variables for estimating locomotor performance and

Journal of Experimental Biology (2018) 221, jeb172346. doi:10.1242/jeb.172346

categorizing animal behaviors (Broell et al., 2013; Kawabe et al., 2004). As latency existed between the initiation of the escape response and the recording initiation of the event logger, we examined whether the latency was short enough to precisely measure these variables. To measure the exact timing of escape response initiation and the recording initiation of the event logger, we synchronized the acceleration signals of the event logger to those of the reference logger by finding the optimal time difference with the least-squares method. The escape response of fish consists of three distinct stages based on body bends (Weihs, 1973). Peak acceleration usually occurs during the initial bend, or stage 1 of the escape response (Domenici, 2009). Therefore, the peak acceleration timings during stage 1 were used in the analysis.

To specify the sampling frequency required for the precise measurement of the above variables, we examined the effect of sampling frequency on the measured variables. The accelerations of different sampling frequencies (1–500 Hz) were obtained by downsampling the 500 Hz acceleration signals from the event logger. The maximum values of the downsampled accelerations were then compared with those of the raw 500 Hz accelerations. We also calculated the minimum sampling frequency required for detecting the oscillation cycles of the acceleration signals, which usually reflects the tail beat frequencies of fish (Kawabe et al., 2003). At least two points within an oscillation period are necessary to detect the oscillation; thus, we regarded the required sampling frequency as reciprocal to one-half of the oscillation period. In this analysis, we used *x*-axis accelerations, as tail beats produce mainly lateral accelerations (Kawabe et al., 2003).

Experiment 2: field performance test using yellowtail kingfish

We examined the accuracy of the event logger's recording initiation system under natural conditions by attaching an event logger and reference logger to free-ranging *S. lalandi* and comparing the obtained acceleration values. This experiment was conducted off the Neptune Islands Group (Ron and Valerie Taylor), Marine Park, Australia (S35°14′, E136°04′) from October to November 2015.

Three fish (98, 99 and 102 cm total length) were caught by hand line and tagged on board. Fish were placed on a rubber mat and their head was covered with a wet towel while the gills were continuously ventilated with a saltwater hose. In compliance with local animal ethics procedures, fish were not anesthetized. We attached the logger package consisting of a radio tag (model MM130B, Advanced Telemetry Systems, Isanti, MN, USA), an event logger, a reference accelerometer logger (ORI400-D3GT, 12 mm diameter×45 mm length, 9 g, 135 mAh; Little Leonardo Co.) and a time-scheduled release mechanism (Little Leonardo Co.) (Watanabe et al., 2004) to each fish. The tagging procedure of the logger package was similar to that in experiment 1. The fish were released promptly after tagging, and the tagging procedure never exceeded 3 min. The sampling frequency, threshold value and per-activation recording period of the event logger were set to 500 Hz, 2.0 ***g*** and 10 s, respectively. The reference logger was set to continuously measure 3-axis accelerations at 20 Hz. Approximately 45, 37 and 18 h after release, the logger packages fell off the fish, and emerged afloat for recovery. The packages were located using radio signals and recovered.

Two of the three event loggers worked properly and were thus used in the data analysis. We synchronized the acceleration signals from the event logger to those from the reference logger using the least-squares method. Subsequently, we examined whether the event loggers were accurately activated, by comparing the activation events with the threshold excess in the acceleration signals obtained from the reference loggers. The maximum acceleration values and minimum oscillation period obtained through the event loggers were compared with those obtained through the reference loggers.

RESULTS AND DISCUSSION

Calibration of the detection accelerometer in the event logger

In all four set threshold values, the maximum accelerations were higher in the trials where the event logger was activated compared with those in which the event logger was not activated. The acceleration range at the 1.6 and 2.4 ***g*** thresholds, however, slightly overlapped between the activated and non-activated trials (Table S1). The calibration formula was obtained by a logistic regression and successfully classified 95.5% (191/200) of thrust events (Fig. 1A). The mean time lag between the instance when the acceleration exceeded the threshold and the instance when the recording was initiated was approximately 1.11×10^{-2} s (Table S1). There was a strong positive correlation between the maximum acceleration values obtained from the event logger and the reference logger (Fig. 1B; R^2=0.99, n=101, P<0.01).

