

Acoustic telemetry and accelerometers: a field comparison of different proxies for activity in the marine environment

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Different proxies for activity are used in the field of acoustic telemetry, a leading technology for the study of behaviour in the aquatic environment. Acoustic telemetry poses some shortcomings that may condition data interpretation. Here, we assessed some approaches commonly used to infer activity from acoustic telemetry data using acceleration biologgers as a benchmark. Specifically, we assessed (1) the performance of internal acceleration transmitters, (2) the consequences of averaging acceleration data into increasing time bins, (3) the occurrence of sampling bias in telemetry data acquisition, and (4) the performance of the number of detections and the depth range as proxies for activity. Despite some constraints of acoustic telemetry, acceleration transmitters had a good performance. Conversely, the number of detections and the depth range did not match well the activity estimates provided by acceleration biologgers. Besides, our results pointed to some issues in models concerning the predictive power of acceleration transmitters (linear predictor) over acceleration biologgers, warned about potential sampling bias associated with data acquisition with acoustic telemetry, and highlighted the relevance of considering inter-individual differences in behavioural studies. Finally, we provided some methodological perspectives that should be considered to plan fieldwork, analyse data, and interpret results on animal activity obtained with acoustic telemetry.

Keywords: activity inference, animal movement, behaviour interpretation, biologging, detection frequency, fish behaviour.

Introduction

The study of animal behaviour has gained relevance over the years due to its importance for biodiversity conservation and for understanding ecosystem functioning (Nagelkerken and Munday, 2016). Acoustic telemetry has become one of the leading technologies for the study of behaviour in aquatic animals due to its multiple advantages; namely, data can be recorded for long periods (i.e. months) and are associated to location, and animals do not need to be recaptured for the data being retrieved (Hussey *et al.*, 2015). Acoustic transmitters can incorporate multiple sensors (e.g. temperature, pressure, or acceleration) that provide a wide variety of alternatives to study different aspects of the animal behaviour (e.g. Kessel *et al.*, 2016; Alós *et al.*, 2017; Aspillaga *et al.*, 2019).

Activity is among the most frequently studied traits in animal behaviour research. The broad nature of the term, defined by Immelman and Beer (1989) as “an individual animal’s general, or specific, movement”, allowed activity to be inferred from various approaches. One common approach for inferring animal activity from acoustic transmitter data has been to use distance travelled (either horizontal or vertical) as a proxy for activity level (Gandra *et al.*, 2018; Brazo *et al.*, 2021). An alternative approach consists in counting the number of detections (i.e. signals emitted by the acoustic transmitters that are successfully received by one or more hydrophones) per time bin, which is usually interpreted as an indicator of animal activity (Koeck *et al.*, 2014; Gandra *et al.*, 2018). Many species hide in refuges during resting periods for multiple reasons

(e.g. avoid predators or strong marine currents, and so on). Instead, when they are engaged in other vital functions such as breeding or foraging, it is assumed that they are more exposed (i.e. detectable). This has led to the idea of a positive correlation between the number of detections and activity level (e.g. Koeck *et al.*, 2014; Gandra *et al.*, 2018).

Despite its great potential, however, acoustic telemetry presents some technical limitations that might bias the data obtained (Cooke *et al.*, 2016; Brownscombe *et al.*, 2019) and thus, the interpretation of the activity patterns. For instance, tracked individuals may be very active at spatial scales smaller than the resolution capabilities of the receivers’ array design or even without displacing (Cooke *et al.*, 2016). Also, both the detection range and the number of detections may be influenced by environmental factors (Payne *et al.*, 2010; Huvneers *et al.*, 2016), habitat complexity, or the degree of exposition of the animals to the receivers (Swadling *et al.*, 2020). Although proper validation procedures for using distance travelled and number of detections as proxies for activity are lacking, they are still widely utilized in the literature (e.g. Brazo *et al.*, 2021).

