

RESEARCH ARTICLE

Measuring abnormal movements in free-swimming fish with accelerometers: implications for quantifying tag and parasite load

Franziska Broell*, Celene Burnell and Christopher T. Taggart

ABSTRACT

Animal-borne data loggers allow movement, associated behaviours and energy expenditure in fish to be quantified without direct observations. As with any tagging, tags that are attached externally may adversely affect fish behaviour, swimming efficiency and survival. We report on free-swimming wild Atlantic cod (*Gadus morhua*) held in a large mesocosm that exhibited distinctly aberrant rotational swimming (scouring) when externally tagged with accelerometer data loggers. To quantify the phenomenon, the cod were tagged with two sizes of loggers (18 and 6 g; <2% body mass) that measured tri-axial acceleration at 50 Hz. An automated algorithm, based on body angular rotation, was designed to extract the scouring movements from the acceleration signal (98% accuracy). The algorithm also identified the frequency pattern and associated energy expenditure of scouring in relation to tag load (% body weight). The average per cent time spent scouring (5%) was independent of tag load. The vector of the dynamic body acceleration (VeDBA), used as a proxy for energy expenditure, increased with tag load ($r^2=0.51$), and suggests that fish with large tags spent more energy when scouring than fish with small tags. The information allowed us to determine potential detrimental effects of an external tag on fish behaviour and how these effects may be mitigated by tag size. The algorithm can potentially identify similar rotational movements associated with spawning, courtship, feeding and parasite-load shedding in the wild. The results infer a more careful interpretation of data derived from external tags and the careful consideration of tag type, drag, buoyancy and placement, as well as animal buoyancy and species.

KEY WORDS: Swimming performance, Parasite load, *Gadus morhua*, Signal processing, Atlantic cod, Scouring

INTRODUCTION

Quantifying the spatial–temporal distribution of free-ranging animals in the marine environment is problematic because of the paucity of direct observations (Cooke et al., 2004; Preston et al., 2010). This can be partially overcome by using a variety of tags that range from conventional tags (e.g. Petersen or Floy tags; Petersen, 1896; McFarlane et al., 1990) to more advanced electronic tags (Cooke et al., 2004; Bograd et al., 2010). Animal-borne archival tags can provide a means to monitor movements of aquatic animals and their environment through *in situ* measurements such as acceleration, temperature and depth. Such data can be used to

indirectly quantify variation in behaviour, energetics and physiology, and to infer how animals interact with each other and their environment (Cooke et al., 2004) for habitat modelling and conservation management (Bograd et al., 2010; Whitney et al., 2010). For example, micro-storage accelerometer tags allow for remote measurements of fine-scale movements and behaviour among free-swimming fish in time and space in controlled mesocosm environments (Gleiss et al., 2010; Broell et al., 2013; Noda et al., 2014; Wright et al., 2014; Broell and Taggart, 2015), as well as in the wild (Kawabe et al., 2003a,b; Tsuda et al., 2006; Whitney et al., 2010; Carroll et al., 2014).

The use of accelerometer tags in bio-logging studies has increased because of their commercial availability, data-storage capabilities and versatility of attachment (Ropert-Coudert and Wilson, 2005; Rutz and Hays, 2009). As with any tagging, external or internal, tag attachments can alter the natural behaviour and physiology of the tagged fish (Ross and McCormick, 1981; Greenstreet and Morgan, 1989; Barrowman and Myers, 1996; Björnsson et al., 2011; Cooke et al., 2012; Jones et al., 2013). *In situ* capture–recapture or tag-recovery studies using conventional or electronic tags are typically based on the assumption that there is no significant effect of the tag on the fish and that tags are not lost or shed through erratic swimming (Bridger and Booth, 2003). If invalid, this assumption can lead to compromised estimates of the metrics used to estimate population size and distribution as well as activity patterns and energy budgets (Bridger and Booth, 2003; Drenner et al., 2012). This is especially problematic in bio-logging studies where data from a few (typically <10) individuals is collected to make inferences about entire populations (Cooke et al., 2004).

In fisheries applications, the general criterion used to minimize potentially adverse tag effects is the ‘2% rule’, which assumes that tag effects are negligible if tag mass is <2% of the body mass of the tagged animal (Winter, 1996), regardless of the attachment method. However, tag mass is not the only factor influencing tag impact (Jepsen et al., 2015), and per cent weight is regarded by many, and ourselves, to be a questionable metric (Brown et al., 2006; Smirich and Kelly, 2014) because it assumes a 1:1 scaling effect of tag and animal, which is invalid. For some aquatic animals, tag mass may have little or no effect, especially in organisms with bladders or lungs that can adjust their buoyancy (Jones et al., 2013). Other factors influencing tag impact include the tag dimensions, volume, buoyancy and attachment position, all of which significantly affect drag (Hoerner, 1965; Musyl et al., 2011; Jones et al., 2013; Jepsen et al., 2015). Therefore, these variables require consideration prior to field deployment to ensure that fish behaviour and movement are unaffected by the tag and attachment designs (Smirich and Kelly, 2014; Jepsen et al., 2015).

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List of symbols and abbreviations

$A_{f,L}$	cross-sectional area of large (cylindrical) tag
$A_{f,S}$	cross-sectional area of small (rectangular) tag
a_{\max}	maximum whole body acceleration
$a_{\max,x}$	maximum lateral acceleration
A_w	wetted surface area of a fish
c_d	fish drag coefficient calculated from characteristic shape
$c_{d,L}$	drag coefficient of large (cylindrical) tag
$c_{d,S}$	drag coefficient of small (rectangular) tag
C_i	rotation segment
F_d	drag force
FN	false negative
FP	false positive
g_0	gravitational acceleration
l	length (m)
l_w	sliding window length in the algorithm
m	mass (kg)
\dot{M}_{O_2}	rate of oxygen consumption
N	total number of fish used in the study
N_D	sample size (subscript indicates data subset: D=all fish, S=small tags, L=large tags)
OLS	ordinary least square
P	power
t_{C_i}	the cross-over points
$t_{C_i,1}; t_{C_i,2}$	start end and index of rotation segment
$t_{C_i,\max}$	instantaneous acceleration at time index where $\theta_{C_i,\max}$
TN	true negative
TP	true positive
T_s	percentage of time spent scouring
u	swim speed ($m\ s^{-1}$)
VeDBA	vector of the dynamic body acceleration ($\sqrt{a_x^2 + a_y^2 + a_z^2}$)
W	algorithm sliding window
x	(subscript) lateral acceleration
y	(subscript) forward acceleration
z	(subscript) vertical acceleration
θ_{C_i}	angle between the acceleration component in the x – z plane and reference alignment
$\theta_{C_i,\max}$	maximum angle in the x – z plane as identified in C_i
θ_R	angle of rotation
θ_{tag}	initial tag orientation; projection of the time-averaged acceleration vector in the x – z plane
θ_{Th}	threshold angle
ρ	density of water

As a behavioural response to tag burden, tag shedding has been reported extensively for various fish species; however, it is rarely quantified in relation to changes in natural behaviour and associated energy expenditure (Barrowman and Myers, 1996; Björnsson et al., 2011; Musyl et al., 2011). While direct observations of tag loss and associated swimming behaviour are limited, shortnose sturgeon (*Acipenser brevirostrum*), rainbow trout (*Oncorhynchus mykiss*) and salema (*Sarpa salpa*) fitted with transmitters attached below the dorsal fin have been observed to scour vigorously against tank enclosures, leading to external tag loss and skin abrasions (Mellas and Haynes, 1985; Collins et al., 2002; Jadot, 2003). This distinctive and repeated scouring-associated rotational movement (flashing, scraping) in the

vertical–lateral plane has also been observed in Atlantic cod (*Gadus morhua*) in order to dislodge parasites (Jeffrey Hutchings, Department of Biology, Dalhousie University, personal communication).