Experiment 1: laboratory performance test using red seabream

The event logger initiated recording at $1.64\times10^{-2}\pm1.21\times10^{-2}$ s (mean±s.d.; n=11) after the initiation of the escape response. In all of the 11 trials, the initiation occurred before the first half of the stage 1 escape response, which indicated that the recording latency was short enough to detect the oscillation of the acceleration signals with precision. Successful recording rates of maximum acceleration

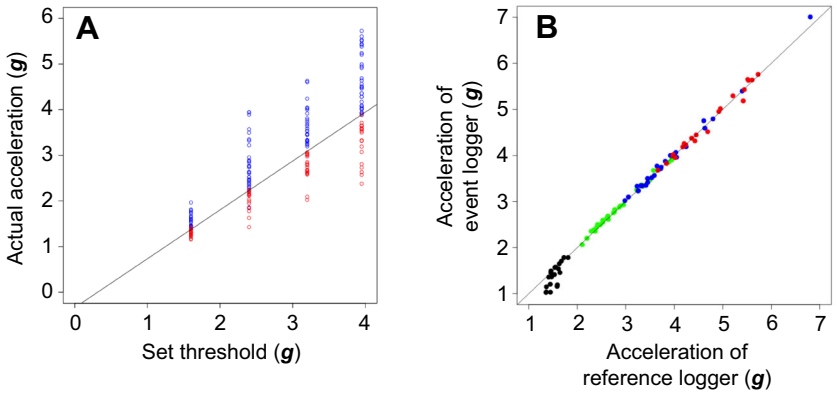

Fig. 1. Calibration of the detection accelerometer. (A) Activations (blue circles) and non-activations (red circles) of the event logger were plotted for the set threshold (1.6, 2.4, 3.2 and 3.95 ***g***) and the actual acceleration. The line indicates the cut-off threshold, determined by logistic regression. The activation accuracy was 0.955 (n=200). (B) The relationship between the acceleration values (maximum absolute values of the 3-axis accelerations) obtained through the reference logger and those obtained through the event logger. The line indicates y=x. Black, green, blue and red dots represent the set thresholds of 1.6, 2.4, 3.2 and 3.95 ***g***, respectively (R^2=0.99, n=101, P<0.01).

