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METHODS & TECHNIQUES

Use of a gyroscope/accelerometer data logger to identify alternative feeding behaviours in fish

Yuuki Kawabata[1,*], Takuji Noda[2], Yuuki Nakashima[1], Atsushi Nanami[3], Taku Sato[3], Takayuki Takebe[3], Hiromichi Mitamura[2], Nobuaki Arai[2], Tomofumi Yamaguchi[1,3] and Kiyoshi Soyano[1]

ABSTRACT

We examined whether we could identify the feeding behaviours of the trophic generalist fish *Epinephelus ongus* on different prey types (crabs and fish) using a data logger that incorporated a three-axis gyroscope and a three-axis accelerometer. Feeding behaviours and other burst behaviours, including escape responses, intraspecific interactions and routine movements, were recorded from six *E. ongus* individuals using data loggers sampling at 200 Hz, and were validated by simultaneously recorded video images. For each data-logger record, we extracted 5 s of data when any of the three-axis accelerations exceeded absolute 2.0 *g*, to capture all feeding behaviours and other burst behaviours. Each feeding behaviour was then identified using a combination of parameters that were derived from the extracted data. Using decision trees with the parameters, high true identification rates (87.5% for both feeding behaviours) with low false identification rates (5% for crab-eating and 6.3% for fish-eating) were achieved for both feeding behaviours.

INTRODUCTION

Cataloguing discrete behaviours (i.e. ethogram) is an essential step toward the understanding of interactions between behaviours and internal states (e.g. metabolic rate, cognitive ability, etc.) of animals. Acceleration data-loggers are a useful tool to categorize behaviours in free-ranging animals (Campbell et al., 2013; Nathan et al., 2012; Sakamoto et al., 2009), but only a few studies have applied this technique to identify feeding behaviours of predators (Broell et al., 2013; Naito et al., 2013; Noda et al., 2013; Watanabe and Takahashi, 2013). A recent study suggested that it would be possible to identify feeding strikes of predatory fish if the sampling frequency was sufficiently high (>100 Hz) (Broell et al., 2013). In addition, it was found that the identification accuracy was greater if the data were obtained from a data logger that incorporated a gyroscope and an accelerometer compared with data from only an accelerometer was used (Noda et al., 2013). However, as far as we are aware, no studies have been conducted using this method on distinguishing prey types.

Previous laboratory studies using high-speed video cameras have elucidated the modulation of feeding kinematics depending on prey types in various predators (Anderson, 1993; Deban, 1997; Ferry-

Graham et al., 2001; Montuelle et al., 2012; Nemeth, 1997). In addition to jaw motion, body motions such as body posture, angular velocity and forward velocity were found to be different between prey types in these animals. Thus, a data-logger incorporating a gyroscope and an accelerometer, that can measure angular velocity and acceleration with high sampling frequency, might be usable for distinguishing feeding behaviours of these predators on different prey types.

In this study, we used a novel gyroscope/acceleration data logger, which can monitor three-axis angular velocities as well as three-axis accelerations, with the aim of identifying the feeding behaviours of a trophic generalist fish, the white-streaked grouper *Epinephelus ongus* (Bloch 1790), on different prey types.

RESULTS AND DISCUSSION

The results of this study indicate that we can successfully identify *E. ongus* feeding behaviours on both crabs (crab-eating) and fish (fish-eating) using the gyroscope/acceleration data logger. Firstly, among the *E. ongus* behaviours recorded, 17 crab-eating, 34 fish-eating, 42 escape responses (escape), nine intraspecific attacks (intra-attack), 27 intraspecific escapes (intra-escape) and 16 routine movements (routine) were detected by a set threshold (2.0*g*) (supplementary material Table S1), from a total of 17 crab-eating, 34 fish-eating, 42 escape, 48 intra-attack and 48 intra-escape behaviours recorded by a video camera. Secondly, the featured parameters were calculated (supplementary material Table S2) after extracting the subsequent 5 s of data and then dividing into the first phase (2.1 s) and second phase (2.9 s) (see Materials and methods and supplementary material Fig. S1 for details). Finally, each of the feeding behaviours was identified by a decision tree using specific parameters (Figs 1, 2). Using this paradigm, we achieved high true identification rates (87.5% for both feeding behaviours) with low false identification rates (4.4% for crab-eating and 5.6% for fish-eating) for both feeding behaviours (Figs 1, 2, Tables 1, 2).