Accelerometers have proved to be very useful to describe and quantify different aspects of animal behaviour, such as activity patterns and body posture (Wilson *et al.*, 2019), and have a great potential to be combined with spatial data (McClintock *et al.*, 2013). Indeed, accelerometers allow to record even subtle movements that occur at fractions of seconds and that do not imply any displacement. The advent of acoustic transmitters equipped with accelerometers (hereafter,

acceleration transmitters) provided new possibilities to study aquatic animal behaviour in the wild (Murchie *et al.*, 2011; Cooke *et al.*, 2016). Despite the usefulness of this technology (Wilson *et al.*, 2013; Kneebone *et al.*, 2018), some particularities should be considered to design a field study and interpret the data produced by accelerometers embedded in acoustic transmitters (Murchie *et al.*, 2011; Cooke *et al.*, 2016). First, acceleration transmitters use raw accelerations recorded within a user-defined time interval or sampling window size (hereafter, SWS) to estimate each RMS (Root Mean Square) value, a measure of activity. Then the range of possible RMS values are split into a series of 256 discrete numbers (the maximum number of values that can be represented by one byte), to transmit and store the data. Once the data are retrieved from the receptors, they are reconverted from discrete numbers to acceleration units, which ranges between zero (absence of movement) and the maximum RMS value according to the sensor sensitivity and its corresponding settings. This procedure triggers a trade-off between the activity range that can be measured and the instrument resolution (i.e. the minimum incremental value of the input signal required to cause a detectable change in the output). Second, the high energy cost of transmitting acoustic signals, combined with limited battery lifespan and the impossibility of simultaneously recording acceleration and transmitting data, forces acceleration transmitters to record intermittently, at lower sampling frequencies, and using narrower acceleration ranges compared to the standards provided by traditional (archival, non-acoustic) accelerometers (Cooke *et al.*, 2016). Battery lifespan is, however, in the order of months for an acoustic transmitter compared with archival accelerometers, which may record for a few weeks before the batteries run out. Beyond these technical aspects, operational issues may also affect the quality and/or usefulness of the data recorded. Frequently, the study design may demand binning acceleration data into time intervals encompassing several SWS (Runde *et al.*, 2020). This loss in the temporal resolution may produce a drop in the accuracy of the activity estimates. Finally, although the internal placement (intra-gastric or loose in the coelomic cavity) of acoustic transmitters is widespread due to its advantages over external attachment (Brownscombe *et al.*, 2019), the consequences of bearing an acceleration transmitter loose within the fish, without a stable (i.e. fixed) position, remain unclear, and may produce an increasing dynamic signal that rises mean activity estimation (Wilson *et al.*, 2019).

This study aims to assess the performance of different activity proxies derived from acoustic telemetry data that are typically used to infer activity patterns in aquatic animals, and to test the effects of some technical constraints and operational particularities of acceleration transmitters that may limit their usage for the study of animal activity. To do so, we equipped dusky groupers with internal acoustic transmitters bearing an accelerometer and a depth sensor, and with externally attached acceleration biologgers that continuously store acceleration data at higher resolutions. We compared data from both devices by using acceleration biologgers as a benchmark due to its fixed attachment mode and less technical limitations compared to the acceleration transmitters, i.e. wider acceleration measurement range, higher recording frequencies and continuous recording (Cooke *et al.*, 2016). To our knowledge, this is the first study in which common proxies for activity derived from acoustic telemetry, such as the number of detections, changes in depth or acceleration,

are evaluated in field conditions by using an independent tri-axial acceleration biologger. Thus, specific goals of this paper were to (1) assess the performance of acceleration transmitters for measuring activity in aquatic animals, (2) evaluate the effects of the time bin size (TBS) when binning activity from acceleration transmitters, (3) assess potential biases in activity data acquisition with acoustic telemetry; and (4) assess the comparative performance of three common proxies for activity derived from acoustic telemetry, not based on acceleration metrics (total and unique number of detections, and change in depth).

Material and methods

Species and study area

The present study was carried out on the dusky grouper *Epinephelus marginatus* (Lowe, 1834) at the Cabo de Palos—Islas Hormigas Marine Fishery Reserve (Murcia, Spain, Western Mediterranean). This marine protected area, declared in 1995, harbours a series of seamounts (“bajos”) aligned in west–east direction, two of which reach the surface and result in the Hormiga and Hormigón islets, around which a no-take area was established (Figure 1). These seamounts are rocky reefs typically surrounded by a low-slope sandy bottom of detritic nature (García-Charton and Pérez-Ruzafa, 1998).