Journal of Experimental Biology (2018) 221, jeb172346. doi:10.1242/jeb.172346

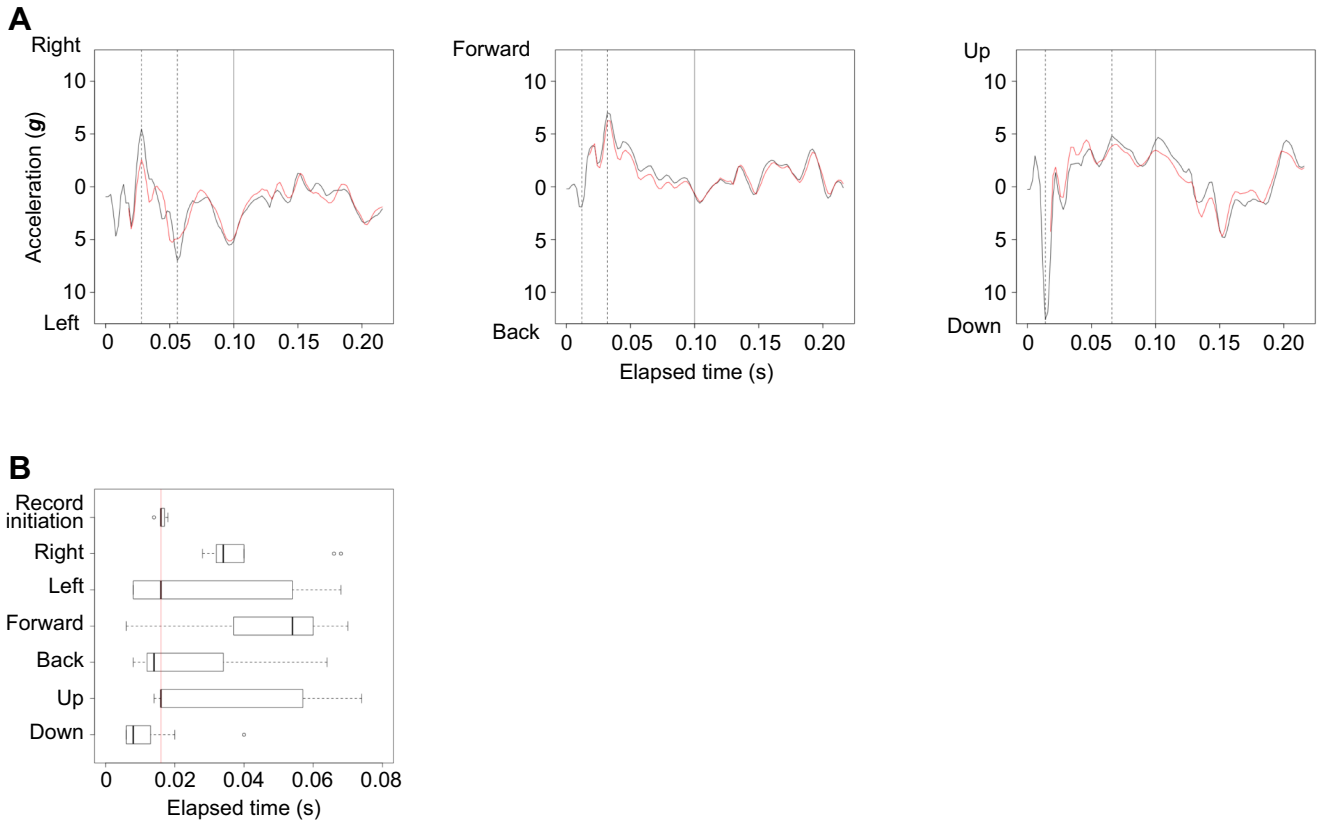

Fig. 2. Performance test of the event loggers attached to the red seabream. (A) Typical acceleration signals during the escape response of red seabream. Black and red traces indicate the accelerations recorded by the reference logger and those recorded by the event logger, respectively. The solid and dashed vertical lines indicate the end of the stage 1 escape response, and the instances when acceleration reached peak values, respectively. (B) Boxplot of record initiation latency, and the instances when acceleration reached peak values. The boxes, right whiskers and left whiskers indicate interquartile range (IQR), maximum value or Q_3+1.5IQR, and minimum value or Q_1−1.5IQR, respectively. The red line indicates the median latency of record initiation (n=11).

values by the event logger in the stage 1 escape response are shown in Fig. 2. Of the 11 trials, 11 rightward (100%), 6 leftward (55%), 10 forward (91%), 5 backward (45%), 9 upward (82%) and 2 downward (18%) maximum accelerations were successfully recorded by the event logger. Depending on which of the six came first, the maximum acceleration values occurred at $8.55\times10^{-3}\pm2.54\times10^{-3}$ s (n=11) after the escape response initiation.

The maximum accelerations became smaller as the sampling frequency decreased. The median value of the downsampled acceleration signals became less than 95% of the original values at 50.0–166.7 Hz and less than 75% of the original values at 22.7–100.0 Hz (Fig. S2). The minimum oscillation period median of the acceleration in the x-axis was 4.8×10^{-2} s, and the required sampling frequency for detecting the oscillation was estimated at 41.7 Hz.