Epinephelus ongus exhibited larger pitch motions to pick up crabs (supplementary material Movies 1–6); the ratio of the range of pitch angular velocity to the range of yaw angular velocity in the first phase ($\text{Range}_{\text{Pitch}-1}/\text{Range}_{\text{Yaw}-1}$) of the crab-eating behaviour was larger than that of the fish-eating, escape, intra-attack and intra-escape behaviours (ANOVA, $P<0.01$; Tukey–Kramer test, $P<0.05$; Fig. 1C). *Epinephelus ongus* did not move substantially during the second phase of routine behaviour; the mean vector sum of the angular velocities in the second phase ($\text{Mean}_{\text{MG}-2}$) of the routine behaviour was lower than those of the crab-eating, fish-eating, escape and intra-escape behaviours (ANOVA, $P<0.01$; Tukey–Kramer test, $P<0.05$; Fig. 1D). Thus, $\text{Range}_{\text{Pitch}-1}/\text{Range}_{\text{Yaw}-1}$ was used to discriminate crab-eating from fish-eating, escape, intra-attack and intra-escape behaviours (Fig. 1A,C), and $\text{Mean}_{\text{MG}-2}$ was used to discriminate crab-eating from routine behaviour (Fig. 1A,D). The sum of sensitivity (true identification rate) and specificity

[1]Institute for East China Sea Research, Nagasaki University, Taira-machi, Nagasaki 851-2213, Japan. [2]Graduate School of Informatics, Kyoto University, Yoshidahonmachi, Kyoto 606-8501, Japan. [3]Research Center for Sub-tropical Fisheries, Seikai National Fisheries Research Institute, Fisheries Research Agency, Fukai-Ota, Ishigaki 907-0451, Japan.

*Author for correspondence (yuuki-k@nagasaki-u.ac.jp)
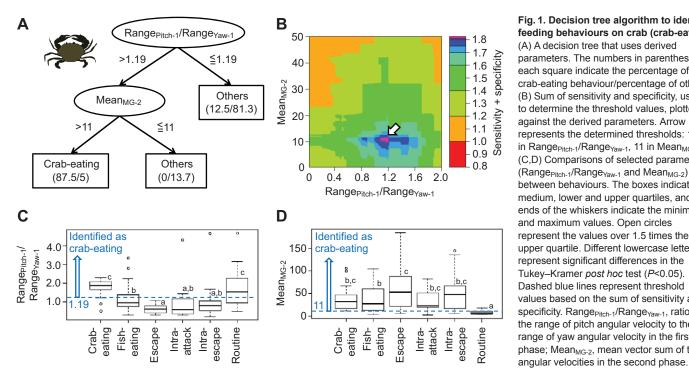
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Fig. 1. Decision tree algorithm to identify feeding behaviours on crab (crab-eating). (A) A decision tree that uses derived parameters. The numbers in parentheses in each square indicate the percentage of crab-eating behaviour/percentage of others. (B) Sum of sensitivity and specificity, used to determine the threshold values, plotted against the derived parameters. Arrow represents the determined thresholds: 1.19 in $Range_{Pitch-1}/Range_{Yaw-1}$, 11 in $Mean_{MG-2}$. (C,D) Comparisons of selected parameters ($Range_{Pitch-1}/Range_{Yaw-1}$ and $Mean_{MG-2}$) between behaviours. The boxes indicate the medium, lower and upper quartiles, and the ends of the whiskers indicate the minimum and maximum values. Open circles represent the values over 1.5 times the upper quartile. Different lowercase letters represent significant differences in the Tukey–Kramer *post hoc* test ($P<0.05$). Dashed blue lines represent threshold values based on the sum of sensitivity and specificity. $Range_{Pitch-1}/Range_{Yaw-1}$, ratio of the range of pitch angular velocity to the range of yaw angular velocity in the first phase; $Mean_{MG-2}$, mean vector sum of the angular velocities in the second phase.

