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Title: From “where” and “when” to “what” and “why”: archival tags for monitoring “complex” behaviours in fish.

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Abstract: Understanding the movements (“where” and “when”) and behaviour (“what” and, hopefully, “why”) of individuals and populations is key to answering fundamental questions in fish ecology. The use of archival tags in telemetry studies of marine fish have, by and large, involved recording “simple” measurements of variables such as pressure (giving depth), temperature and light over extended timescales. These have then been used to provide information about location and movement of individuals. However, our understanding of more complex behaviours (i.e. what fish are doing as different from spatial movements) has usually been inferred from movement data because it has not been possible to record directly specific behavioural events such as feeding or spawning. This is because the events are usually infrequent, irregular and often quite brief and so not amenable to a technology based on taking regular but infrequent records of continuously available variables. The recent implementation of new sensors (e.g. physical movement, tri-axial accelerometers), rapid (< 30 Hz) sampling capabilities, enhanced memory and more complex data capture protocols has led to the development of archival tags that can be used to detect and record complex behaviours such as feeding and spawning. We describe recent developments with archival tags and their use to monitor feeding and spawning in fish together with the application of tri-axial accelerometry that can be used to quantify behaviour and metabolic rate. These can then be used to assess the cost of behaviours with a view to understanding how appropriate they are as responses to environmental variability.

Keywords: telemetry, behaviour, data storage tag

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Introduction

A key driving force in the development of marine fish telemetry over the past three to four decades has been the need to observe the movements and behaviour of free-ranging animals in their natural environment (Metcalf et al. 2002; Ropert-Coudert and Wilson 2005). Although there is a range of devices currently available that measure and record "simple" environmental variables such as temperature, pressure (to give depth) and ambient daylight that can be used to describe horizontal and vertical movements, few devices are able to provide information about more complex behaviours, such as feeding or spawning or integrated measures of activity that can be used to quantify behaviour and metabolic rate.

This is because specific behavioural events are usually infrequent, irregular and often quite brief and so not amenable to a technology based on taking regular but infrequent records of continuously available variables. Here we describe recent developments in archival tag technology that attempt to fill this gap. We present results that show it is possible unambiguously to detect more complex behaviours like feeding and spawning and we consider new challenges that such devices present in terms of data sampling and processing.

Tag developments 1: Feeding

Feeding affects growth, survival and reproductive success of marine fish (see Wootton 1990) and is therefore a fundamental aspect in studies of fish ecology (see Gerking, 1994) and a key parameter in models of population and ecosystem dynamics (Daan 1987; Magnússon 1995). If a preferred prey is scarce, a predator may be able to survive extended periods without feeding (Love 1980), but enforced starvation will reduce growth and fecundity, compromising survival and contribution to future generations. To avoid this, a predator may switch to feed on a different prey, or may move to another locality in order to find the preferred prey. Results from electronic tagging studies carried out with Atlantic cod (*Gadus morhua*), a predatory fish, show that levels of activity differ between seasons, and those seasonal patterns of activity differ between environments (Righton et al. 2001). It is likely that these differences in activity reflect differences in foraging behaviour but, without direct measurements of feeding, it is not possible to identify how the differences in behaviour in space and time relate to differences in feeding success. Measuring feeding behaviour in the wild is therefore an important factor in understanding the mechanisms driving the movements, migrations and habitat use of predatory marine fish (Heithaus et al. 2002). However, obtaining the necessary information is difficult because of the problems associated with monitoring feeding behaviour in the wild over seasonal, let alone annual, time scales.

In attempting to quantify feeding, analysis of stomach samples can be useful, but is limited because it only provides information about what a predator has eaten at specific locations and times (Polunin and Pinnegar 2002); it does not provide behavioural time series data about when and where feeding occurs. Stomach sampling methods can also be biased due to difficulties in identifying different prey items and differential digestion rates for different prey types, and problematic because many fish predators only feed intermittently and may regurgitate food on capture (Staniland et al. 2001). Analysis of tissue samples using stable isotopes, body lipids etc. provides broad information about who eats whom (Fry 1988; Owens 1987; Post 2002) and can highlight changes in diet over the course of a fish's life, but is limited in providing detailed information about temporal and spatial patterns in feeding activity.

To monitor feeding events directly, we have developed an archival tag suitable for free-ranging fish to monitor feeding activity of cod (Metcalf et al 2009). Cod feed by aspirating food into their buccal cavity by a rapid opening of the mouth. Our approach has been to develop a device that monitors jaw movements, and hence feeding, and is based on the design of the inter-mandibular angle sensor (IMASEN) described by Wilson et al. (2002) for use with penguins and by Hochscheid et al. (2005) for use with sea turtles. The IMASEN detects jaw movements by monitoring the relative movement between a small, powerful disc magnet and a Hall-effect magnetic field sensor. Our aim has been to develop a device that will be able to monitor the frequency and pattern of feeding of cod in the wild over seasonal timescales in relation to location, environmental conditions, and geographical movements.

Cod possess a semi-protrusible jaw and initial studies of the articulation of the jaw apparatus indicated that the movements of the maxilla are slight when the fish is only ventilating, but rapid and extensive during feeding. We therefore concluded that the most effective location for the movement sensing system would be with the magnet attached to the caudal end of the maxilla, and the magnetic field sensor at the angle of the jaw at about 5 mm from the magnet. We anticipated that this arrangement should give a good dynamic performance and a high probability of distinguishing feeding from ventilation.

Jaw movements were measured by monitoring the relative movement between a small (3 mm * 2 mm), powerful Neodymium disc magnet and a Hall-effect magnetic field sensor. The output of the Hall-effect sensor was recorded using a modified Cefas G5 data storage tag (Cefas Technology Limited). The operating range of the sensor depends on the field strength of the magnet. When used with a 3 mm magnet (in feeding trials), the sensor had a useful operating range of up to about 10 mm. With larger magnets (e.g. 9 mm diameter * 3 mm used in spawning trials) the useful operating range increased to about 30 mm.

The sensor package was about 23 mm * 6 mm * 4 mm, the lead was 2 mm in diameter (the lead length depended on size of fish). To improve biocompatibility, the sensor was embedded in a thin silicon rubber coat and the leads ran through thin-walled silicon rubber tube. The tag case was 19 mm dia. * 90 mm and fabricated from polycarbonate. The complete tag weighed about 36 g in air (depending on lead length) and about 6 g in seawater. These prototypes were designed to be re-usable and so were air-filled and have replaceable batteries. As a consequence, the tag was about twice the size that has been subsequently achieved with solid-potted devices.