To investigate the effect of external accelerometer tag burden on free-swimming *G. morhua* held in a large mesocosm, we quantified the short-term effect of different tag loads on the swimming behaviour associated with tag shedding, i.e. scouring. To identify and quantify the distinctive acceleration patterns generated by scouring, we first developed an automated algorithm to extract the scouring-associated rotational movement from the acceleration time series. We then used the results to quantify the scouring behaviour in relation to tag load and the amount of time individuals spent scouring, energy expenditure, fish size and time of day, where for the last of these there is limited knowledge of swimming behaviour during night-time conditions.

MATERIALS AND METHODS**Study animals**

Atlantic cod (*Gadus morhua* L., $N=22$) of total length (l) ranging from 0.47 to 0.72 m (mean \pm s.d., 0.61 ± 0.069 m) with mass (m) between 0.95 and 3.4 kg (2.0 ± 0.66 kg) were collected near Nova Scotia, Canada. Data on the free-swimming fish were collected in a large mesocosm (Dalhousie University) with a diameter of 15.24 m, a depth of 3.54 m at the perimeter and 3.91 m at the centre, and a volume $684\ m^3$ held at $11\pm 1.5^\circ\text{C}$. Experiments were conducted over 6 trial-days spanning a month. Each individual fish swim trial lasted between 24 and 30 h with a recovery period of 3–5 days.

Accelerometers

We used two tri-axial accelerometer tag models (Maritime bioLoggers, Halifax, Canada): the cylindrical MBLog PT-1 (hereafter referred to as the ‘large’ tag) and the rectangular MBLog PT-2 (hereafter referred to as the ‘small’ tag) (Table 1). Both tags were set to record tri-axial acceleration at 50 Hz (10-bit resolution) at $\pm 6\ g_0$. Drag coefficients for the tags were determined using the characteristic shape and length given high Reynolds number flow ($Re > 10^4$) (Table 1). For both tags, the ratio between tag and body mass was $< 2\%$ (Table 1).

Swimming experiments

Cod were anaesthetized with MS222 ($40\ \text{mg}\ \text{l}^{-1}$), measured for l and m and permanently tagged using rectangular Petersen Disc tags to which the accelerometer was attached for swim trials. The Petersen discs were attached using two nickel pins, which ensured that the discs were stable and could not rotate (see Broell et al., 2013, for tag attachment details). Fish were randomly assigned a small or large tag (Fig. 1) for each swim trial. Fish swam *ad libitum* with no external stimulus save a natural daylight cycle. Following each trial, the accelerometer was detached and the animals recovered in a holding tank (2.0×2.0 m). At least 22 h of free-swimming data were collected for each individual for a total of 1200 h of data. Data from the same individual carrying the same size tag were combined,

Table 1. Specifications for externally attached large and small tags used in free-swimming trials of Atlantic cod

Tag	Model	Shape	Dimensions (cm)	Mean mass (g)	Tag frontal area (cm^2)	Mean tag load (range) (%)	Drag coefficient	Sample size
Large	MBLog PT-1	Cylindrical	2.3 diameter \times 5.0 length	18.8	4.15	1.1 (0.57–2.1)	0.825	22
Small	MBLog PT-2	Rectangular	2.5 l \times 1.7 w \times 1.1 d	6.1	1.87	0.42 (0.17–1.7)	1.05	20

Mean mass is the mass in air.

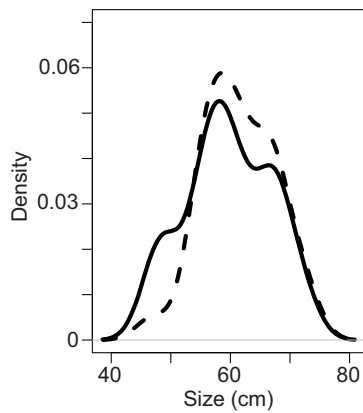


Fig. 1. Probability density function of size distributions of Atlantic cod tagged with small and large tags. Small tags, $N_S=20$, dashed line; large tags, $N_L=22$, solid line.

resulting in $N_D=42$ datasets with $N_S=20$ from fish carrying small tags and $N_L=22$ from fish carrying large tags.

Animal care and sampling protocol for the tagging surgery for this study were approved by Dalhousie University (permit number 12-049) in accordance with the Canadian Council for Animal Care standards.

Extracting scouring from the time series

Scouring movements were characterized by a change in orientation of the tag as the animal rotated on its side to scrape its body along a substrate in the water column. Such movements varied in duration, ranging from short (~ 3 s) to long (10–60 s). Typically, shorter duration movements were characterized by high acceleration while longer duration scouring was characterized by lower maximum acceleration during which the fish continued to beat its tail (Fig. 2). To extract such movements, we made use of the fact that gravitational acceleration (g_0) is recorded by the tag, and when the fish was in its natural vertical (upright) position, gravitational acceleration was recorded in a combination of axes. When the animal rotates laterally (up to 90 deg), the contribution of g_0 to the different axis can be used to measure rotation. For example, if most of g_0 is recorded in the vertical (z) axis, during lateral rotation the contribution of g_0 to the lateral (x) axis increases until all of g_0 is recorded in x , corresponding to a full 90 deg rotation ('roll'; Fig. 2).

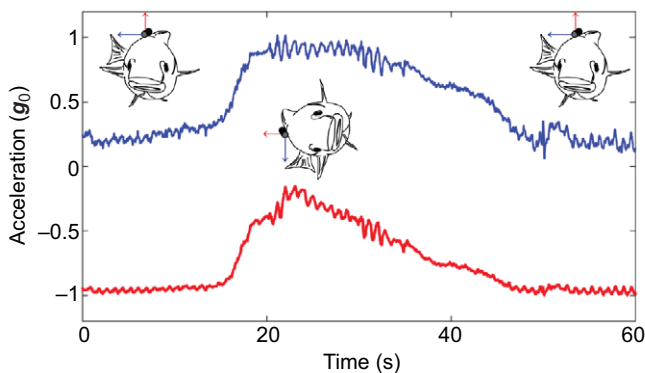


Fig. 2. Illustration of fish movement and associated example of acceleration time series as the accelerometer tag rotates during scouring. When the fish is in the upright position, acceleration (g_0) is measured in the vertical axis (red), and when the fish turns laterally, gravitational acceleration is measured in the lateral axis (blue). The higher frequency variation is the tail beat.