This experiment showed that the event logger recorded accelerations during most parts of the escape response, with sufficient temporal resolution. Although there was latency in initiating the recording, which prevented accurate recordings of maximum values of leftward, backward and downward accelerations during the stage 1 escape response, the logger successfully recorded the maximum acceleration values in the opposite directions (i.e. rightward, forward and upward accelerations) and oscillation cycles with high accuracy. The difference in successful recording rates between opposite directions in the same axis was related to the asymmetrical waveform of the acceleration signals (see Fig. 2). The asymmetrical waveform may be due to the gravitational, propulsive and centripetal accelerations, and to the logger attachment site (i.e. left side of the fish body); however, further research is required to explicitly clarify the cause of this asymmetry.

The latency in the record initiation was a combination of time lag from escape initiation to threshold detection and time lag from threshold detection to record initiation. Although the former time lag can be modified by a set threshold value, the latter time lag is mechanically fixed as the mean of 1.11×10^{-2} s (Table S1). Because the first maximum value among six directional accelerations occurred at 8.55×10^{-3} s after the escape response initiation, recording all maximum values during the stage 1 escape response of this species was difficult with the present system. Nonetheless, the time to maximum acceleration should be species and behavior specific even for small and agile animals; thus, the latency could be short enough to record maximum acceleration values in all directions for other studies. Additionally, the latency will be shorter as sensor technology continues to advance.

The escape response of red seabream included abrupt acceleration changes and thus more than 166.7 Hz of sampling frequency was required to measure the exact peak accelerations, and more than 41.7 Hz for estimating tail beats. This result is consistent with the conclusion by Broell et al. (2013) that accelerometers with a sampling frequency of more than 30 Hz are required to identify the escape and predatory behaviors of fish.

Experiment 2: field performance test using yellowtail kingfish

Each of the acceleration signals recorded by the two reference loggers, namely packages 1 and 2, exceeded the set threshold nine