The tag is also equipped with 2 terminals that allowed it to be connected to the host software on a PC. This is necessary for the initial setting of the logging regime, but also allows the sensor gain and offset values to be adjusted to optimise performance once the sensor and magnet were in place in the fish but before the body of the tag was attached or implanted. In this study, we did not attempt an absolute calibration of the sensor *in situ* (i.e. determine signal strength generated by measured jaw movement). Instead we ensured that jaw movements of a magnitude judged to be similar to those expected during ventilation provided sufficient signal that they could be readily detected. In subsequent analysis, jaw movements (speed and amplitude) during coughing, yawning, feeding etc. could then be expressed in relation to ventilation movements. This provides a method for "scaling" jaw movements "*in situ*" that could accommodate small variations in signal strength during deployment as a consequence of slight movement of either the magnet or sensor

The feeding trials were carried out at the Cefas Laboratory in Lowestoft in 2005/06. Details of the tag and sensor implantation methods and subsequent feeding experiments are given in Metcalfe et al. (2009), here we provide the key results from these studies.

Recovery and onset of feeding

We have so far successfully instrumented 5 cod. All fish recovered successfully from the surgery. In one fish, the sensor became dislodged after 5 days and the study was terminated. Of the other 4 fish, jaw movements were successfully recorded up to 14, 16, 16 and 22 days following surgery, respectively.

Jaw movements

Jaw movements (at least ventilation movements, and "yawns" and "coughs" when they occurred) were recorded in all 5 fish, at least for the first few days of the trial. Only one fish resumed normal feeding during the period of the trial, but numerous feeding events were successfully recorded from this individual. In this preliminary description of results, we present and have analysed a small number of representative examples of various types of jaw movement. In this we have expressed the amplitude and speed (expressed as the first difference in the sensor data time series, i.e. the absolute difference between successive sensor output values) of jaw movements in relation to those observed during normal ventilation in the same individual during each logging period.

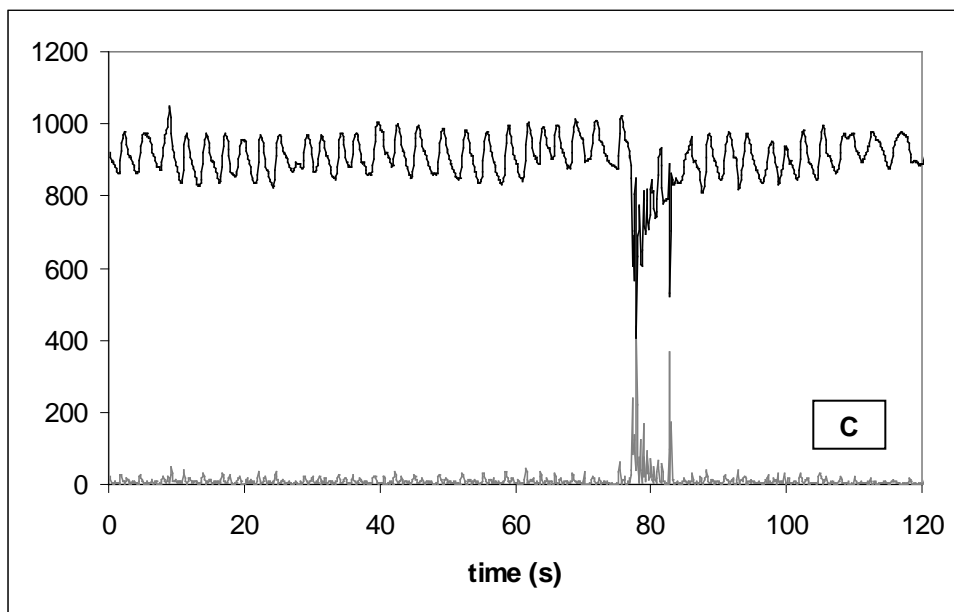
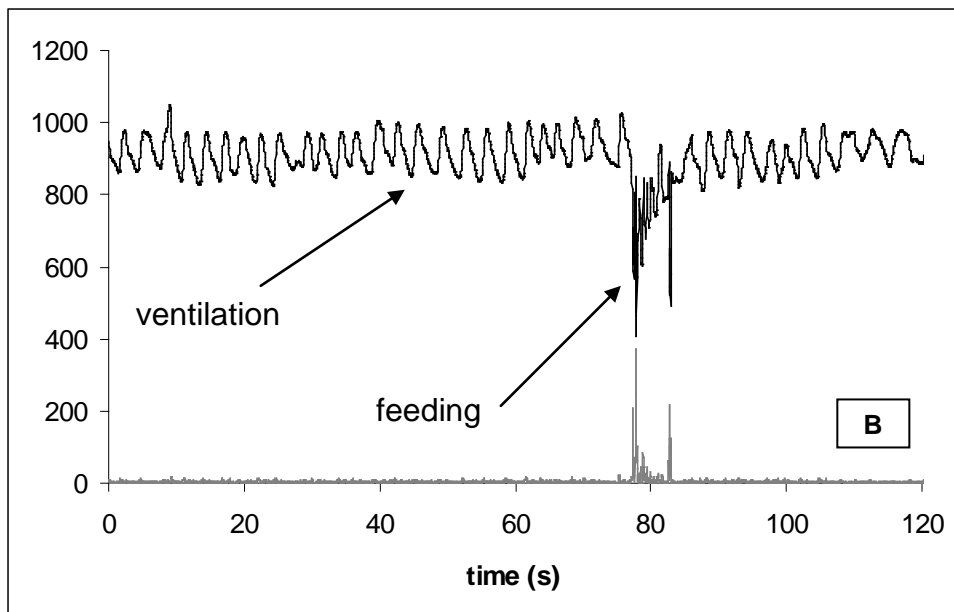
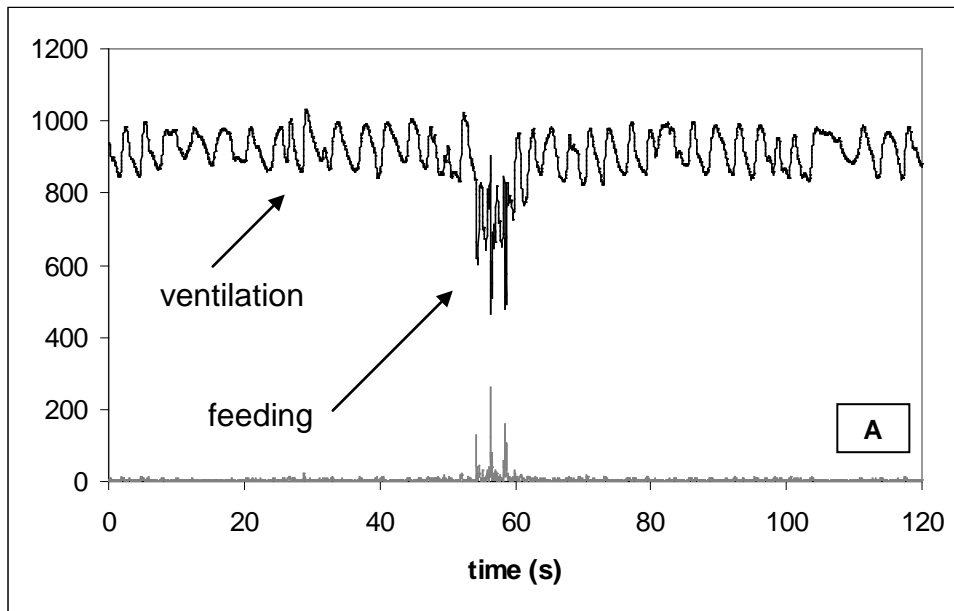