This shift in gravitational acceleration can be used to identify scouring movements. To extract this movement, the algorithm was designed to determine the angle in the $x-z$ plane relative to the long-term average of the mean gravity relative to the tag (Fig. 3). If this angle exceeded the pre-set threshold θ_{Th} , a scouring event was identified. Here, scouring was defined when an animal rotated at least $\theta_{Th}=45$ deg. At the centre of the algorithm is a sliding window of length l_W , with an overlap of 5%. Within each window, the cross-over points (t_{C_i}) between the static acceleration in the x and z axes (Fig. 4) using a zero-crossing approach are established (Kedem, 1986; Stein, 2000; Broell and Taggart, 2015). Static acceleration was calculated by applying a 2 s moving average to the time series (see Shepard et al., 2008; Wright et al., 2014). Each rotation segment C_i within window W was bracketed by time $t_{C_i,1}$ and $t_{C_i,2}$. Within each segment, the angle θ_{C_i} between the acceleration component in the $x-z$ plane and reference alignment (vertical gravity) was calculated. The angle of rotation θ_r within each segment was then calculated by comparing θ_{C_i} with the initial orientation of the tag, θ_{tag} . The largest rotation angle, $\theta_{C_i,max}$, was then compared to the threshold value θ_{Th} . If $\theta_{C_i,max}$ was larger than θ_{Th} , the segment was classified as a scouring movement (e.g. Fig. 5). The beginning and end of the scouring event was then defined by the first and last roll angle to exceed the threshold, thereby bracketing $\theta_{C_i,max}$ within the segment. This algorithm not only allowed for variable tag orientation, and sliding window size, but by adjusting the angle threshold parameter it also allowed for an adjustment to the degree of rotation of interest. By examining the sign of the rotation angle, this algorithm also extracted the directionality of the scouring event, i.e. left-lateral or right-lateral side (Fig. 5C,D).

The sensitivity and specificity of the algorithm was determined using a test data-set composed of a random selection of 10% of the experimental data spanning over 1000 positive scouring events where all windows were visually classified. Accuracy, precision, recall or sensitivity, and F-measure (the weighted average between precision and recall) were calculated as follows:

$$\text{Accuracy} = (\text{TP} + \text{TN}) / (\text{TP} + \text{FP} + \text{TN} + \text{FN}),$$

$$\text{Precision} = \text{TP} / (\text{TP} + \text{FP}),$$

$$\text{Recall or Sensitivity} = \text{TP} / (\text{TP} + \text{FN}),$$

$$\text{F-measure} = (2 \times \text{precision} \times \text{recall}) / (\text{precision} + \text{recall}),$$

where TP, TN, FP, FN signify true positive, true negative, false positive and false negative, respectively.

Other detection methods (e.g. wavelet analysis) could not be used because the energy in the frequency spectrum for scouring (~ 1 Hz) was similar to that of steady swimming (e.g. tail beat frequency of ~ 1 Hz; see Broell and Taggart, 2015).

Statistical analysis

All scouring events were analysed using conventional methods (mean-comparison) using the time spent scouring over the entire time series (hereafter referred to as T_s), maximum lateral acceleration ($a_{max,x}$) and maximum magnitude of acceleration (a_{max}) after correction for gravitational acceleration using a 2 s moving average filter (Shepard et al., 2008; Wright et al., 2014). Parameters were assessed in relation to animal length l (m), tag type (S, small; L, large) and tag load. Tag load was expressed as the ratio between tag mass and fish body mass (tag mass/fish mass $\times 100$).

The energy spent during scouring was also analysed as a function of tag type. While energy expenditure could not be calculated using

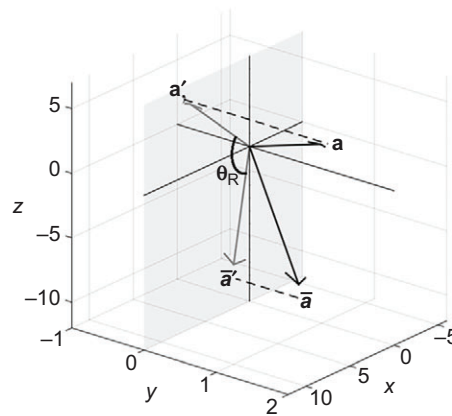
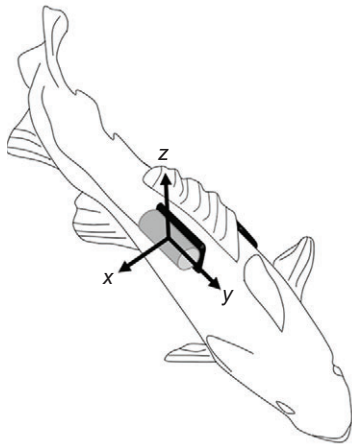


Fig. 3. Visualization of angular roation.

(A) Illustration of accelerometer tag attachment to Atlantic cod. (B) Illustration of angle projection on the $x-z$ plane where \mathbf{a} is acceleration at time t_i , $\bar{\mathbf{a}}$ is the time-averaged acceleration vector (i.e. direction of acceleration when the fish is upright). In this case, the tag is tilted in the positive $x-y$ direction relative to the fish. \mathbf{a}' is the projection of $\bar{\mathbf{a}}$ in the $x-z$ (lateral-vertical) plane, where the fish has rotated ~ 120 deg, with \mathbf{a}' the projection of \mathbf{a} in the $x-z$ plane, and θ is the angle between \mathbf{a}' and $\bar{\mathbf{a}}$. θ_R , angle of rotation.

respirometer calibrations (e.g. Wright et al., 2014), the nearly linear relationship between VeDBA and the rate of oxygen consumption, \dot{M}_{O_2} , in a comparable species (Wright et al., 2014), suggests that the vector norm:

$$\text{VeDBA} = \sqrt{a_x^2 + a_y^2 + a_z^2}, \quad (1)$$

as outlined in Wright et al. (2014), is a valid proxy for energy expenditure. Mean VeDBA was calculated for each scouring event after data were corrected for gravitational acceleration using a moving average filter with a window length of 2 s.

A time series of T_s (\pm s.d.) as a function of experimental day for all fish was calculated and differences between day and night scouring were assessed. Directionality of scouring movement was also assessed to determine whether animals spent more time scouring on the right-lateral side, where the accelerometer tags were attached.

Algorithm computations and statistical analyses were performed using R (v0.98.977, R Foundation for Statistical Computing, Vienna, Austria) and MATLAB R2014b (The MathWorks, Natick, MA, USA). All estimates are provided as means \pm 1 s.d. unless otherwise noted.