The dusky grouper is a demersal top predator species strongly associated with rocky substrates, where it usually seeks small cavities for shelter (Concini *et al.*, 2018). Due to the ecological and economic role of this species, as well as its conservation status in the Mediterranean (categorized as Endangered by the IUCN), it raises great scientific concern (Concini *et al.*, 2018). Its strong site attachment (Concini *et al.*, 2018), high recapture rate and the relative ease of handling makes it ideal for combining acoustic telemetry with biologging techniques.

Passive acoustic telemetry and fish tagging

A total of two arrays of acoustic receivers (model VR2W, Vemco Ltd, Bedford, NS, Canada), were deployed, one around the Hormigón islet (HG) ($n = 13$), and the other around the “Bajo de Dentro” seamount (BD; $n = 10$; Figure 1) between August 2016 and April 2017. The receivers were placed less than 100 m apart (Welsh *et al.*, 2012). This, together with the estimated 250-m detection range for the area (Hackradt, 2012), maximized the probability for the acoustic signals to be detected by the receivers whenever the tagged individuals were in the vicinity of the rocky reefs and outside the caves. For each detection, the receivers registered date and time, a unique ID for each fish (fish ID), and either an acceleration or a pressure (depth) value. A total of two reference tags, i.e. transmitters located at known places that emit an acoustic pulse at fixed and known time intervals (600 s in this study), were placed in each array of acoustic receivers. These tags are used to estimate standardized detection frequency (SDF) values that may be used as a minimum threshold value for an acceptable level of propagation capacity in a specific area. The use of reference tags is increasingly encouraged (see Payne *et al.*, 2010 for further details).

We used two types of tri-axial accelerometers simultaneously to estimate activity in free-living fish: an internal acceleration transmitter (model V13AP, Vemco, Inc.) and an external acceleration biologger (model X16-mini, Gulf Coast Data