(1–false identification rate), a criterion to determine the optimal threshold (see Materials and methods for details), revealed a peak (1.83) at thresholds of 1.19 and 11 in the $Range_{Pitch-1}/Range_{Yaw-1}$ and $Mean_{MG-2}$, respectively (Fig. 1B), at which the true identification rate was 87.5% (14/16) and the false identification rate was 5% (4/80; Fig. 1, Table 1). In the more conservative cross-validation test, in which we derived the decision tree algorithm from five individuals at a time and tested identification success on the remaining individual, the true identification rate was 75% (12/16) and the false identification rate was 6.3% (5/80; Table 3).

Epinephelus ongus exhibited a strong fast-start motion during fish-eating and escape compared with the other behaviours (supplementary material Movies 1–6). The standard deviation of the lateral acceleration in the first phase (SD_{AX-1}) of fish-eating and escape was higher than that of the other behaviours (ANOVA, $P<0.01$; Tukey–Kramer test, $P<0.05$; Fig. 2C). *Epinephelus ongus* showed strong yaw motion during escape compared with fish-eating (supplementary material Movies 2, 3); the ratio of the range of yaw angular velocity to the range of roll angular velocity in the first phase ($Range_{Yaw-1}/Range_{Roll-1}$) of escape was larger than that of fish-
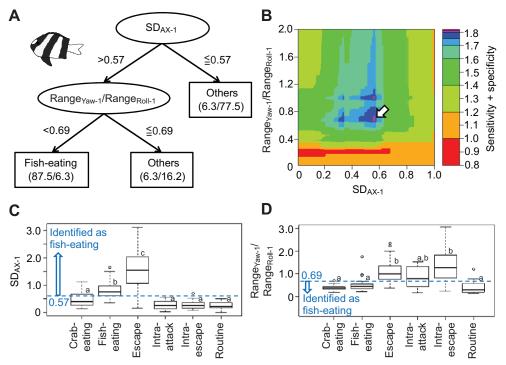

Fig. 2. Decision tree algorithm to identify feeding behaviours on fish (fish-eating). (A) A decision tree that uses derived parameters. The numbers in parentheses in each square indicate the percentage of fish-eating behaviour/percentage of others. (B) Sum of sensitivity and specificity, used to determine the threshold values, plotted against the derived parameters. Arrows represent the determined thresholds: 0.57 in SD_{AX-1}, 0.69 in $Range_{Yaw-1}/Range_{Roll-1}$. (C,D) Comparisons of selected parameters (SD_{AX-1} and $Range_{Yaw-1}/Range_{Roll-1}$) between behaviours. The boxes indicate the medium, lower and upper quartiles, and the ends of the whiskers indicate the minimum and maximum values. Open circles represent the values over 1.5 times the upper quartile. Different lowercase letters represent significant differences in the Tukey–Kramer *post hoc* test ($P<0.05$). Dashed blue lines represent threshold values based on the sum of sensitivity and specificity. SD_{AX-1}, standard deviation of the lateral acceleration in the first phase; $Range_{Yaw-1}/Range_{Roll-1}$, ratio of the range of yaw angular velocity to the range of roll angular velocity in the first phase.

Table 1. Decision tree results for identifying feeding behaviour on crab (crab-eating), in which the same data set was used for deriving the decision tree algorithm and for testing identification success

	Crab-eating	Fish-eating	Escape	Intra-attack	Intra-escape	Routine
Crab-eating	**14 (87.5)**	3 (18.8)	0 (0)	0 (0)	0 (0)	1 (6.3)
Others	2 (12.5)	**13 (81.3)**	**16 (100)**	**16 (100)**	**16 (100)**	**15 (93.8)**

Number (%) of trials identified correctly are shown in bold.