RESULTS

Algorithm efficiency

The identification probability for scouring movements in the test data had an accuracy of 98.7%, a precision of 94.2%, a sensitivity of 92.9% and an F -measure of 0.936. This demonstrates that the algorithm was highly effective in detecting and classifying scouring events.

Statistical analysis

Size distributions of fish used for each tag type were not significantly different (Student's t -test, $P>0.05$; Fig. 1) and this allowed us to compare tag types independently of a fish-size effect.

Time spent scouring

T_s ranged from 0 to 20% ($4.2\pm 3.6\%$) and there was no relationship between T_s and tag load (Table 2, Fig. 6A). Tag type was not a significant confounding factor (or interaction) when T_s was regressed against animal size, and animal size did not affect T_s (ordinary least square, OLS, with interaction, $P>0.05$; Fig. 6C). T_s did not differ between tag type (Fig. 6B; Wilcoxon sign rank sum test, $P>0.05$) and T_s was significantly higher during the day (80%) than during the night (20%; Fig. 7). T_s increased significantly from

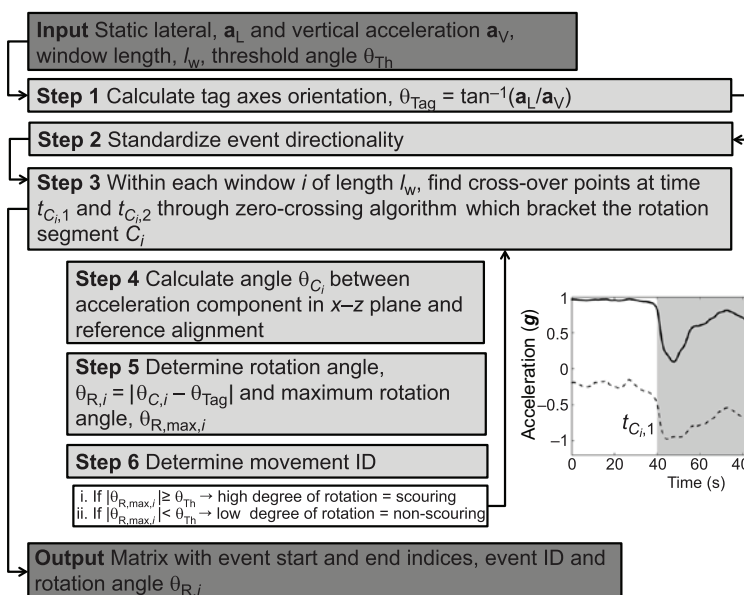


Fig. 4. Flow chart of the extraction algorithm used to extract scouring movements based on angular rotation in the $x-z$ plane. θ_{Tag} is the $x-z$ plane orientation of the sensor on the fish, θ_{Th} is the threshold angle that denotes vertical-lateral rotation (here, $\theta_{\text{Th}}=45$ deg). The rotation angle θ_{C_i} is calculated within the rotation segment C_i , bracketed by cross-over points $t_{C_i,1}$ and $t_{C_i,2}$, which are found through a zero-crossing algorithm (Broell and Taggart, 2015). If the maximum event rotation angle $\theta_{R,\text{max},i} = |\theta_{C_i} - \theta_{\text{Tag}}|$ exceeds θ_{Th} , then scouring movement is identified. The output of the algorithm is a matrix containing start and end indices of events, event ID and the event rotation angle $\theta_{R,\text{max},i}$.

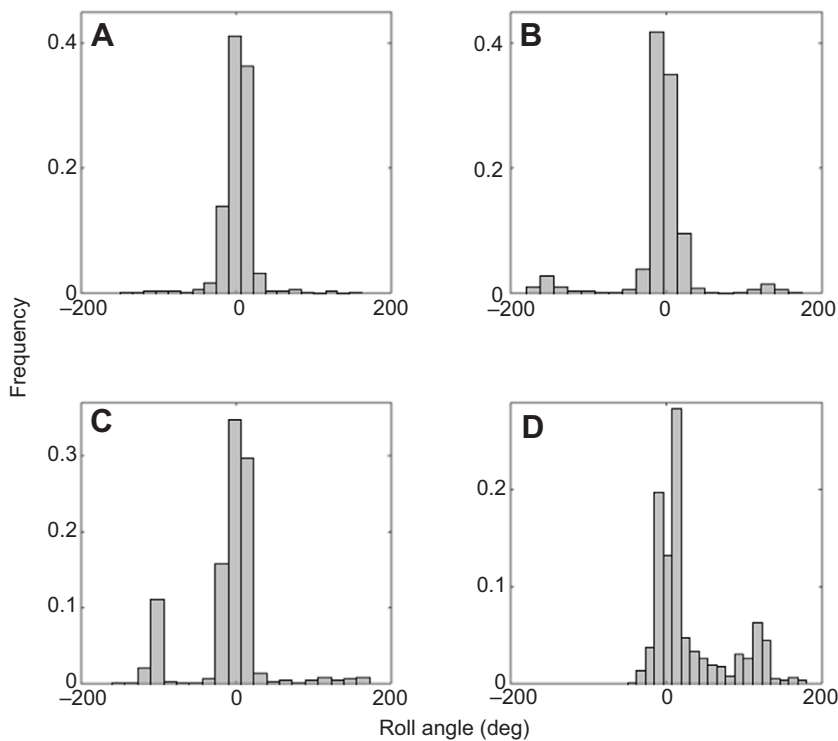


Fig 5. Normalized histogram of roll angles within extracted window segments for four different cod. Fish are shown scouring on both the lateral-left (A) and lateral-right (B) side, and mostly on the left (C) and right (D) lateral side.

an average of 3% to 8% after 6 experimental days regardless of recovery time among experimental days (Fig. 8). On average, fish spent $69.8 \pm 1.7\%$ of scouring time on the right-lateral side where the tag was attached.

Maximum acceleration

Lateral maximum acceleration, $a_{\max,x}$, ranged from 0.05 to $1.63 g_0$ ($0.37 \pm 0.28 g_0$) and the maximum magnitude of acceleration, \mathbf{a}_{\max} , ranged from 0.44 to $2.26 g_0$ ($0.63 \pm 0.46 g_0$). Both parameters were positively related to tag load (log–log OLS, $r^2=0.61$ and 0.70 , respectively; Table 2, Fig. 6D,G). $a_{\max,x}$ and \mathbf{a}_{\max} were significantly greater (Wilcoxon sign rank sum test, $P>0.05$; Fig. 6E,H) for fish tagged with large tags ($0.52 \pm 0.29 g_0$ and $0.94 \pm 0.43 g_0$, respectively) than for those tagged with small tags ($0.20 \pm 0.10 g_0$ and $0.21 \pm 0.28 g_0$, respectively). Animal size did not affect either parameter (OLS with interaction, $P>0.05$; Fig. 6F,I).