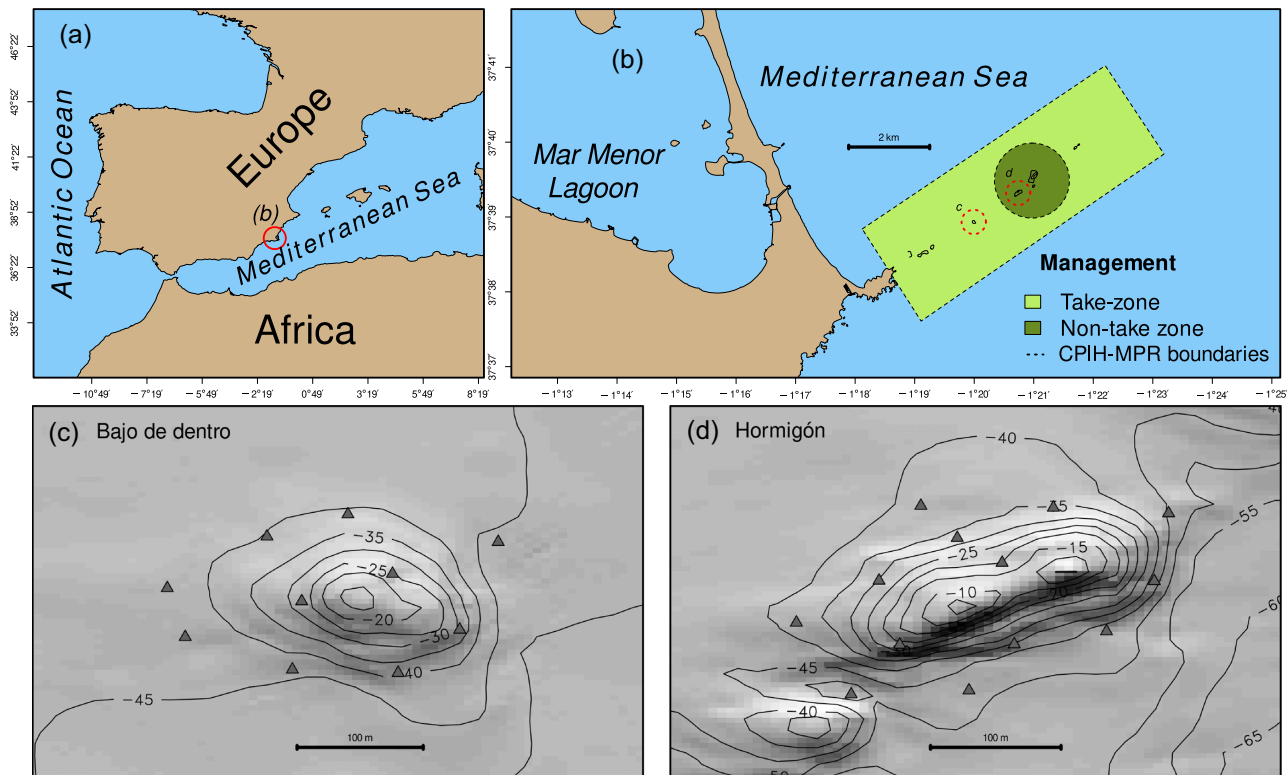


Figure 1. Location of the Cabo de Palos—Islas Hormigas Marine Fishery Reserve (CPIH-MPR) (a) and of the study sites: Bajo de Dentro reef area and Hormigón islet (b). The grey triangles show the location of the acoustic receivers in each area (c) and (d).

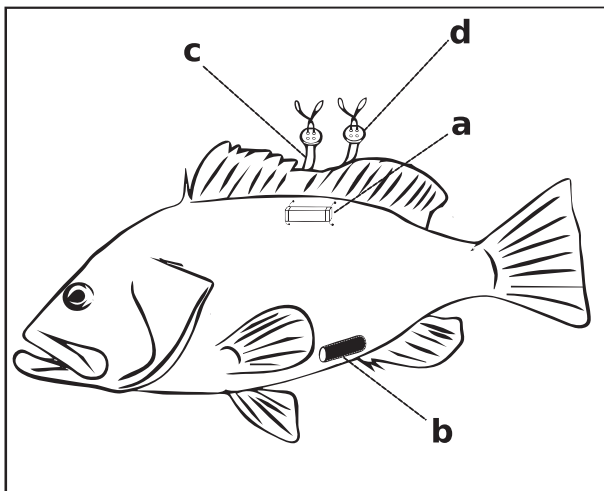


Figure 2. Schematic representation of the attachment of the acceleration biologgers (a) and acceleration transmitters (b) in free-living dusky groupers with the use of biodegradable monofilament surgical sutures (c), and sterile buttons (d).

Concepts, LLC, Waveland, MS USA; [Figure 2](#)). A total of 16 dusky groupers were captured with baited traps (eight from HG and eight from BD), all of them were adults ranging in size between 50 and 92 cm total length (fish weights: 2–12 kg). Once anaesthetized, a 3-cm incision was made in the ventral cavity of each fish to introduce the V13AP acoustic tag, which was sealed using surgical glue to avoid the permeability of the wound. In 10 of those individuals (H4–H8 from HG and D4–D8 from BD), an additional X16-mini acceleration

biologger was fixed externally below the dorsal fin by using biodegradable monofilament surgical suture (Monomax 1 HR37, B. Braun Inc) and two sterile buttons ([Figure 2](#)). The weights in the air of these devices were ~ 16 and 13 g for the acceleration biologger and the acoustic transmitter, respectively. In no case they exceeded 1% of the fish body mass (following Smircich and Kelly, 2014). We did not observe any difference in behaviour between fish equipped and not equipped with an externally attached biologger. The acceleration biologgers were recovered through fish recapture by using baited traps between 14 and 45 d after releasing. The regional authority *Consejería de Agua, Agricultura, Ganadería y Pesca—Región de Murcia*, after the approval by the Ethics Committee on Animal Experimentation of the University of Murcia (licence number A13150108), granted us the corresponding authorizations to capture, mark and release the dusky groupers, and to deploy the array of receivers within this marine protected area. All operations complied with the regulations expressed in the aforementioned licence and in the recommendations “Animal Research: Reporting of *In Vivo* Experiments” (ARRIVE guidelines, see Percie du Sert *et al.*, 2020), and were performed by licensed scientists, which ensured minimizing fish stress. Further details on handling, anaesthesia and tagging procedures are provided in Online Resource 1.