Table 2. Decision tree results for identifying feeding behaviour on fish (fish-eating), in which the same data set was used for deriving the decision tree algorithm and for testing identification success

	Fish-eating	Crab-eating	Escape	Intra-attack	Intra-escape	Routine
Fish-eating	**14 (87.5)**	4 (25)	1 (6.3)	0 (0)	0 (0)	0 (0)
Others	2 (12.5)	**12 (75)**	**15 (93.8)**	**16 (100)**	**16 (100)**	**16 (100)**

Number (%) of trials identified correctly are shown in bold.

eating (ANOVA, $P<0.01$; Tukey–Kramer test, $P<0.05$; Fig. 2D). Therefore, SD_{AX-1} was used to discriminate fish-eating from crab-eating, intra-attack, intra-escape and routine behaviours (Fig. 2A,C), and $Range_{Yaw-1}/Range_{Roll-1}$ was used to discriminate fish-eating from escape (Fig. 2A,D). The sum of sensitivity and specificity revealed a peak (1.81) at thresholds of 0.57 and 0.69 in SD_{AX-1} and $Range_{Yaw-1}/Range_{Roll-1}$, respectively (Fig. 2B), at which the true identification rate was 87.5% (14/16) and the false identification rate was 6.3% (5/80; Fig. 2, Table 2). In the more conservative cross-validation test, the true identification rate was 87.5% (14/16) and the false identification rate was 8.8% (7/80; Table 4).

Although the overall identification success was high, some behaviours were more likely to be misidentified than the others. In general, intra-attack, intra-escape and routine behaviours were rarely misidentified as either feeding behaviour [0% (0/16) or 6.3% (1/16) of the false identification rates even in the cross validation tests; Tables 3, 4], while escape was more likely to be misidentified as fish-eating [18.8% (3/16) of the false identification rate in the cross validation test; Table 4]. Previous studies that compared escape responses and feeding strikes (fish-eating) in predatory fishes revealed that both feeding strikes and escape responses have several mechanical types, and in some types, the motions were similar between the two behaviours (Broell et al., 2013; Harper and Blake, 1991; Noda et al., 2013). Even in the present study, there were overlaps in the distributions of accelerations and angular velocities between the fish-eating and escape behaviours (Fig. 1C, Fig. 2C; supplementary material Table S2), and thus some escape events were misidentified as fish-eating.

In addition, crab-eating and fish-eating were sometimes confused with each other, even though there were significant differences in $Range_{Pitch-1}/Range_{Yaw-1}$ and SD_{AX-1} between the two behaviours (Fig. 1C, Fig. 2C). This is because, in a few cases, *E. ongus* attacked and swallowed crabs without a large pitch motion but with its body rolled, and in other cases, *E. ongus* attacked fish with large pitch motions, probably adjusting its body posture towards the vertically evading fish.

Over the last two decades, researchers have attempted to record the feeding behaviours of predators in nature using electronic devices, such as animal-borne video cameras (Davis et al., 1999; Watanabe and Takahashi, 2013), stomach/oesophageal temperature and impedance telemetry (Austin et al., 2006; Hanuise et al., 2010; Meyer and Holland, 2012), and accelerometers/hall sensors attached to jaws or heads (Hanuise et al., 2010; Naito et al., 2013; Watanabe and Takahashi, 2013; Wilson et al., 2002). However, very few studies have attempted to distinguish prey types (Wilson et al., 2002), except for studies using cameras. The present study shows that as long as the mechanical motions are distinct in each of the feeding behaviours, the gyroscope/acceleration data logger is usable for distinguishing prey types. Body motions in various predators such as lizards, salamanders, frogs and other reef fishes were reportedly different between prey types (Anderson, 1993; Deban, 1997; Ferry-Graham et al., 2001; Montuelle et al., 2012; Nemeth, 1997), and thus this method could also be applied to these predators.