Proxy for energy expenditure

VeDBA was positively related to tag load (log–log OLS, $r^2=0.51$; Table 2, Fig. 9A), with large tags displaying significantly higher VeDBA during scouring movements ($P<0.05$). VeDBA was

independent of fish size ($P>0.1$; Fig. 9C). When VeDBA was compared within individuals during times when they were tagged with a small versus large tag, VeDBA was higher for fish tagged with large tags in more than 80% of cases. Of those where VeDBA increased, the increase varied amongst individuals with an average of 62% and a range of 26% to 88%, confirming an increase in VeDBA with tag load across individuals.

DISCUSSION

Based on high-frequency acceleration data, we have developed an algorithm to detect and identify rotational movement in the lateral–vertical plane of fish that is associated with a variety of behaviours; the algorithm has a high efficiency, with 98.7% accuracy and 94.2% precision. The efficiency was achieved by a relatively simple algorithm based on the rotation of the three-dimensional coordinate system of the tag given the orientation of the animal. Not only is this algorithm independent of tag attachment and orientation, it also can be easily modified to identify and differentiate various degrees of rotation through the adjustment of the input cut-off threshold. Furthermore, a rotation in a different plane (e.g. forward–vertical) could easily be implemented to extend the algorithm’s applicability to identify various aberrant swimming behaviours among other species, i.e. those deviating from steady continuous swimming (e.g. Broell and Taggart, 2015), such as similar erratic swimming observed with other behaviour-associated movements as a modal action-pattern in at least 81 fish species (Wyman and Walters-Wyman, 1985). For example, cichlids (*Entropus* spp.) incorporate scouring as a means of courtship and pair formation (Wyman and Walters-Wyman, 1985), ludericks (*Girella tricuspidata*) rotate when feeding on seagrass epiphytes (Matthew Taylor, New South Wales Department of Primary Industries, Australia, personal communication), and various salmonids exhibit comparable swimming patterns when building spawning redds (Evans, 1994; Esteve, 2005). Despite the widespread observations of this behaviour, there remains a lack of evidence that explicitly examines rotational

Table 2. Relationship between tag effect (tag mass/body mass) and response parameters

Response	Intercept	Slope	<i>P</i> -value	<i>r</i> ²	<i>N</i>	Model type
T_s			0.96	0	42	Linear
$a_{\max,x}$	2.82 ± 0.51	0.79 ± 0.10	<0.05	0.61	42	log–log
\mathbf{a}_{\max}	4.1 ± 0.50	0.94 ± 0.10	<0.05	0.70	42	log–log
VeDBA	0.71 ± 0.43	0.50 ± 0.08	<0.05	0.51	42	log–log

T_s , percentage of time spent scouring; $a_{\max,x}$, maximum lateral acceleration; \mathbf{a}_{\max} , maximum magnitude of acceleration; and VeDBA, vector of the dynamic body acceleration (a proxy for energy expenditure).

Intercept or proportionality constant, slope or exponent is provided (mean \pm s.d.) if the predictor is significantly different from zero, with *P*-values from ordinary least squares.

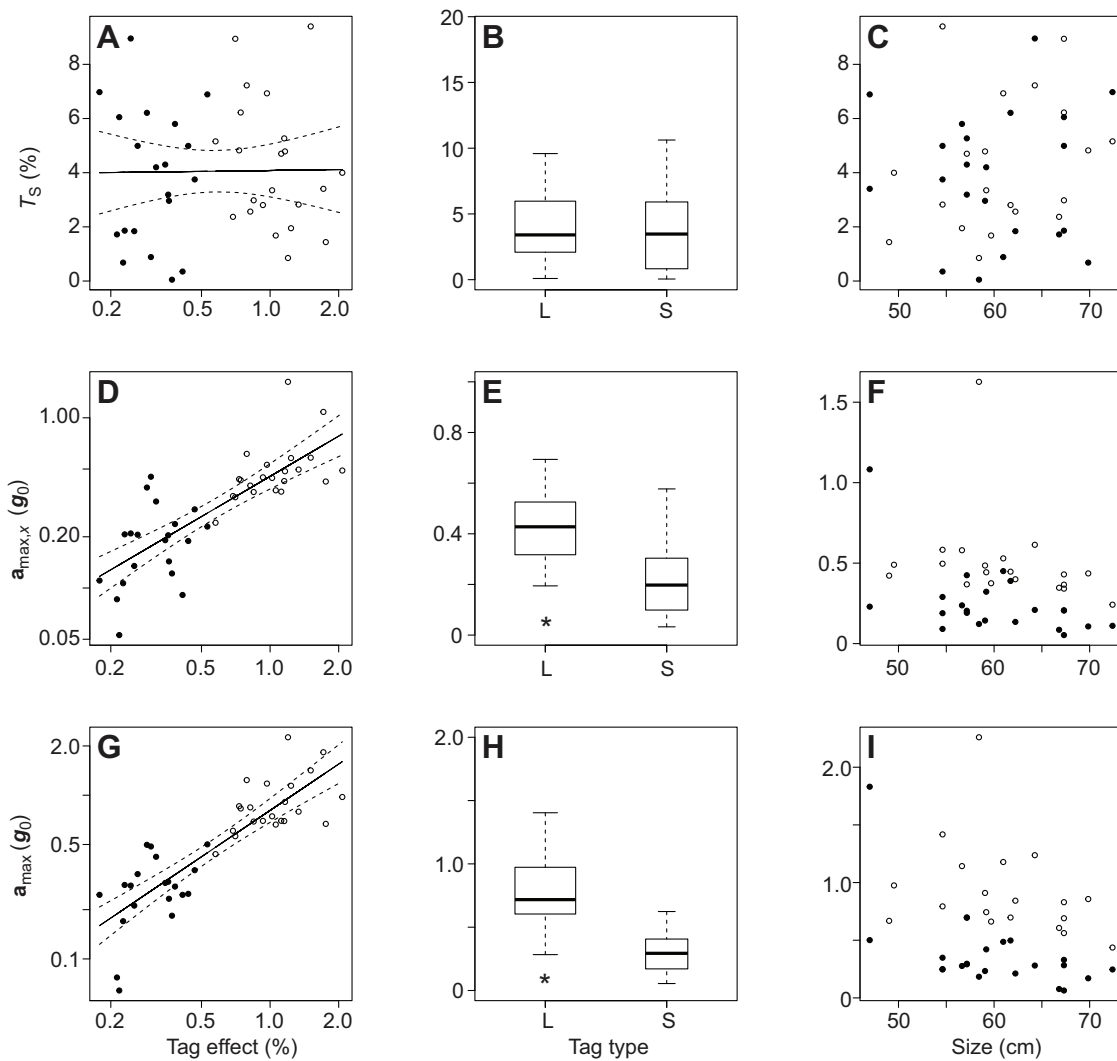


Fig. 6. Summary of acceleration parameters as a function of tag effect. Percentage time spent scouring (T_s), maximum lateral acceleration ($a_{max,x}$, g_0) and maximum acceleration norm (a_{max} , g_0) as (A,D,G) a function of tag effect expressed as percentage tag mass/fish mass, (B,E,H) box and whisker plots illustrating differences between tag type (L, large; S, small) and (C,F,I) a function of fish size. In all panels, open circles represent the large tag, filled circles represent the small tag. For box and whisker plots, the box illustrates the inter-quartile range (IQR), the bar the median and the whiskers ± 1.5 IQR.

swimming among fish species (Wyman and Walters-Wyman, 1985). Therefore, the algorithm not only allows for the identification of a behaviour specific to scouring but also can potentially be applied to acceleration data collected from similar movements associated with

parasite load, spawning, courtship or feeding and foraging in the wild.