Devices features and settings

The V13AP acceleration transmitter, compared to the X16-mini acceleration biologger, records acceleration at lower frequencies (5 vs. 12 Hz) and within narrower acceleration measurement ranges (29.4 vs. ± 156.8 ms⁻²). Also, they provide

a single activity value [RMS, Equation (1)] for customizable SWS, instead of raw tri-axial accelerations. In contrast, the bi-logger records acceleration continuously (data are not transmitted but stored in internal memory) and, most important, allows raw data (i.e. tri-axial acceleration) to be obtained. The main advantages of the acceleration transmitters over the bi-loggers are that they may record data for longer time periods (up to years), do not require to recapture the fish to retrieve the data, and data include information about position. In this study, the expected battery lifespan was 214 d for the V13AP and 8 d for the X16-mini.

The acoustic transmitters were set to send activity and pressure alternatively within a random delay of 60–180 s (average: 120 s). Given that the acceleration transmitters start recording acceleration immediately after each depth record transmission, it was possible to calculate the time bins for which they recorded. This, together with the synchronization method used, allowed data from the acoustic transmitters and the acceleration bi-loggers to be matched. We describe the synchronization method in detail in Online Resource 2. It is based on the assumption that, if data from two devices are correlated over time because of their nature, the maximum correlation between their measures will be obtained when they are synchronized. To do that, we constructed a profile for the correlation strength (Pearson correlation) between both data series, by implementing a set of relative time delays between both devices. Following Vemco recommendations, acceleration transmitters were set to record tri-axial acceleration at 5 Hz for a fixed SWS of 57 s.

Raw accelerations recorded by the V13AP transmitters are internally separated into their dynamic and static components by using the low-pass filter “Butterworth”, with a 3.5-s cut-off (D.M.W., Vemco, pers. comm., January 2020). Then, RMS activity values are calculated, transmitted and stored. RMS ranged between 0 and 4.91 ms^{-2} , with a resolution of 0.02 ms^{-2} . Acoustic transmitters had an output power of 153 dB. The pressure sensor was set to a maximum depth of 68 m, with accuracy and resolution of 3.4 and 0.3 m, respectively. To account for differences in clock drift among receivers, these were time-synchronized using the VUE software (Vemco).

Data analysis

Acceleration data processing

The expressions for the activity metrics RMS and aVeDBA are, respectively,

$$RMS = \frac{\sqrt{\sum_{i=1}^n (X_{dyn}^2 + Y_{dyn}^2 + Z_{dyn}^2)}}{n}, \quad (1)$$

$$aVeDBA = \frac{\sum_{i=1}^n \sqrt{(X_{dyn}^2 + Y_{dyn}^2 + Z_{dyn}^2)}}{n}, \quad (2)$$

where X_{dyn} , Y_{dyn} , and Z_{dyn} represent the dynamic acceleration (ms^{-2}) in the X, Y, and, Z axes, respectively; and n , the total number of acceleration measurements for the SWS (it is the product of the size of the sampling-window in sec and the recording frequency in Hz; further details in Online Resource 3). Following the manufacturer’s suggestion for the V13AP, we also used a 3.5-s running mean to separate raw accelerations obtained with the bi-loggers into their static and dynamic components.

For goal 1, we estimated RMS from bi-loggers (coincidentally with acceleration transmitters) to avoid any unwanted influence of the activity metrics on the results. For goals 2–4, we estimated the average vectorial dynamic body acceleration (aVeDBA), defined for a given time bin. The magnitude of aVeDBA estimates are much less affected than the magnitude of RMS estimates grouped into time bins of varying sizes; hence, we preferred to calculate aVeDBA over grouped RMS for the bi-logger data to achieve goals 2, 3, and 4 (further details in Online Resource 3).