Journal of Experimental Biology (2018) 221, jeb172346. doi:10.1242/jeb.172346

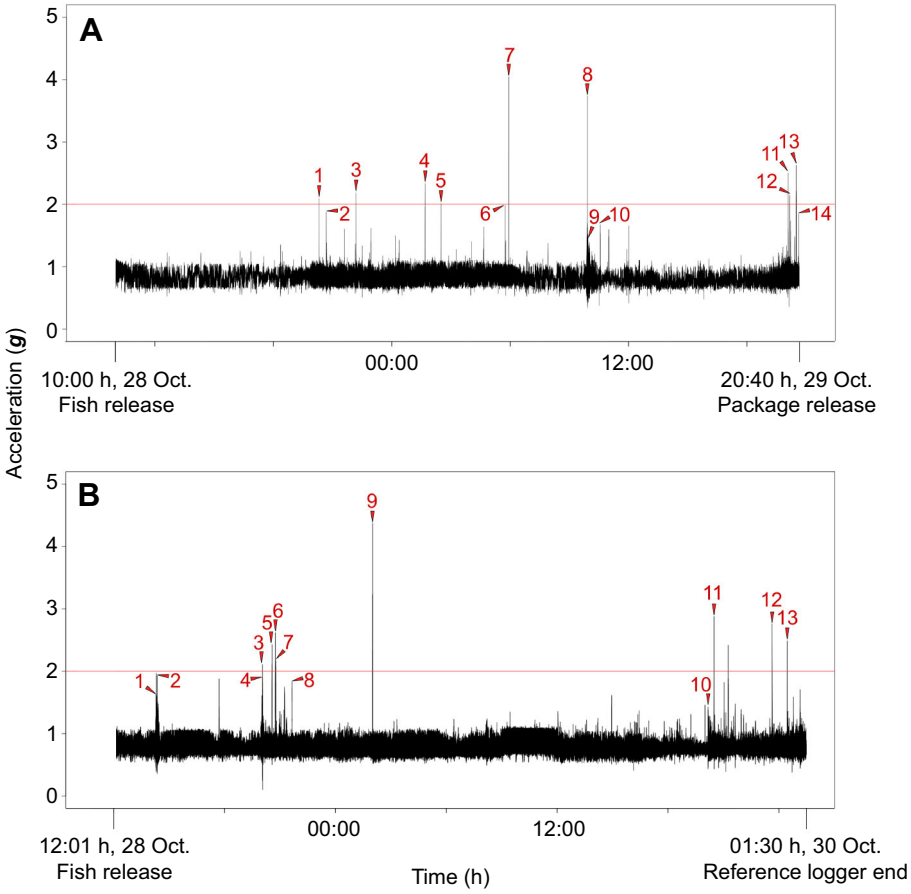

Fig. 3. Activations of the event loggers attached to free-ranging yellowtail kingfish. A and B show data from two different fish. The activation events (numbered red arrowheads) are shown against the maximum absolute values of the 3-axis accelerations recorded by the 20 Hz reference loggers.

times. The event logger of package 1 was activated in all nine cases, while that of package 2 was activated in eight of the nine cases. The maximum acceleration value of the remaining case was 2.42 ***g***. In addition to the nine and eight activations, both event loggers were activated another five times each, when the acceleration measured by the reference loggers surged, but did not exceed the threshold (mean 1.72±0.20 ***g***, n=10; Fig. 3). With the exception of the rightward, leftward and backward acceleration values in package 2, the maximum values obtained through the event loggers were larger than those obtained via the reference loggers (Table S2, Fig. S3).

These results show that the event logger was accurately activated in response to accelerations above threshold. The event logger failed to detect one acceleration that exceeded threshold; however, this could have been caused by a slight positional difference between the event logger and the reference logger. The event logger was also activated several times when the acceleration measured by the reference logger did not exceed 2.0 ***g***. Although these activations could be the result of false detection by the detection accelerometer (see Table S1), it is more likely that the activations are related to the 400 Hz samplings of the detection accelerometer, which allows the detection of momentary high acceleration with higher probabilities than the 20 Hz samplings of the reference logger (see Fig. S3).

Conclusions

The burst locomotor performance of large aquatic animals is increasingly being measured *in situ* using accelerometers (Marras et al., 2015; Watanabe et al., 2012). Generally, small animals are more agile and quicker in their movements; therefore, small and high-frequency accelerometers are required to measure their burst movements. However, because of the critical trade-off between the sampling frequency and device size (or recording duration), producing such small high-frequency accelerometers has been technically challenging. The present study shows that the event logger is small but works with a high sampling frequency for a relatively long period, and thus it is applicable to the *in situ* measurement of the burst locomotor performance in small and agile animals.

The event logger system is similar to on-board data processing, in the sense of discarding unnecessary data before recording. Generally, on-board data processing operates by summarizing the information inside the tags, which allows us to save battery and minimize memory usage. Previous studies demonstrated that the acceleration data could be processed into activity level (Payne et al., 2016) or the occurrence of specific behaviors, such as jaw opening, flipper stroking and burrowing (Adachi et al., 2014; De Almeida et al., 2013; Naito et al., 2013). However, few on-board processing methods have been reported to determine the types of burst movements, possibly because of the low sampling frequencies of accelerometers and the limited number of established processing algorithms (but see De Almeida et al., 2013; Horie et al., 2017). In addition, such processing would limit the scope of analysis, as it cannot provide the various kinematic variables simultaneously. In contrast, the event logger works with a simple algorithm, which records certain raw acceleration data with a high sampling frequency, and thus allows *post hoc* analysis from various kinematic aspects. Such raw high-frequency acceleration data would be especially useful for exploring burst behaviors, which have not been studied well. Additionally, the *post hoc* analysis of

high-frequency acceleration data would allow identification of specific behaviors such as feeding and escaping (Broell et al., 2013), which helps answer the ecological question of when, where and how animals feed and escape predators. Therefore, we believe that this new logger will contribute to the exploration of burst movements in various animals, and to the further development of animal-borne accelerometer methods.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: Y.K.; Methodology: Y.K.; Software: N.N., Y.K.; Formal analysis: N.N., Y.K.; Investigation: N.N., A.M., R.K., N.P., C.H., Y.Y.W., Y.K.; Writing - original draft: N.N., Y.K.; Writing - review & editing: N.N., R.K., N.P., C.H., Y.Y.W., Y.K.; Visualization: N.N., Y.K.; Supervision: Y.K.; Project administration: Y.K.; Funding acquisition: R.K., N.P., C.H., Y.Y.W., Y.K.