By changing the threshold angle (θ_{Th}), the algorithm can easily be adjusted to detect and identify different degrees of rotation and

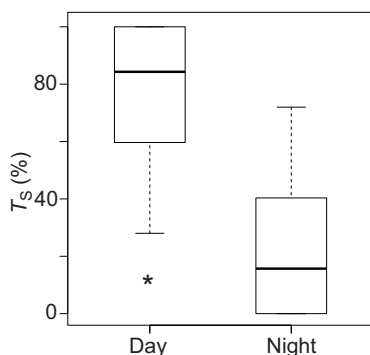


Fig. 7. Box and whisker plot of T_s during daytime versus night-time. The box illustrates the IQR, the bar the median and the whiskers ± 1.5 IQR.

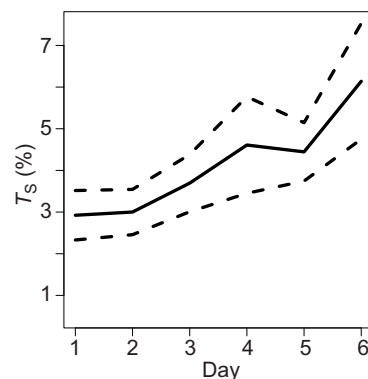


Fig. 8. Trend in T_s over the 6 day trial period for all fish. The solid line is the mean and the dashed lines are 95% standard errors around the mean.

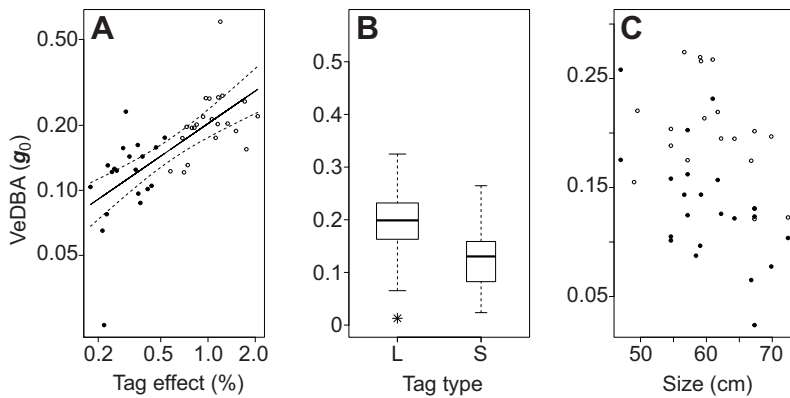


Fig. 9. VeDBA as a proxy for energy expenditure. VeDBA is shown as (A) a function of tag effect (% tag mass/fish mass), (B) box and whisker plots illustrating differences between tag type (L, large; S, small) and (C) a function of fish size. In all panels, filled circles represent the small tag, open circles represent the large tag.

therefore the classification of movements associated with various behaviours beyond scouring, such as above. Furthermore, the algorithm is robust and both input parameters (window overlap and window length) have little effect on algorithm efficiency (<1%). As the initial orientation of the tag on the animal (i.e. the angle between the lateral and vertical axis in the frame of reference of the acceleration sensor) is incorporated in the design of the algorithm, constant tag orientation amongst individuals or even within a single individual is not essential. It is further possible to determine the scouring direction (clockwise or anticlockwise) by using the sign of the rotation angle and thereby delivering even more fine-scale behavioural information.

Usability

Typically, accelerometer measurements do not provide rotational information such as angular velocity and the direction of movement. A gyroscope can directly measure angular velocity, and if the initial attitude is known, any new attitude achieved through rotational movement can be estimated using the attitude change calculated from the gyroscope measurements (Noda et al., 2013). Therefore, a gyroscope sensor could easily and directly measure rotations in any plane. However, because of battery and tag-size constraints, tags are frequently deployed with a single sensor, and accelerometers are typically preferred over gyroscopes. Accelerometer sensors not only deliver crucial information, such as a proxy of energy expenditure and behaviour, but also draw less power than gyroscopes. For example, a sensor chip commonly used in biologging tags (InvenSense MPU-9250 2015, <http://store.invensense.com/datasheets/invensense/MPU9250REV1.0.pdf>) with a typical operating circuit in the 3-axis gyro mode requires a supply of 3.2 mA, while in the 3-axis accelerometer mode it requires 0.45 mA – nearly 7-fold less at the same operating supply voltage. This is especially important for data-logging applications in fish, where tag size, which is a direct function of battery size and power consumption, is severely constrained by fish body size. Here, we have shown that rotational movement can be well identified using the tri-axial acceleration signal without the use of a gyroscope sensor and can be of considerable value in studies where only accelerometer tags are deployed.

Tag effect

Energetic consequences of tag load: chronic and acute effects

Reduced swimming performance of tagged fish has been observed in various salmonids (Greenstreet and Morgan, 1989; McCleave and Stred, 1975) and perciformes (Mellas and Haynes, 1985; Ross and McCormick, 1981). However, <2% tag load (i.e. tag mass/body mass; Winter, 1996) is often assumed to not significantly affect swimming ability and behaviour. Despite adhering to the 2% tag-

load rule, we found that all tagged animals spent a significant amount of time scouring – a behaviour often observed in Atlantic cod to dislodge parasites (Jeffrey Hutchings, Department of Biology, Dalhousie University, personal communication). Our findings indicate that there may be more fine-scale effects of tag load that have not yet been considered given traditional metrics such as tag retention and survival (e.g. Ross and McCormick, 1981; Greenstreet and Morgan, 1989; Barrowman and Myers, 1996; Björnsson et al., 2011; Cooke et al., 2012). Another important point to note is that despite a ‘small’ tag load of less than 2%, significant tag effects were observed, including some individuals that spent up to 20% of their time scouring. The total time the animals spent scouring was independent of tag load and this indicates that lower tag load does not necessarily result in reduced tag effect. The acute cost and physical damage that is caused by scraping the body to dislodge the tag can damage skin and provide the opportunity for secondary infections to occur. Secondary infections can affect animal behaviour and can have energetic consequences, and affect growth rate, reproductive performance and survival (Barber et al., 2000).

The chronic cost is the cost to the animal due to energy expenditure associated with added drag as well as tag load. While individual fish exhibited high variability in scouring behaviour and associated VeDBA, generally, fish that carried a tag with a higher tag to body mass ratio exhibited higher lateral and full-body acceleration during such scouring movements, which implies that they used more energy when attempting to dislodge a larger tag. Specifically, VeDBA increased 5-fold when tag load (related to body mass) was doubled from 1% to 2%. Subsequently, these fish exhibited significantly higher maximum lateral acceleration, $a_{\max,x}$ and whole-body acceleration, a_{\max} . Therefore, the scouring force, F_d , exhibited must be higher, as:

$$F_d \propto ma_{\max}, \quad (2)$$

where m is fish body mass, and this naturally leads to an increase in energy expenditure (Videler, 1993).