The SWS remained constant throughout the study for the acceleration transmitter (i.e. 57 s). However, this value was different to estimate RMS (goal 1) and aVeDBA values from bi-logger data (goals 2–4). In goal 1, the SWS for the bi-logger data was 57 s; in goals 2 and 4, it was equivalent to the size of the time bins used; and in goal 3, it was 20 s.

Goal 1: performance of acceleration transmitters

The acoustic transmitters were placed internally, and thus relatively free within the coelomic cavity and exposed to the intestinal movements. Under the assumption that the acceleration bi-logger represents better the activity pattern of fish given its type of attachment and settings (detailed in “Devices features and settings”) we compared the activity estimates obtained with both devices using linear mixed-effect models (LME). Activity estimates from the bi-logger (Act_{bio}) and from the acceleration transmitter (Act_{trans}) were used, respectively, as the dependent and the explanatory variables for model fitting. Data were log-transformed to meet model assumptions. To test for potential non-linear relationships between the data obtained with both devices, we fitted polynomial forms of degrees 1–5, and estimated the explained variances.

Goal 2: effects of binning activity from acceleration transmitters

Beyond the features of the V13AP acoustic transmitters for recording and sending acceleration data, not all the transmissions sent are heard by the receivers. Therefore, the number of observations used to estimate the average activity values are not constant. Here, we explored the predictive power of the data obtained with the acoustic transmitters at different TBSs. Specifically, we modeled Act_{bio} as a function of the average activity values from the acceleration transmitters (Act_{trans}), the number of activity detections (n_{det}), which is indicative of the fraction of time for which acceleration has been sampled, and their interaction ($Act_{trans} \times n_{det}$). It is expected that the accuracy of the activity estimates provided by the acceleration transmitters increases with n_{det} . Besides, as dusky groupers are less active within their refuges (JMP, pers. obs.), which may cause a drop in the number of detections received, it is expected that a large number of records in each time bin (high value of n_{det}) correlates with higher activity levels. To achieve this goal, we used LME models to examine the relationship between Act_{bio} , and different combinations of the variables Act_{trans} , n_{det} , and $Act_{trans} \times n_{det}$ at time bins of 6 min ($n = 3\,960$), 15 min ($n = 2\,027$), 30 min ($n = 1\,079$), 60 min ($n = 561$), and 120 min ($n = 284$). All data were log-transformed to facilitate meeting model assumptions (see below).

Goal 3: potential sampling-bias in data acquisition

A non-representative or biased activity sample of the tagged fish might be obtained using acoustic telemetry if the overall

activity levels were different among habitats (e.g. swimming in the water column vs. resting in their refuges) with distinct properties for transmitting the acoustic signals. To test that possibility, we used data from acceleration biologgers and compared activity values (aVeDBA) between sampling windows in which there were no detections (neither activity nor depth data, referred as reference windows) and those in which the receivers got a data pulse (hereafter, detection windows), by using a SWS of 20 s. This SWS was chosen based on a trade-off between a SWS small enough to represent the activity properly around the detection time and large enough to avoid increasing substantially the imbalance between both types of windows. We used the unpaired two-sample Wilcoxon test for each fish individually to test for differences in activity values between the reference windows, which are considered a random sample that represents accurately the true distribution of activities of the individual at SWS of 20 s, and the detection windows. We first applied a two-sided test. In the case of rejecting the null hypothesis of equality in the central tendency (i.e. median) of the distribution of both window types, we applied a one-tailed test to check if the activity was higher or lower for the detection windows than for the reference ones. We also calculated the effect size (r), a useful measure to assess the magnitude of the differences between window types (Tomczak and Tomczak, 2014).