Figure 1. Two examples (a & b) of jaw movements during normal ventilation and feeding on single sandeels (data logged at 30 Hz). Fig. c is the same feeding event presented in Fig. b, but with the data resampled at 10Hz. The upper black line in each figure is the raw time series data; the lower grey line is the first difference in the sensor data time series, i.e. the absolute difference between successive sensor output values (Metcalf et al, 2009). The y-axis gives arbitrary sensor output values.

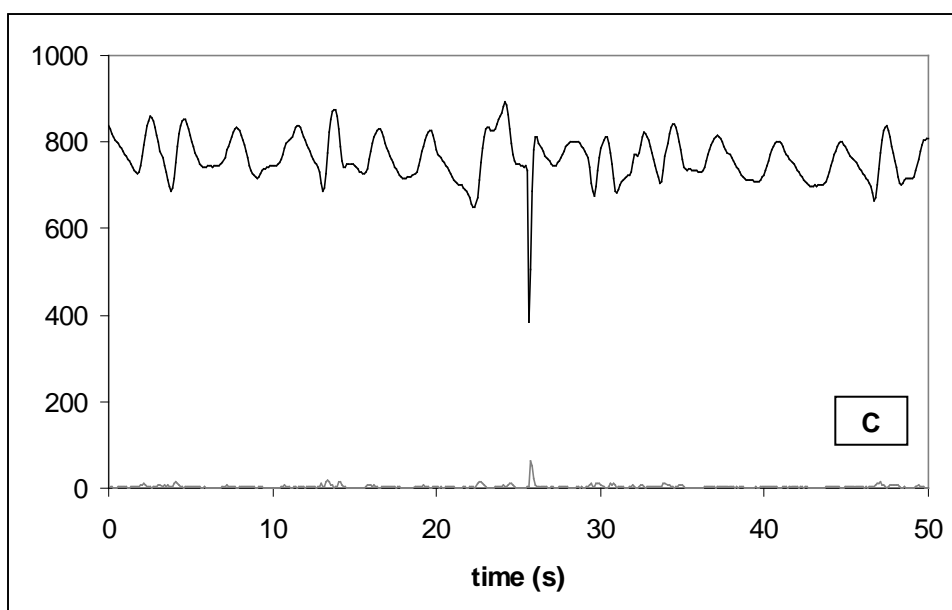
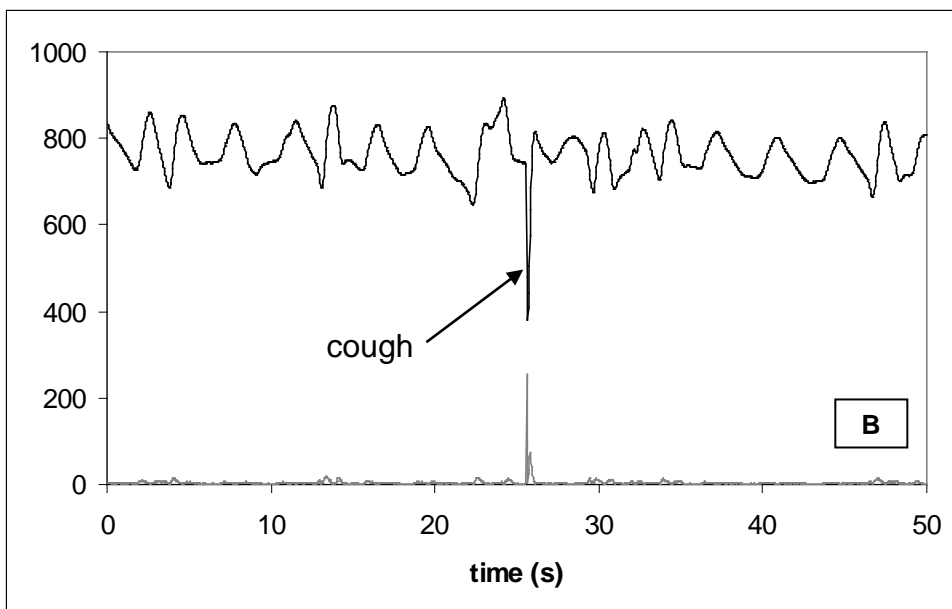
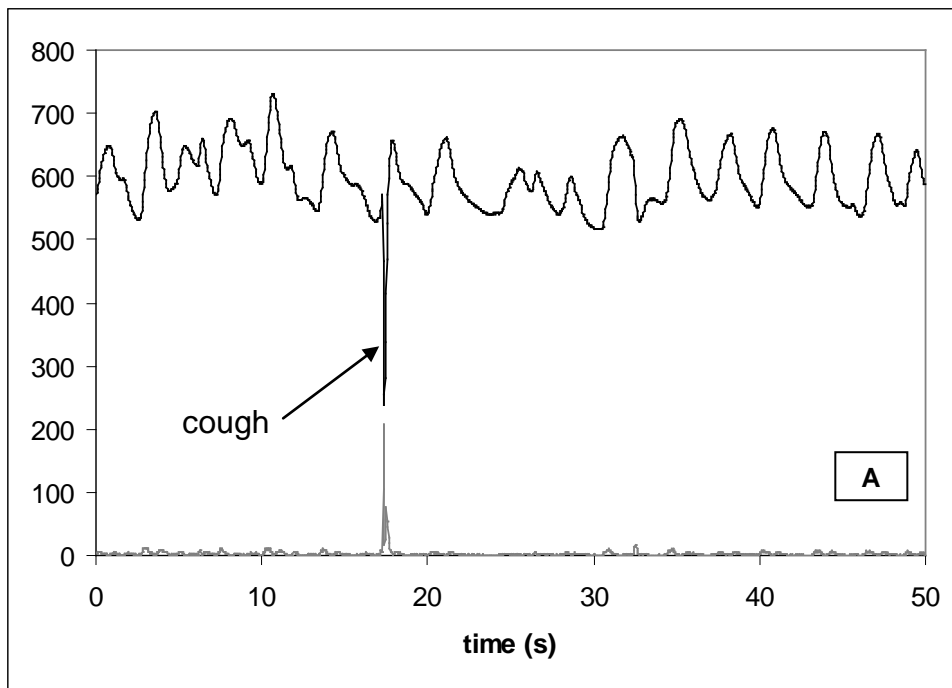