The strategy for allocation of energy is an important contributor to physiological (e.g. oxygen consumption and heart rate) and behavioural (e.g. reproduction, foraging) ecology (Clark et al., 2010) and growth. An increased energy expenditure associated with a tag-shedding response in fish could result in reduced reproductive rates, growth rates or survival.

Tag load confounding factors

For aquatic organisms with the capability to regulate buoyancy through swim bladders (or lungs), the effect of tag load, as the mass

of the tag and fish in air, is negligible in comparison to the drag coefficient, frontal area and increased drag (Jones et al., 2013). Our results are confounded by other factors beyond just tag weight, given the large difference in tag frontal area (5.14 cm² versus 1.87 cm²) as well as tag length and shape, which affect the friction drag. Thus, tag load expressed as a percentage of body weight does not reflect the true tag load. In an attempt to disentangle mass and other tag effects, we separated tag types and examined for each the effect of tag-to-fish frontal area ratio (tag frontal area/fish frontal area) within tag type (mass term disappears). While the increase in the parameters (a_{\max} , \mathbf{a}_{\max} , VeDBA) persists within tag type, the amount of explained variation was marginal, indicating that other factors (mass, buoyancy, etc.) are likely to be involved. Given the strong correlation between tag load expressed as weight and tag load expressed as frontal area ($r^2=0.9$), as a result of the same aspect ratio, the experimental design did not allow us to disentangle the underlying effects that are responsible for the observed pattern in increased a_{\max} , \mathbf{a}_{\max} and VeDBA. However, it remains the case that the 2% body rule may not be a valid metric given the other variables that affect tag burden (tag buoyancy, shape, friction, etc.), and even if the percentage mass load is small, the effect on the animal as a result of the confounding factors may be high. Furthermore, the time spent scouring in our study was clearly independent of tag mass or tag frontal area, which, in turn, suggests that the observed effect of tag burden is likely attributable to irritation, rather than tag properties, and there is no simple means of assessing irritation.

Additionally, externally attached tags have been shown to influence the hydrodynamics around the fish and can lead to decreased swimming performance and associated energy expenditure given increased frictional drag and flow resistance (Arnold and Holford, 1978; Ross and McCormick, 1981; Mellas and Haynes, 1985; Bridger and Booth, 2003; Jones et al., 2013; Janak et al., 2014). An increase in drag causes a proportional increase in power output of the tagged animal, described by:

$$\begin{aligned} P &= \mathbf{F}_d u \\ \text{or} \\ P &\propto c_d u^3, \end{aligned} \quad (3)$$

where c_d is the drag coefficient and u is swimming speed (Jones et al., 2013). Therefore, increased drag requires an increase in power output by the animal at constant speed (Jones et al., 2013). For example, for a 73 cm fish ($c_d=0.01$; Blake, 1983) swimming at 1 m s⁻¹, a first principle approximation of the drag force:

$$\mathbf{F}_d = 0.5\rho u^2 c_d A, \quad (4)$$

where A_f is the cross-sectional area of the tag and ρ the density of the water, reveals that \mathbf{F}_d increases from 1.24 N for the small tag ($c_{d,S}=1.05$, $A_{f,S}=0.00027$ m²) to 1.26 N for the large tag ($c_{d,L}=0.825$, $A_{f,L}=0.00038$ m²). This incremental drag increase is nearly independent of tag size, because the difference in theoretical drag from the tag is negligible compared with drag from fish of different sizes (cm) ($\mathbf{F}_{d,25\text{ cm}}=0.13$ N, $\mathbf{F}_{d,42\text{ cm}}=0.36$ N, $\mathbf{F}_{d,73\text{ cm}}=1.1$ N at 1 m s⁻¹). Therefore, an increase in animal size will probably not be able to mitigate drag effect of the tag. While here, only energetic consequences of tag-load reducing behaviour were investigated, the added drag due to tag load would probably increase the estimated energy expenditure during routine swimming movement and exacerbate the overall energy expenditure. Arnold and Holford (1978) suggest that a tag of similar drag coefficient ($c_d=0.6$) only

increases total drag by 5–7% in Atlantic cod during routine swimming. In their calculations, the authors did not observe or quantify scouring movement because experiments were conducted in a flume and not on free-swimming fish. This potentially leads to an underestimated tag effect. Given the tags in this study, and based on the ratio between tag drag:

$$\mathbf{F}_d = A_f c_{d,S} \quad (5)$$

and animal drag:

$$\mathbf{F}_d = A_w c_d, \quad (6)$$

where A_w is the wetted surface area of a fish, the increase in drag for a 73 cm fish would be 12% and 13% for the small and large tag, respectively, much higher than in Arnold and Holford (1978) for the same sized fish (1%). Because the cross-sectional areas of the tags used here are 3–4.5 times larger and drag coefficients are significantly higher, the estimated added drag is higher. While this increase may not significantly affect swimming ability (Arnold and Holford, 1978; Cooke, 2003), given our findings that relate to scouring behaviour, tag effect studies that only investigate added tag drag may underestimate tag effect.

Given our observations, a decrease in tag load (even below the 2% body rule) may be able to counteract the chronic costs associated with increased energy expenditure during scouring movements and drag; however, acute costs associated with physical damage will probably be constant because they are independent of tag load. This is a significant result, as generally a decrease in tag load has been assumed to lead to a decrease in tag effect, but there is no means of decreasing irritation, and this suggests external tagging will always incur a cost.

Diurnal patterns

Cod spent a significantly greater amount of time scouring during the day (80%) than during the night (20%) and exhibited preferential scouring on the right-lateral side where the tag was attached, suggesting that they experience the asymmetry in the tag load. Typically, if a single-sided load is attached to a buoyant normally upright object (e.g. a submarine), it creates a rolling movement because the weight and drag are not equally distributed and neutral, causing an angle of list and/or angle of loll – referred to as the trim or ballasting problem. As it is only during the day that cod, a visual predator and schooling species, experiences sufficient light for visual referencing of its position (dispersed versus aggregated; Brodeur and Wilson, 1996; Axenrot et al., 2004), we assume that only then do they have a substrate reference for scouring. It is equally possible that it is only during the day that the angle of tilt caused by the asymmetrical tag load is apparent to the fish and therefore they try to compensate (Webb, 2002) and/or remove the load. If it is indeed related to the angle of list and/or the asymmetrical load, it becomes essential that tag load (external or internal tags) is mounted symmetrically around the centre of gravity and possibly the centre of buoyancy, though the latter is probably much more difficult to achieve with a physostomous fish.