MATERIALS AND METHODS
Ethics statement
Animal care and experimental procedures for the tagging surgery and live predator–prey experiments were approved by the Institutional Animal Care and Use Committee (permit no. ECSER12-02) in accordance with the Guidelines for Animal Experimentation of Nagasaki University.

Table 3. Results of the more conservative cross-validation test for identifying feeding behaviour on crab (crab-eating), in which we derived the decision tree algorithm from five individuals at a time and then tested identification success on the remaining individual

	Crab-eating	Fish-eating	Escape	Intra-attack	Intra-escape	Routine
Crab-eating	**12 (75)**	3 (18.8)	0 (0)	0 (0)	1 (6.3)	1 (6.3)
Others	4 (25)	**13 (81.3)**	**16 (100)**	**16 (100)**	**15 (93.8)**	**15 (93.8)**

Number (%) of trials identified correctly are shown in bold.

Table 4. Results of the more conservative cross-validation test for identifying feeding behaviour on fish (fish-eating), in which we derived the decision tree algorithm from five individuals at a time and then tested identification success on the remaining individual

	Fish-eating	Crab-eating	Escape	Intra-attack	Intra-escape	Routine
Fish-eating	**14 (87.5)**	4 (25)	3 (18.8)	0 (0)	0 (0)	0 (0)
Others	2 (12.5)	**12 (75)**	**13 (81.3)**	**16 (100)**	**16 (100)**	**16 (100)**

Number (%) of trials identified correctly are shown in bold.

Study animals

Epinephelus ongus is an abundant generalist predator in the Indo-Pacific coral reefs, where it feeds mainly on benthic crustaceans and fishes (supplementary material Table S3). Six *E. ongus* [total length (TL): 254±24 mm] were collected by hook-and-line while snorkelling around the Yaeyama Islands, Okinawa, Japan, and were transferred to the Research Center for Subtropical Fisheries, Seikai National Fisheries Research Institute, Fisheries Research Agency, Okinawa, Japan. The fish were held in two 2000 l circular fibre-reinforced plastic (FRP) tanks for at least 2 days prior to experimental testing.

Two different prey types – the mangrove swimming crab, *Thalamita crenata* (Portunidae) (carapace length: 26±7 mm), and the whitetail dascyllus, *Dascyllus aruanus* (Pomacentridae) (TL: 33±9 mm) – were utilized in this study. These species were chosen because they are abundant in the *E. ongus* habitat and because the primary prey types of *E. ongus* are benthic crustaceans and fishes such as Portunidae and Pomacentridae, respectively (supplementary material Table S3).

Data-logging device

We employed a data logger incorporating a three-axis accelerometer and a three-axis gyroscope (LP-BLKU02, Biologging Solutions Inc., Kyoto, Japan; 60×5×13 mm, mass in air 6.5 g, sampling frequency 200 Hz, recording duration 150 min, resolution 16 bit). This device allowed for multiple scheduled recordings (e.g. 30 min of recording each day).

Attachment procedure

The fish were first anaesthetized using 0.1% 2-phenoxyethanol until they reached stage-4 anaesthesia. Next, two small holes (~2 mm in diameter) were drilled into their dorsal musculature above their approximate centre of mass (39% of TL), and the logger was attached using two plastic cables that passed through the holes and were set on the right side of the body. The surgery had no observable effects on fish swimming or feeding behaviours.