Goal 4: performance of three common proxies for activity

To achieve this goal, we assessed the performance (in terms of predictive power as linear predictors) of the variables “number of unique detections” (Unique), “number of total detections” (Total), and “depth-range” (Depth), derived from telemetry data, as proxies for activity. Total and Unique represent the number of detections of each V13AP tag considering all detections received by multiple hydrophones or time-unique transmissions, respectively. Depth represents the change in depth undergone by each V13AP tag. These three variables were calculated for 15-min, 30-min, and hourly time bins, being the latter the time unit more commonly used in the literature (Payne *et al.*, 2010; Koeck *et al.*, 2014). As the number of detections can be highly affected by the environmental conditions (Huvneers *et al.*, 2016), we excluded from the analyses those time bins with a SDF value (dimensionless proportion) below 0.8 (SDF *sensu* Payne *et al.*, 2010), excluding, therefore, those individual time bins in which the ability of the receivers’ array to detect the acoustic signals had been reduced by at least 20% compared to average conditions in the area. We analysed data at two different time scales: a short-term scale (in the range of a few days), for which data from the acceleration biologgers was available (six fish ID), and a long-term scale (about 6 months), for which only data from the acoustic transmitter was available (16 fish ID). Given that both accelerometers have different technical characteristics, and that fish behaviour may be affected during a few days after tagging, we considered useful to evaluate the performance of the proxies for activity at the two temporal scales. In the short-scale scenario, we used 15-min, 30-min, and hourly activity estimates from the acceleration bilogger (Act_{bio}) as the benchmark for activity (response variable) and fitted different LME models containing only one of the explanatory variables at a time: unique detections, total detections or depth range. On the long-scale scenario, we ran the same set of models but using 15-min, 30-min, and hourly activity averages from the acceleration transmitters (Act_{trans}) as the benchmark for activity

(response variable). The performance of the three proxies was evaluated by comparing each fitted model with the corresponding null model. Data were log-transformed to meet model assumptions after adding 0.1 to each observation to deal with a few zeros in the data set. The explained variance for each model was also estimated for interpretation purposes.

General statistical analyses and modelling tools

All statistical analyses were performed using the R software v.3.6.2 (R Core Team, 2021). The inclusion of fish ID as a random factor in the models for goals 1, 2, and 4 (either as a varying intercept and as varying both intercept and slope) was evaluated by comparing MLE fits against generalized least squares models (GLS). LME and GLS models were performed using the R package “nlme” (Pinheiro *et al.*, 2018). The random terms in LMEs were evaluated by fitting the models using restricted maximum likelihood (REML). The fixed terms in the models for Goal 1 were tested using maximum likelihood (ML). Final models were fitted by REML in all cases (Zuur *et al.*, 2009). All models were visually validated by checking normality and homoscedasticity of residuals (Zuur *et al.*, 2010). We used the Akaike Information Criterion (AIC) for comparison between competing models. A difference of 2 or greater between the AIC values for two models being compared (i.e. $\Delta AIC \geq 2$) was taken as indicative of differences between them, and the model with the lower AIC was retained (Burnham and Anderson, 2002). We also estimated the Bayesian Information Criterion (BIC) for comparing competing models in Goal 1 (Schwarz, 1978), to avoid the selecting of more complex (i.e. overfitted) models (Aho *et al.*, 2014). The variances explained by the models were calculated using two goodness-of-fit measures (Nakagawa and Schielzeth, 2013), with the MuMIn R package (Barton, 2020): marginal goodness-of-fit (r^2_m), which indicates the variance explained by the fixed factors, and conditional goodness-of-fit (r^2_c), which shows the variance accounted for by both the fixed and the random terms. The non-parametric unpaired two-sample Wilcoxon test for goal 3 and the effect size were performed using the functions “wilcox.test” and “wilcox_effsize”, available in the “base” package of the R software. A p -value of 0.05 was used to determine statistical significance.