Fig 2. Two examples (a & b) of jaw movements during normal ventilation and coughing (data logged at 30 Hz). Fig. c is the same cough presented in Fig. b, but with the data resampled at 10Hz. The upper black lines, lower grey lines and y-axis values are as for Fig 1. (Metcalfe et al., 2009)

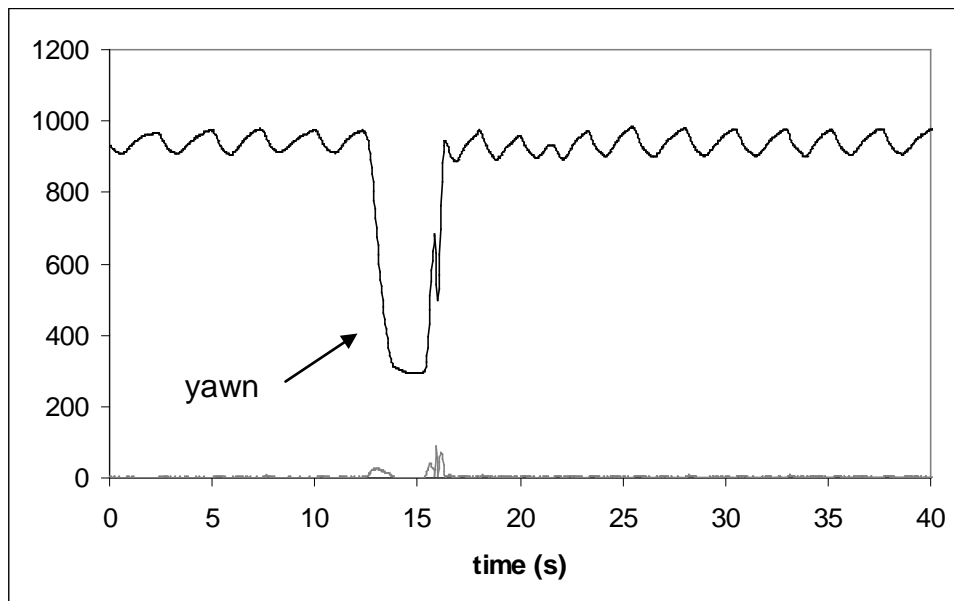
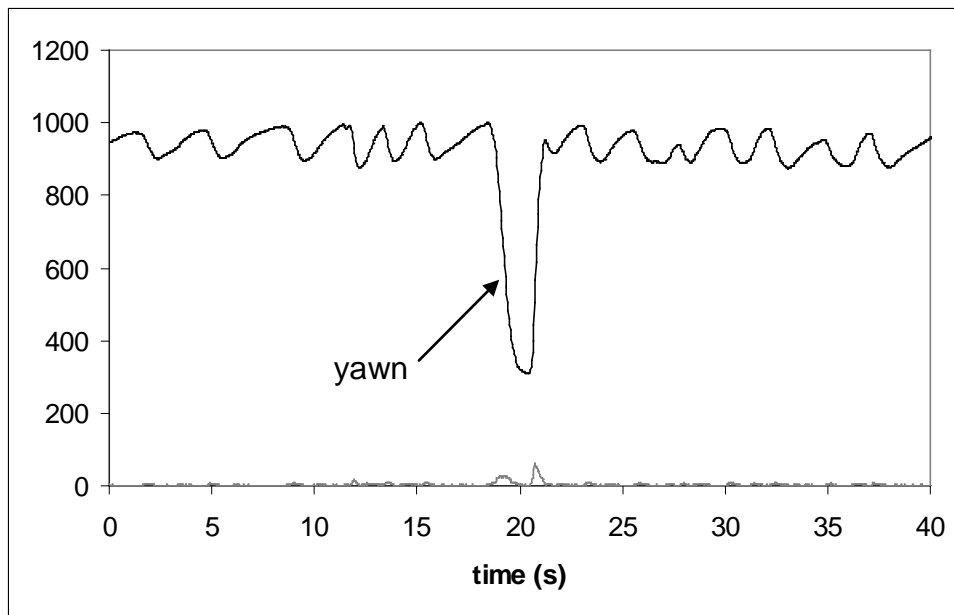


Fig 3. Two examples of jaw movements during normal ventilation and yawning. The upper black lines, lower grey lines and y-axis values are as for Fig 2. (Metcalf et al., 2009)

i. Ventilation

Ventilation was recorded in 5 cod, at least during the first few days following surgery. Typical ventilation movements are presented in Fig. 1. In this study, ventilation rate ranged from about 16 to 27 min^{-1} but was typically about 20 min^{-1} . While we have no data for unequipped conspecifics (the holding tank was too large for such small jaw movements to be monitored visually with any accuracy), this is considerably lower than that ($\sim 30 \text{ min}^{-1}$) measured in this species by Kinkead et al. (1991), particularly in view of the lower temperature (10-11 $^{\circ}\text{C}$) of their study. In comparison with feeding, coughing and yawning, jaw movements during ventilation were regular, slow and of low amplitude.

ii. Feeding

Although feeding (i.e. ingestion of food items) was observed and recorded in only one cod, this fish fed on many occasions. Jaw movements during two such feeding events are

presented in Fig 1. Typical characteristics of a feeding event are numerous rapid movements over a period of several seconds, the amplitudes of which are 3 to 4 times that of ventilation and the speeds of which are frequently 5 to 10 times faster than the maximum observed during ventilation over the preceding 20 s.

iii. Coughs

Coughs (observed directly during feeding trials as large, rapid jaw movements) were observed and recorded in 3 cod. Jaw movements during two coughs are presented in Fig. 2. Typical characteristics of a cough are a single movement over a period of less than a second, the amplitude of which is 3 to 5 times that of ventilation and the speed of which can be at least 5 to 10 times faster than the maximum observed during ventilation over the preceding 20 s. While the speed and amplitude of a cough may be very similar to that of feeding, the event may be discriminated on the basis that it is a single event lasting less than a second.

iv Yawns

Yawns (observed directly during feeding trials as large, slow jaw movements) were observed and recorded in 3 cod. Jaw movements during two yawns are presented in Fig. 3. Typical characteristics of a yawn are a single movement over a period of several seconds, the amplitude of which is at least 3 to 5 times that of ventilation with few if any movements faster than 5 to 10 times the maximum observed in the preceding 20 s. While the amplitude of a yawn may be very similar to that of feeding or coughing, the event may be discriminated on the basis that it is a single event lasting several seconds during which jaw movement is usually much slower than during feeding.