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Supplementary information
Supplementary information available online at
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References

Adachi, T., Maresh, J. L., Robinson, P. W., Peterson, S. H., Costa, D. P., Naito, Y., Watanabe, Y. Y. and Takahashi, A. (2014). The foraging benefits of being fat in a highly migratory marine mammal. *Proc. R. Soc. Lond. B* **281**, 20142120.

Broell, F., Noda, T., Wright, S., Domenici, P., Steffensen, J. F., Auclair, J.-P. and Taggart, C. T. (2013). Accelerometer tags: detecting and identifying activities in fish and the effect of sampling frequency. *J. Exp. Biol.* **216**, 1255-1264.

Cooke, S. J., Brownscombe, J. W., Raby, G. D., Broell, F., Hinch, S. G., Clark, T. D. and Semmens, J. M. (2016). Remote bioenergetics measurements in wild fish: opportunities and challenges. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **202**, 23-37.

De Almeida, P. R., Pereira, T. J., Quintella, B. R., Gronningsaeter, A., Costa, M. J. and Costa, J. L. (2013). Testing a 3-axis accelerometer acoustic transmitter (AccelTag) on the Lusitanian toadfish. *J. Exp. Mar. Biol. Ecol.* **449**, 230-238.

Domenici, P. (2009). Escape responses in fish: kinematics, performance and behavior. In *Fish Locomotion: an Eco-Ethological Perspective* (ed. P. Domenici and B. G. Kapoor), pp. 123-170. New Hampshire: Science Publishers.

Føre, M., Alfredsen, J. A. and Gronningsater, A. (2011). Development of two telemetry-based systems for monitoring the feeding behaviour of Atlantic salmon (*Salmo salar* L.) in aquaculture sea-cages. *Comput. Electron. Agric.* **76**, 240-251.

Gleiss, A. C., Wilson, R. P. and Shepard, E. L. C. (2011). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods Ecol. Evol.* **2**, 23-33.

Horie, J., Mitamura, H., Ina, Y., Mashino, Y., Noda, T., Moriya, K., Arai, N. and Sasakura, T. (2017). Development of a method for classifying and transmitting high-resolution feeding behavior of fish using an acceleration pinger. *Anim. Biotelem.* **5**, 12.

Kawabata, Y., Noda, T., Nakashima, Y., Nanami, A., Sato, T., Takebe, T., Mitamura, H., Arai, N., Yamaguchi, T. and Soyano, K. (2014). Use of a gyroscope/accelerometer data logger to identify alternative feeding behaviours in fish. *J. Exp. Biol.* **217**, 3204-3208.

Kawabe, R., Kawano, T., Nakano, N., Yamashita, N., Hiraishi, T. and Naito, Y. (2003). Simultaneous measurement of swimming speed and tail beat activity of free-swimming rainbow trout *Oncorhynchus mykiss* using an acceleration data-logger. *Fish. Sci.* **69**, 959-965.

Kawabe, R., Naito, Y., Sato, K., Miyashita, K. and Yamashita, N. (2004). Direct measurement of the swimming speed, tailbeat, and body angle of Japanese flounder (*Paralichthys olivaceus*). *ICES J. Mar. Sci.* **61**, 1080-1087.

Marras, S., Noda, T., Steffensen, J. F., Svendsen, M. B. S., Krause, J., Wilson, A. D. M., Kurvers, R. H. J. M., Herbert-Read, J., Boswell, K. M. and Domenici, P. (2015). Not so fast: Swimming behavior of sailfish during predator-prey interactions using high-speed video and accelerometry. *Integr. Comp. Biol.* **55**, 719-727.