Validity of data in the field

Many studies now use implanted tags (Bridger and Booth, 2003; Cooke et al., 2004) because they have a variety of advantages such as higher tag retention, reduced biofouling, and reduced added drag that may affect swimming ability, and thus survival rates (Bridger and Booth, 2003). However, in certain environments and experimental settings, external tags are necessary (Cooke, 2003;

Johnson et al., 2015) though they are not always ideal (Methling et al., 2011; Tudorache et al., 2014). This is especially true for pop-up satellite tags (PSAT), which have significant effects of added drag to the body (Bridger and Booth, 2003; Methling et al., 2011; Tudorache et al., 2014). Others (e.g. Thorstad et al., 2000; Cooke, 2003) did not observe adverse short-term effects of tags with a similar tag load for fish that, unlike cod, spend little of their time on the bottom (e.g. salmon, except when spawning), and rolling behaviour was not observed in either case. Similar observations on shortnose sturgeon (Collins et al., 2002) have shown that these animals ‘occasionally’ scrape the substrate, causing eventual tag loss. Other research using similar tags and attachment methods (Broell and Taggart, 2015) on saithe (*P. virens*) did not show a similar behavioural reaction to tag load, but these animals are pelagic species and did not exhibit scouring as observed in cod. Consequently, scouring may be species specific and more apparent in species associated with a benthic habitat.

Effect of missing scouring events

The identification of scouring movements is crucial not only to determine potential tag effects but also to differentiate such behaviour from routine swimming movements and other behaviours (e.g. feeding, migration, etc.). If such movements are overlooked or misidentified, energy and activity budgets and related physiological estimates may be compromised. This is especially crucial given that some algorithms that are designed to identify burst acceleration movements associated with a feeding or escape response (Broell et al., 2013; Noda et al., 2013, 2014) are based on comparing the variance amongst lateral and vertical or forward acceleration within movements. During scouring movements, fish also exhibit burst acceleration characterized by higher variance between the lateral and vertical axis when compared with other behaviours and therefore could easily be misidentified as a feeding or escape response. To ensure the identification of such events, it is also crucial to ensure sufficient accelerometer sampling frequency: scouring movements, similar to feeding and escape responses in other fish (Broell et al., 2013), can occur over short time scales (<1 s), and if sampling frequency is too low (<10 Hz), such movements may be overlooked or misidentified due to aliasing (Broell et al., 2013). This too could lead to compromised estimates of energy expenditure, but, more importantly, a failure to challenge the assumption that the effect of the tag on behaviour and survival of the fish is minimal. Only by quantifying that tagging activities have little effect on animal welfare and behaviour can data from such tags be used to make predictions on routine behaviour and movement (McMahon et al., 2013).

Algorithm as parasite indicator with internally attached tags

Demersal fish such as Atlantic cod have been observed to dislodge parasites (Barber et al., 2000; Øines et al., 2006) by scraping their lateral side along the bottom substrate. Documenting the functional significance of scouring with respect to parasite load is particularly important for cod (and salmon) given their increasing economic value in aquaculture production (Lysne et al., 1994), which can be compromised by external parasite infestations (Øines et al., 2006), and thus monitoring such behaviour becomes diagnostic. Infections in cod can induce altered time allocations for foraging and reproduction, reduced swimming performance, increased energy expenditure and changes in habitat selection, which may have implications for anti-predator behaviour, growth and ultimately survival (Barber et al., 2000; Jones and Taggart, 1998). While in this study the externally attached tags elicited a response in cod that is

similar to parasite infestation, if accelerometer tags were attached internally and symmetrically, they would probably not elicit scouring behaviour and all scouring movements recorded would then relate to parasite infection. Such data could be used to quantify a response to parasitic infections and the onset of disease. Beyond diagnosing parasitic infections in species such as cod, this would prove especially useful in identifying disease, given most fish species lose equilibrium in advanced stages of disease, which is exhibited by lateral–vertical rotations due to loss of balance (e.g. whirling). In an aquaculture setting, this could help in diagnosing infected fish, by monitoring parameters studied here such as the percentage time spent scouring or loss of equilibrium, and when an individual exceeds a predetermined threshold it could then be removed to help contain the infection. This would be useful given the continuous advancement in miniaturization and low-cost sensor and telemetry applications that would allow for large-scale direct observations and an *in situ* diagnostic of infection.

Limitations

Dorso-lateral rotations as observed during scouring may also occur during other movement-associated behaviours such as feeding, courtship and spawning. Given the design of the algorithm we provide, it would be difficult to differentiate among different rotational behaviours if they occur in the same movement ($x-z$) plane and to the same degree. Fish that were observed in this study did not exhibit other rotational behaviours that could confound the classification. For field or aquaculture applications, the algorithm would have to be optimized to account for other burst acceleration movements based on statistical parameters that are capable of differentiating among different behaviours (feeding, escape, scouring).

In this study, it was not possible to collect direct measurements of energy expenditure through conventional techniques (e.g. calorimetry, Walsberg and Hoffman, 2005; or \dot{M}_{O_2} , Clarke and Johnston, 1999) because of the need to collect data from free-swimming fish. However, given past research, it is reasonable to assume that the dynamic body acceleration, VeDBA (Wright et al., 2014; Gleiss et al., 2010), can be used as a proxy for energy expenditure, as it is assumed to be proportional to energy expenditure. While this proxy is useful in determining relative changes in energy expenditure, it does not allow us to make deductions on ‘real’ energy expenditure (e.g. \dot{M}_{O_2}). While the use of this proxy may be a debatable approach (see Noda et al., 2013), especially when comparing across individuals, it is reassuring to find that when VeDBA was compared within individuals during times when they were tagged with a small versus large tag, VeDBA was higher for fish tagged with large tags in more than 80% of cases. Of those where VeDBA increased, the increase varied amongst individuals, with an average of 62% and range from 26% to 88%, confirming an increase in VeDBA and probably associated energy expenditure with tag load.

Conclusions

Reduced swimming performance of tagged fish has been observed in various salmonids (Greenstreet and Morgan, 1989; McCleave and Stred, 1975) and perciformes (Mellas and Haynes, 1985; Ross and McCormick, 1981). However, the effects of tagging are typically not addressed, and there are few studies that have quantified fine-scale post-tagging behavioural responses in fish. This study has shown that even if relatively small tags (<2% body mass) are used on fish, there are significant effects on behaviour and probably associated energy expenditure. To further quantify the effect of external tags,

assessing specific drag of the external tag is important. The results of this study have potential implications for the nature of tag deployments in the wild where external attachment methods are used. Based on the observations here, it may be worth considering additional factors when determining tag load and type, especially for demersal fish associated with the benthic environment and species where a history of parasite load reducing behaviour is known.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

C.T.T. conceived of and secured funding for the research. F.B. and C.T.T. each contributed to the design and execution of the experimental studies. F.B. helped design the accelerometers, F.B. and C.B. conducted the analyses and prepared the manuscript with help and advice on writing and interpretation of the results from C.T.T. All authors agreed on the form and content of the manuscript for publication.

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