Data logging frequency

In this initial study, jaw movement data were logged at 30 Hz, the maximum sampling frequency of the Cefas G5 data storage tag. During data analysis it became apparent that it should be feasible to sample data at lower frequencies without losing key features that allow discrimination between feeding and other jaw movements. To investigate this further, we have re-sampled a number of the 30 Hz data sets (above) to provide 10 Hz data sets (Fig 2c: feeding & Fig. 3c: coughing). Despite the 3-fold reduction in sampling frequency, even comparatively rapid jaw movements such as feeding (Fig 2) and coughing (Fig 3) can be readily discriminated from normal ventilation and from each other using the same basic criteria applied to data gathered at 30 Hz (above). Therefore, a tag with 16 MB memory as described, could log jaw movement data at 10 Hz for up to 288 h.

We have not yet conducted studies with different prey types, but it is known that in piscivorous fish, prey handling time is affected by prey size and type (Juanes et al. 2002) so it may well be possible to use jaw movement data to provide more detailed information about feeding than that obtained by simply recording the frequency of feeding events. For example, Wilson et al (2002) has shown that using a similar device with penguins, jaw movements could be used to determine prey mass with “reasonable accuracy”, and that there was some indication that prey type could be resolved.

Tag developments 2: Spawning

Understanding the location and timing of spawning is a key requirement for understanding stock identity and stock dynamics of many fish species. Currently, this is difficult and costly to derive from plankton (i.e. egg) surveys and consequently our understanding of the location and persistence (year-on-year) of spawning grounds for species such as cod is only vague. Also, a more detailed understanding of behaviour (e.g. vertical movements and distribution) in relation to spawning events will be valuable in predicting the effectiveness of management measures designed to protect adult fish on spawning grounds. Furthermore, spawning fish are known to be particularly sensitive to environmental change, for example they show a smaller thermal window than immature conspecifics (Pörtner and Farrell, 2008). Thus, knowledge of their optimal spawning temperature is important in studies on biological effects of climate change. Like feeding, spawning is difficult to detect or observe directly. Therefore, because many of the technological requirements needed to monitor feeding activity could be used to monitor spawning activity, we have gone on to investigate implementing a similar approach to monitoring spawning activity.

Source of fish and holding conditions prior to surgery

For this study, experiments with cod were conducted at the Institute of Marine Research (IMR) in Bergen, Norway over the winter spawning period in 2007/08. A number of females with predicted spawning dates in February and March 2008 were selected for tag implantation. Following this operation each female was returned to the main tank and temporarily kept in a separate partition to better evaluate the individual recovery.

Tag and sensor implantation

Cod were anaesthetised in seawater using a cocktail of benzocaine (60 ppm) and metomidate (5 ppm) and placed ventral side up in a sponge-lined trough with their gills irrigated with seawater containing anaesthetic (as above, but at 6 ppm and 0.5 ppm, respectively).

To implant the magnet, a small incision was made in the skin level with, but about 30 mm to the left of, the cloaca (Fig. 2) and a small pocket running up to the cloaca was created by blunt dissection. A Neodymium disc magnet (9mm x 3 mm) that had been coated in a thin layer of silicon rubber (Dow-Corning, 743 RTV) was then inserted and the wound was closed with two or three sutures.

To implant the tag and magneto-sensor, a 30 mm mid-line incision was made in the skin approximately 70 mm anterior to the cloaca. A subcutaneous tunnel running back to the cloaca was created by blunt dissection and the tag sensor and lead were advanced posteriorly. Once the sensor and lead was in place, the tag was connected to a PC running the tag host software and sensor gain and offset adjusted to provide optimal sensor operation. The body wall was then opened through the 30 mm incision made previously and the electronic package was inserted into the peritoneal cavity. The sensor lead was anchored in place with a single suture at the caudal end of the peritoneal wound. The incision was closed with 5-7 single sutures and the wounds treated with a topically applied antibiotic (Cicatrín (GlaxoSmithKline) in Orahesive (ConvaTec Ltd.) protective powder (~50%/50%)). Fish were then transferred to a small (50 l) recovery tank with plentiful running seawater for a period of 10-20 minutes until normal ventilation and upright swimming activity had resumed. Fish were finally returned to their large holding tank (30 m³) where they remained for the following 26 days prior to being moved to the observation tanks.

Observations of spawning behaviour

To facilitate this study, the IMR 200-m³ circular tank was divided into 10 spawning compartments (Kjesbu et al. 1996). Each female was reweighed and a male, matching in length, was located and reweighed. Each selected pair was then introduced into each of the spawning chambers and egg-collecting devices installed at the outlets. The daylight was set to follow the natural cycle and all feeding was stopped. Each instrumented female was checked for wound healing one week later. Although progressing, the antimicrobial agent flumequine, dissolved in physiological saline water, was injected (50 mg·kg⁻¹) to reduce any inflammation.

The first release of eggs was detected on 6 February 2008. The standard protocols for egg collection and egg diameter measurements were followed (Kjesbu et al. 1991). However, as the present focus was on spawning time instead of fecundity, precise daily temperature recordings and egg staging were emphasised. Incubation temperature (T_2) was set equal to ambient water temperature (8.5-9 °C) over the relevant period of time. Each chamber was cleaned for eggs in the early morning, although a few eggs from each single batch typically still could be detected on the second and third day. The eggs were subsequently staged according to the scale of Fridgeirsson (1978) for cod. However, as the eggs considered were only up to one day old (1-128 blastomers), the more detailed information on development rates for such young eggs found in Kjesbu (1989) was consulted to establish a stage-specific formula based on the Q_{10} -rule (accuracy: $\approx \pm 1$ h; precision: ± 0.1 h) (Witthames et al. in press). More specifically, the development rate of interest (R_2) was set to be a function of the previously observed rate R_1 at temperature T_1 and the stage-specific Q_{10} value (in general around 2): $R_2 = R_1 \times Q_{10}^{(T_2 - T_1)/10}$. Only batches where the fertilisation rate was high (> 80%) were considered as low fertilisation rates are linked with 'holding' of eggs in the ovarian lumen over various lengths of time (Kjesbu 1989). A female that spawned irregularly died on 6

March 2008 following the production of five egg batches. All remaining males and females in the Circular tank were reweighed at removal on 11 March 2008, any scar from the previous operation photographed and the tag/sensor dissected out.