Murchie, K. J., Cooke, S. J., Danylchuk, A. J. and Suski, C. D. (2011). Estimates of field activity and metabolic rates of bonefish (*Albula vulpes*) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry. *J. Exp. Mar. Biol. Ecol.* **396**, 147-155.

Naito, Y., Costa, D. P., Adachi, T., Robinson, P. W., Fowler, M. and Takahashi, A. (2013). Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. *Funct. Ecol.* **27**, 710-717.

Noda, T., Kawabata, Y., Arai, N., Mitamura, H. and Watanabe, S. (2013). Monitoring escape and feeding behaviours of cruiser fish by inertial and magnetic sensors. *PLoS ONE* **8**, e79392.

O'Toole, A. C., Murchie, K. J., Pullen, C., Hanson, K. C., Suski, C. D., Danylchuk, A. J. and Cooke, S. J. (2010). Locomotory activity and depth distribution of adult great barracuda (*Sphyraena barracuda*) in Bahamian coastal habitats determined using acceleration and pressure biotelemetry transmitters. *Mar. Freshwat. Res.* **61**, 1446-1456.

Payne, N. L., Gillanders, B. M., Seymour, R. S., Webber, D. M., Snelling, E. P. and Semmens, J. M. (2011). Accelerometry estimates field metabolic rate in giant Australian cuttlefish *Sepia apama* during breeding. *J. Anim. Ecol.* **80**, 422-430.

Payne, N. L., Smith, J. A., van der Meulen, D. E., Taylor, M. D., Watanabe, Y. Y., Takahashi, A., Marzullo, T. A., Gray, C. A., Cadiou, G. and Suthers, I. M. (2016). Temperature dependence of fish performance in the wild: links with species biogeography and physiological thermal tolerance. *Funct. Ecol.* **30**, 903-912.

Sato, K., Watanuki, Y., Takahashi, A., Miller, P. J. O., Tanaka, H., Kawabe, R., Ponganis, P. J., Handrich, Y., Akamatsu, T., Watanabe, Y. et al. (2007). Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proc. R. Soc. Lond. B* **274**, 471-477.

Shepard, E. L. C. and Wilson, R. P. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endang. Species Res.* **10**, 47-60.

Tanaka, H., Takagi, Y. and Naito, Y. (2001). Swimming speeds and buoyancy compensation of migrating adult chum salmon *Oncorhynchus keta* revealed by speed/depth/acceleration data logger. *J. Exp. Biol.* **204**, 3895-3904.

Tsuda, Y., Kawabe, R., Tanaka, H., Mitsunaga, Y., Hiraishi, T., Yamamoto, K. and Nashimoto, K. (2006). Monitoring the spawning behaviour of chum salmon with an acceleration data logger. *Ecol. Freshwat. Fish* **15**, 264-274.

Van Deurs, M., Andersson, A., Vinterstare, J., Didenko, A., Persson, A., Brönmark, C. and Nilsson, P. A. (2017). Using accelerometry to quantify prey attack and handling behaviours in piscivorous pike *Esox lucius*. *J. Fish Biol.* **90**, 2462-2469.

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. 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.* **426-427**, 5-11.

Watanabe, Y. Y. and Takahashi, A. (2013). Linking animal-borne video to accelerometers reveals prey capture variability. *Proc. Natl. Acad. Sci. USA* **110**, 2199-2204.

Weihs, D. (1973). The mechanism of rapid starting of slender fish1. *Biorheology* **10**, 343-350.

Whitney, N. M., Pratt, H. L., Jr, Pratt, T. C. and Carrier, J. C. (2010). Identifying shark mating behaviour using three-dimensional acceleration loggers. *Endang. Species Res.* **10**, 71-82.

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.

Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A. and McNutt, J. W. (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**, 185-189.

Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C. A., Le Maho, Y. and Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. *J. Exp. Biol.* **202**, 3121-3126.