Recording of behaviours

Experiments were performed in a 1000 l circular FRP tank with seawater to a depth of 300 mm. The water temperature during the experiments was 28.13±0.31°C. Three *E. ongus* were introduced into the experimental tank and allowed to acclimate for ~22 h. The data loggers were scheduled to record data at 17:00–18:30 h; this period was chosen because this species increases its foraging activity during crepuscular periods (Kawabata et al., 2011). During the experiments, one to five crabs (*T. crenata*) or fish (*D. aruanus*) were introduced into the tank, and feeding behaviours of *E. ongus* were recorded. We also recorded escape responses and intraspecific interactions to test whether the method can accurately identify each of the feeding behaviours, which can also manifest as burst movements similar to feeding behaviours. Escape responses were elicited by thrusting a PVC pipe near the fish (Broell et al., 2013; Domenici et al., 2004), and intraspecific interactions were recorded by introducing three individuals into the same tank. These behaviours were simultaneously recorded using a USB camera (HD Pro Webcam C920, Logitech International S.A., Morges, Switzerland) 2.8 m above the tank bottom.

Data analyses

We first reconstructed 3D motions of the fish through the three-axis acceleration and three-axis angular velocity datasets [see Luinge and Veltink (Luinge and Veltink, 2005) and Noda et al. (Noda et al., 2014) for detailed analysis in which the reconstructed motions were compared with the video images] to investigate mechanical differences of motions among behaviours, and created animations using the 3D editor Blender 2.68 (The Blender Foundation, 2013). Next, the reconstructed 3D animations and video images were observed to identify distinct parameters of each of the feeding behaviours.

The threshold acceleration value was set to 2.0 g, because all the feeding behaviours exceeded the absolute 2.0 g in at least one of the three axes. We included two phases for calculating parameters, as the fast-start behaviours include the initial fast motions (e.g. strike or escape) and the

subsequent motions (e.g. swallowing prey, swimming or resting). The different cut-off periods (0.1–3.0 s) and total periods (3–13 s) were tested using the sum of sensitivity and specificity, and 2.1 and 5 s were chosen as the optimal periods (supplementary material Fig. S1). Featured parameters (maximum value, mean, range and standard deviation) were calculated based on the three-axis accelerations and three-axis angular velocities in each phase (supplementary material Table S2). On the basis of the distinct motion of each of the behaviours, these parameters and inter-axial parameters (e.g. ratio of maximum forward acceleration to maximum lateral acceleration) were considered and selected for identification analysis. ANOVA and Tukey–Kramer *post hoc* tests were used to determine any significant differences in parameters between behaviours.

We chose a uniform sample size for each of the behaviours (*n*=16) to conduct the identification analysis, because there were no data concerning the occurrence of each of the behaviours in the natural environment. Decision trees were constructed because there was no single parameter that can differentiate each of the feeding behaviours from all other behaviours. The optimal threshold of parameters was obtained from the sum of sensitivity and specificity (Akobeng, 2007; Valenzuela et al., 1997). The sensitivity and specificity represent the rates correctly identified and rejected, respectively, and were calculated as follows: sensitivity=(true positive)/(true positive+false negative) and specificity=(true negative)/(false positive+true negative).

The criterion (sum of sensitivity and specificity) is based on the concept that the optimal threshold should strike a balance between the high true identification rate and low false identification rate of the target event (Akobeng, 2007). We first used the same data set for deriving the decision tree algorithm and for testing identification success. Then, a more conservative cross-validation test was employed, in which we derived the decision tree algorithm from five individuals at a time and then tested identification success on the remaining individual. All the data analyses were performed using R 3.0.1 (R Foundation for Statistical Computing, Vienna, Austria) (see supplementary material Script 1 for the custom-made program).

Competing interests
The authors declare no competing financial interests.

Author contributions
Y.K. designed the experiment. Y.K., Y.N., A.N., T.S., T.T., T.Y. and K.S. conducted the experiment. T.N., H.M. and N.A. designed and developed the data logger. Y.K. and T.N. analysed the data. T.N. created the 3D animation. Y.K. wrote the manuscript. All authors provided critiques on the manuscript.