Cloacal movements during spawning events

Unlike feeding trials (above) where the time of feeding events was recorded precisely by direct visual observation, the time of spawning had to be inferred indirectly by back calculating from the time of egg collection using the state of egg development at the time of collection and estimates of the temperature-dependent rate of egg development. As noted, this provided an estimate of the time of spawning to within approximately ± 1 hour. Accordingly, after concluding the study and recovering the archival tags, the downloaded data was inspected for about 1 hour before and after the calculated time of spawning. It is known from visual observations that spawning in cod involves release of eggs through the cloaca, over a period that may last totally up to 3 min (Rakitin et al. 2001), although typically around 30-60 s (J.E. Skjæraasen, University of Bergen, personal observation). The data records were therefore inspected for events that indicated an opening of the cloaca, followed by its closing, that lasted for this amount of time. An example of a putative spawning event is shown in Fig 4 where, prior to the release of eggs, there are relatively fast, low amplitude movements, probably resulting from swimming movements. There is then a gradual dilation of the cloaca that lasts several seconds; a more gradual closing lasting some 7-10 s follows this. During this slow opening and closing movement, there are relatively fast, mid-amplitude movements, probably resulting from swimming or other bodily movements during the spawning event.

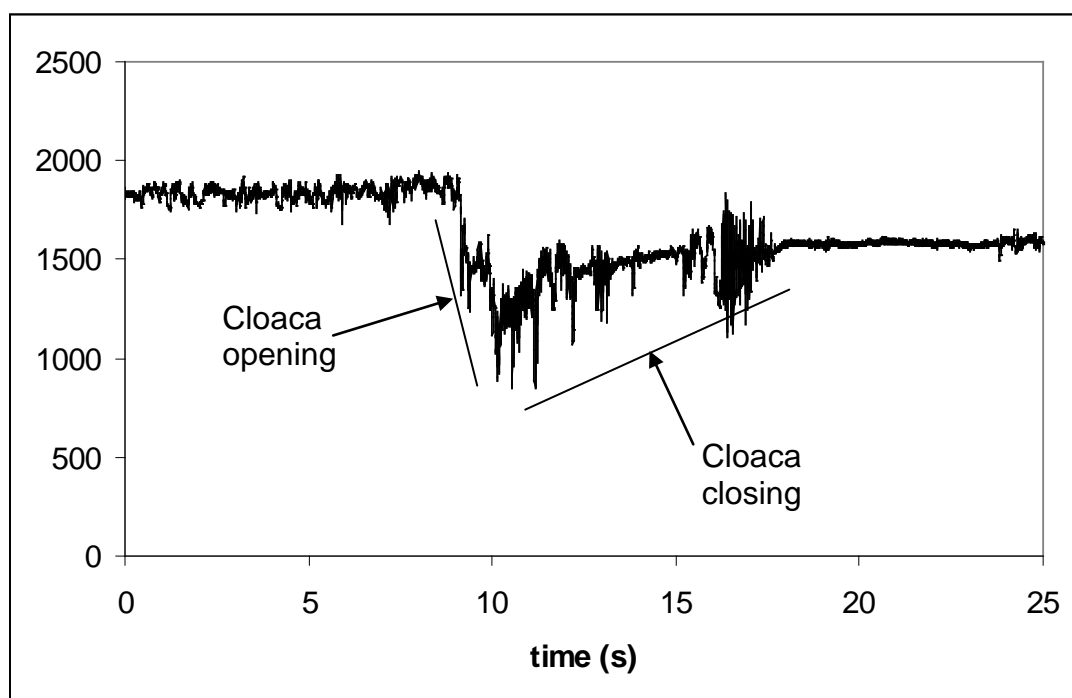


Fig. 4. a putative spawning event recorded from a female cod.

Tag developments 3: integrated measures of activity

While tracking studies of fish have prospered over the past two decades (see Arnold & Dewar 2001), we are still some way from being able to understand decision making by fish in the wild, particularly that relating to their movements and behaviours. For this to be possible it is important to be able to quantify relevant currencies that animals are purported to optimise. These are normally energy and/or time (Shepard et al. 2009). While the two key behaviours of feeding and spawning can be identified using methods described above, there are many more facets to a fish's repertoire than this, many of which can be categorised by the nature of the fish movement undertaken (for instance resting or swimming) or its posture (e.g. communication). The recent development of low power, miniature accelerometers now

permits the high resolution monitoring of both posture and movement of tagged fish so that the behaviour can be resolved as well as its energetic cost (via metrics estimating overall activity). These developments promise an unparalleled ability to quantify the behaviour (see Shepard, 2008b) and ecology of fish as we are increasingly able to estimate primary currencies (time and energy) that modulate fitness related processes.

Acceleration signals

Acceleration needs to be measured in a defined spatial axis, so a complete picture of a fish's body acceleration can only be undertaken if tags contain tri-axial accelerometers to help quantify the 3 spatial dimensions (i.e. in the x, y and z planes). Fortunately, such tags are now available. Acceleration is the first derivative of velocity with respect to time and therefore represents the degree to which the fish region to which the tag is attached changes in velocity in the axes defined by the transducers. Any acceleration trace from a mono-axial transducer is composed of 2 distinct signals (see Shepard et al. 2008a), the static acceleration (due to the earth's gravitational pull) and the dynamic acceleration (which is due to the animal's movement) and these can be separated using signal processing (Shepard et al. 2008a; Sato et al. 2003). The static acceleration can be used to deduce fish posture, as the magnitude or gravitational acceleration depends on the relative position of the logger in relation to the gravitational pull. The dynamic acceleration is a direct function of the change in speed (movement) of the animal carrying the accelerometer. Tri-axial accelerometers used on fish typically sample at sub-second rates and quantify the instantaneous acceleration in the three spatial dimensions, corresponding to surge, heave and sway (Fig. 5), giving a true 3-dimensional representation of movement. Thus, for example, in the case of a fish swimming with lateral undulations, the swaying acceleration registers cyclic accelerations and decelerations, coupled with the tail-beat and its associated amplitude (see Gleiss et al. 2009 for a more detailed discussion).

Accelerometry and Behaviour

Ideally, accelerometer tags should be attached to their carrier animals with known and defined orientation, with the sensor axes aligned with those of the animal (longitudinal, dorso-ventral and lateral). It is important that attachments be tight with little residual movement of the logger so that the signals may be attributed to the movement of the animal body rather than, for example, being due to turbulence in the water flow round the body. Best performance of acceleration loggers is achieved when they are attached near the centre of mass of the animal so that posture can be properly determined while tail-beat activity can still be determined (good signals are achieved despite no major visible movement of the tag). Different behaviours and their intensities can be distinguished based on the frequency and amplitude of acceleration signatures (Fig. 5 and Sakamoto et al. 2009) and/or the frequency of particular postures (Grundy et al. 2009).

Accelerometry and metabolic rate

An exciting consequence of measuring acceleration in all three dimensional axes is that it should correlate with energy expenditure because movement is the major element in the energy expenditure of most free-living animals. Indeed, studies aimed at deriving the overall dynamic body acceleration (ODBA: which is effectively the sum of the dynamic components of all three acceleration axes (Wilson et al. 2006)) from tri-axial acceleration tags used on animals in metabolic chambers shows that ODBA does indeed correlate well with metabolic rate in a number of animals, including birds, mammals (Halsey et al. 2008), amphibians (Halsey et al. unpubl.) and, recently, fish (Fig. 6, Gleiss et al. in press). Thus, the simple use of accelerometer tags on free-living fish can allow us to not only determine the behaviour of the animals, but to determine the energetic costs of the various behaviours.

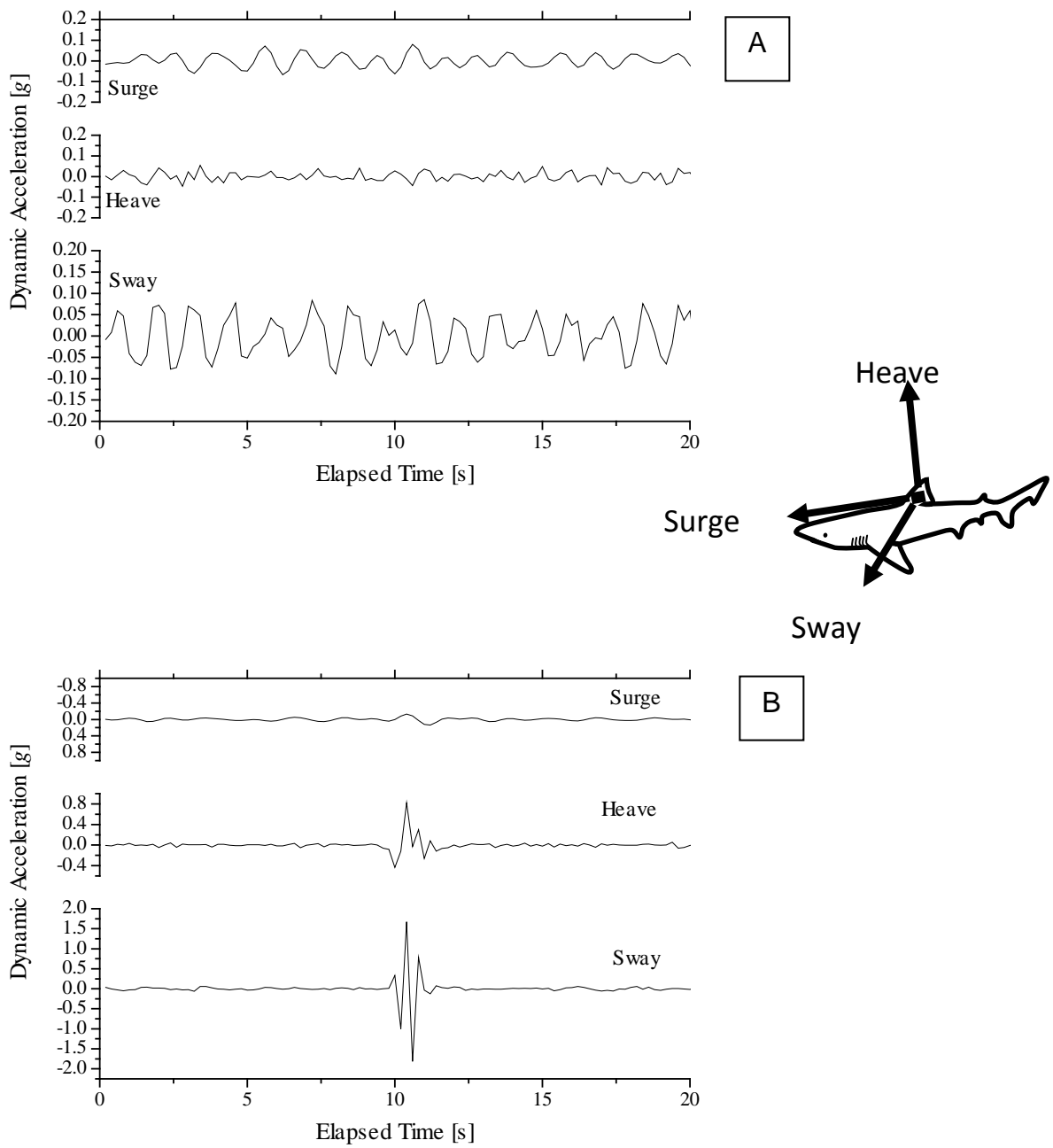


Fig. 5 Acceleration traces of 2 distinct behaviours from a captive lemon shark (*Negaprion brevirostris*). Note the waves in the swaying acceleration representing the tail-beat activity during steady swimming (**A**) in contrast to the periodic elevated swaying amplitude during fast-start swimming (**B**).

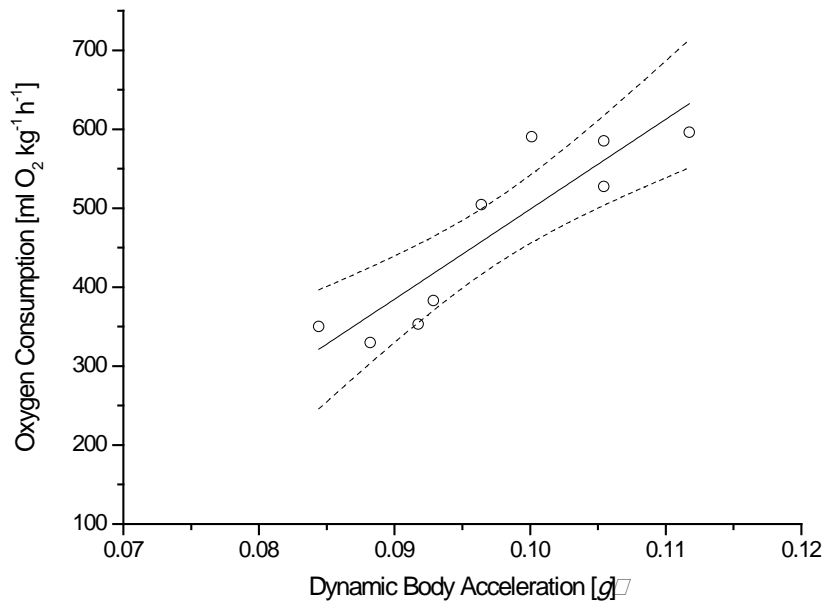


Fig. 6 Linear Regression of oxygen consumption and Dynamic Body Acceleration ($R^2 = 0.78$, $F_{1,7} = 30.633$, $P > 0.005$) for a juvenile hammerhead shark (*Sphyrna lewini*) swimming at a range of speeds in a “Brett-Style” respirometer at the Hawaii Institute of Marine Biology.