Supplementary material
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References
Akobeng, A. K. (2007). Understanding diagnostic tests 3: receiver operating characteristic curves. *Acta Paediatr.* **96**, 644-647.
Anderson, C. W. (1993). The modulation of feeding behavior in response to prey type in the frog *Rana pipiens*. *J. Exp. Biol.* **179**, 1-12.
Austin, D., Bowen, W. D., McMillan, J. I. and Boness, D. J. (2006). Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. *J. Anim. Ecol.* **75**, 408-420.
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.
Campbell, H. A., Gao, L., Bidder, O. R., Hunter, J. and Franklin, C. E. (2013). Creating a behavioural classification module for acceleration data: using a captive surrogate for difficult to observe species. *J. Exp. Biol.* **216**, 4501-4506.

Davis, R. W., Fuiman, L. A., Williams, T. M., Collier, S. O., Hagey, W. P., Kanatous, S. B., Kohin, S. and Horning, M. (1999). Hunting behavior of a marine mammal beneath the Antarctic fast Ice. *Science* **283**, 993-996.

Deban, S. (1997). Modulation of prey-capture behavior in the plethodontid salamander *Ensatina eschscholtzii*. *J. Exp. Biol.* **200**, 1951-1964.

Domenici, P., Standen, E. M. and Levine, R. P. (2004). Escape manoeuvres in the spiny dogfish (*Squalus acanthias*). *J. Exp. Biol.* **207**, 2339-2349.

Ferry-Graham, L. A., Wainwright, P. C., Westneat, M. W. and Bellwood, D. R. (2001). Modulation of prey capture kinematics in the cheeklined wrasse *Oxycheilinus digrammus* (Teleostei: Labridae). *J. Exp. Zool.* **290**, 88-100.

Hanuise, N., Bost, C. A., Huin, W., Auber, A., Halsey, L. G. and Handrich, Y. (2010). Measuring foraging activity in a deep-diving bird: comparing wiggles, oesophageal temperatures and beak-opening angles as proxies of feeding. *J. Exp. Biol.* **213**, 3874-3880.

Harper, D. G. and Blake, R. W. (1991). Prey capture and the fast-start performance of northern pike *Esox lucius*. *J. Exp. Biol.* **155**, 175-192.

Kawabata, Y., Asami, K., Kobayashi, M., Sato, T., Okuzawa, K., Yamada, H., Yoseda, K. and Arai, N. (2011). Effect of shelter acclimation on the post-release survival of hatchery-reared black-spot tuskfish *Choerodon schoenleinii*: laboratory experiments using the reef-resident predator white-streaked grouper *Epinephelus ongus*. *Fish. Sci.* **77**, 79-85.

Luinge, H. J. and Veltink, P. H. (2005). Measuring orientation of human body segments using miniature gyroscopes and accelerometers. *Med. Biol. Eng. Comput.* **43**, 273-282.

Meyer, C. G. and Holland, K. N. (2012). Autonomous measurement of ingestion and digestion processes in free-swimming sharks. *J. Exp. Biol.* **215**, 3681-3684.

Montuelle, S. J., Herrel, A., Libourel, P. A., Daillie, S. and Bels, V. L. (2012). Flexibility in locomotor-feeding integration during prey capture in varanid lizards: effects of prey size and velocity. *J. Exp. Biol.* **215**, 3823-3835.

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.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. and Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *J. Exp. Biol.* **215**, 986-996.

Nemeth, D. (1997). Modulation of attack behavior and its effect on feeding performance in a trophic generalist fish. *J. Exp. Biol.* **200**, 2155-2164.

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.

Noda, T., Kawabata, Y., Arai, N., Mitamura, H. and Watanabe, S. (2014). Animal-mounted gyroscope/accelerometer/magnetometer: In situ measurement of the movement performance of fast-start behaviour in fish. *J. Exp. Mar. Biol. Ecol.* **451**, 55-68.

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.

Valenzuela, T. D., Roe, D. J., Cretin, S., Spaite, D. W. and Larsen, M. P. (1997). Estimating effectiveness of cardiac arrest interventions: a logistic regression survival model. *Circulation* **96**, 3308-3313.

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.

Wilson, R. P., Steinfurth, A., Ropert-Coudert, Y., Kato, A. and Kurita, M. (2002). Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Mar. Biol.* **140**, 17-27.