Solutions to data sampling problems

The detection of “complex” behaviours described above have all required the capacity to record animal movement, either of the whole body or of specific areas of the body, at much higher frequencies that are usually required to monitor spatial movements. Typically, for fish, geolocation (from ambient daylight or tidal data) or patterns of vertical movements can be determined from data logged once per minute, and often even less frequently. To detect feeding, spawning and to use 3-axis accelerometry to quantify behaviour and metabolic rate requires sub-second data logging, at least as fast as 5Hz and often even faster. This requirement leads to an increase in data logging rates of 2 or even 3 orders of magnitude. For devices that are small enough to attach to smaller fish, birds and mammals, this has become feasible as a consequence of the continuing improvements in microelectronic technology. The last 20 years of archival tag development at Cefas have seen the power requirements more than halve (with a consequent reduction in the size/weight of batteries required to run the tag), and the memory density increase by more than 44 fold. Despite these improvements, technical issues remain that still need to be addressed. Although memory density has increased substantially, and is expected to continue to do so, it is not yet feasible to log data from multiple sensors at sub-second frequencies continuously for extended periods (i.e. years) and still retain the small size usually required for wildlife applications. This is because the power required to record and store such large amounts of data is considerable, requiring larger batteries to be used. Even if it were possible to store large amounts of raw data, the subsequent data handling and processing requirements would be substantial. However, even with the current archival tag technology, there is a range of sensor sampling and data handling options that can provide useful solutions. Essentially, these come down to the problem of equitably balancing power and memory usage. We consider the pros and cons of some of these options below.

Intermittent sampling.

Taking feeding as an example, the Cefas G5 feeding tag has the capacity continuously to monitor jaw movements at 10 Hz (judged to be the minimum frequency required) for about 288 h (i.e. about 12 days). This is clearly insufficient to investigate longer-term (e.g. seasonal) changes in feeding pattern. However, by using other data logging regimes (e.g. logging at 10

Hz for 4 h in every 20 h) it is possible to monitor feeding intermittently over the 24 h cycle for several months. Such a logging regime could be further modified so that feeding is logged intermittently for one month in the winter and for one in the summer and hence approaching a capacity to investigate seasonal changes in feeding behaviour.

While this approach is by no means a complete answer for long-term monitoring, it is easy to implement (it is currently available in the G5) and provides raw data that can be analysed and interpreted subsequently (i.e. it is not prone to the problems of on-board processing – see below)

Conditional sampling and pre-trigger sampling

Where particular behavioural events have specific and unique characteristics, there is the potential to implement conditional data sampling where data is only recorded when a particular “condition” is met (i.e. trigger activated or sensor threshold crossed). This has the advantage that, for behaviours that are short lasting, infrequent and irregular, data is only recorded during the events of interest, with better use being made of the available memory. However, this approach requires that the “condition” is suitably and robustly defined to ensure all the events are captured. Also, where the “condition” is identified from one or more of the on-board sensors, there is the requirement continuously to monitor the sensor. So while memory may be conserved, power is still required to collect and process sensor data. Currently in the Cefas G5, the power required is about 50% of that required to collect, process *and store* the data, but alternative approaches to powering the sensor used to trigger sampling are feasible that can further reduce the power costs, for example some dive loggers (and the G5 in “dive mode”) monitor a simple wet/dry switch and use this to trigger logging, thereby significantly reducing the power cost of continuous monitoring and so extending tag life substantially. As with intermittent sampling, conditional sampling has the advantage that raw data is logged and can be analysed and interpreted subsequently.

A further variant of conditional sampling involves pre-trigger sampling. With “simple” conditional sampling, data just prior to the “condition” being met is not recorded. With pre-trigger sampling a defined but variable amount of data is continuously passed through a “pre-trigger” buffer (first in – first out). When the “condition” is met, the data in the pre-trigger buffer, together with the defined quantity of post-trigger data, is written to memory. This way the behavioural event can be fully recorded. Again however, continuously monitoring sensors will have an additional power cost, but this is dependent on the power requirements of the sensors used.

Onboard processing and event detection

Both intermittent and conditional data sampling involve storing raw sensor data. Memory is preserved to some extent by not recording large amounts of “useless” data, but if data is logged at high frequencies there will still be a substantial memory requirement if events are to be recorded over extended periods, and there will be power penalties if there is a requirement to collect and process sensor data. A further option is to process data onboard the tag and simply record the times of events of interest. Again, we will use feeding as an example.

The characteristics of a feeding event (i.e. multiple jaw movements over a few seconds, the speed and amplitude of which are several times larger than those during ventilation) could be readily implemented in an event detection algorithm. In this example, the tag could also be programmed intermittently (say every 6 h) to monitor and analyse short periods (say 60 s) of ventilation so as to update the speed and amplitude threshold criteria. If this raw data were also stored, it could provide verification that the magnet/sensor system was still functioning throughout the logging period (this can be a problem if there is movement of the magnet or sensor after surgery). But the analogous situation wouldn't necessarily occur with all types of behaviours (e.g. spawning), and for some situations (e.g. tri-axial accelerometry) wouldn't be necessary because there would be no issues relating to sensor function. However, accurate event detection would be critically dependent on the robustness of the event detection algorithm and this would probably require extensive laboratory validation prior to tag deployment. Also, event detection will still require sensor data to be monitored and processed continuously, so power requirements (as above) will remain an issue.

Discussion

We show here that archival telemetry is advancing beyond the recording of “simple” variables that are used to derive geolocation, spatial movements and less complex elements of behaviour. It is now possible to record more complex behaviours such as feeding and spawning, identify different swimming modes, and even estimate activity-specific metabolic rate in animals behaving naturally in the wild.

By combining information about these more complex behaviours with information about geolocation and patterns of spatial and vertical movement, it should become possible to identify where specific types of behaviour occur (e.g. detail spawning areas) and to develop a more complete understanding of the interactions between environment, movement and behaviour. Further, the ability to determine activity-specific metabolic rate in animals behaving naturally in the wild puts us in a powerful position to understand how animals might modulate their behaviour to enhance their chances of survival (using time and energy as currencies).

Although the detection of “complex” behaviours described above all require the capacity to sample data at much higher frequencies than are usually required to monitor spatial movements, there is a range of sensor sampling and data handling options that offer an alternative to having to build in large data storage capacity and/or big batteries. These capabilities are already either available or achievable with current technology.

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