Results

Data from acoustic transmitters and acceleration biologgers (detections and raw accelerations, respectively) were heterogeneously distributed among individuals (Table 4.1 and Figure 5.1 in Online Resources 4 and 5, respectively). We obtained 2059 831 unique detections from the acoustic transmitters implanted in the 16 fish tagged. The ratio of depth: activity data provided by the acoustic transmitters was approximately 1:1 ($n_{depth} = 1029\ 143$ and $n_{activity} = 1030\ 688$). A total of seven out of 10 fish that had acceleration biologgers attached were recovered, four were from HG and three from BD. In total, one fish (D4) was completely out of range of the acoustic receivers while the acceleration bilogger was recording; hence, it was excluded from the analyses for goals 1, 2, and 3. Another fish (H5) left the study area a few hours after being released. It was sighted in another reef, 2 km away, after several days, and when it returned to the tagging area a few weeks later, the acceleration bilogger had already stopped recording (Figure 5.1 in Online Resource 5). Still, the available data from H5 was used in this study (Online Resource 4). A total of

39 063 937 acceleration records (850 h) were obtained for the six individuals tagged with the acceleration bilogger and included in the analyses (Online Resource 4). Activity data from the acceleration loggers and the acceleration transmitters were strongly right-skewed, and rarely (0.11%) reached the maximum activity value configured for the acceleration transmitter (Figure 3a).

Goal 1: performance of internal acceleration transmitters

For most of the activity range recorded for the dusky groupers, the RMS values obtained with the acceleration transmitters were larger than those estimated with the acceleration loggers (Figure 4a). Act_{trans} (fixed predictor) explained 88.4% of the total variation in Act_{bio} . Fish ID (random intercept and slope) accounted for an additional 5% in the explained variance (Table 1). A few activity values recorded by the acceleration transmitters clearly broke away from the linear trend at values lower than or equal to -2.847 (0.058 ms^{-2} in its natural scale), justifying the selection of a four-degree model over a straight-line (Figure 4b).

Goal 2: effects of binning activity from acceleration transmitters

The average percentage of time for which acceleration was sampled by the acceleration transmitters varied as a function of the TBS used and ranged between 14.0% (120-min time bins) and 20.4% (6-min time bins; Table 6.1 in Online Resource 6). Both the acceleration transmitters and the loggers registered a decrease in the proportion of close-to-zero activity values as the TBS increased (Figure 3).

The best models selected for each TBS had different fixed structures (Table 2). For the smaller bin sizes (6 and 15 min) only the predictors “ Act_{trans} ” and “ $Act_{trans} \times n_{det}$ ” were included, while for the largest bin sizes (30, 60, and 120 min) the models also included the variable “ n_{det} ” on its own (Table 2). Overall, the predictive power of the fixed predictor of the models enlarged moderately from 73 to 82% as the TBS increased. The inclusion of “ n_{det} ” in the models (on its own and/or within the interaction term) always increased the predictive power of the linear predictor, between 0.5 and 2.9% for time bins of 6, 15, and 30 min, and about 8% for time bins of 60 and 120 min (Table 2). To visualize its effect on model fitting and how it impacts more with larger time bins (e.g. 120 vs. 6 min), Figure 5 shows model predictions when taking only those cases with lower number of detections (10th percentile) in contrast with those with higher “ n_{det} ” (50th and 90th percentiles). Fish ID (random intercept and slope) contributed to explain less as the TBS enlarged (Table 2).

Finally, the models for the smaller time bins did not allow a good prediction of the X16-mini activity estimations at low values of the V13AP activity (Figure 5). This trend disappeared as the TBS increased.

Goal 3: assessment of potential sampling-bias in data acquisition

The median activity was higher for the detection windows than for the reference ones (in which there were no detections) for most tagged fish (Table 3). The overall effect size was small [i.e. effect size (r) < 0.3], although it varied by up to one order of magnitude among individuals. Noteworthy, there were significant differences in activity between reference and detec-

tion windows for four out of the six tagged fish (Table 3 and Figure 7.1 in Online Resource 7), three of them tagged in HG and one in BD. For all these four fish, the central tendency in activity was significantly higher in the detection windows than in the reference ones ($p < 0.05$), which suggest that those individuals were detected more when they were more active.

Goal 4: performance of three common proxies for activity

Overall, depth explained a significant proportion of the variability in Act_{bio} compared to the null model, being this result consistent at both temporal scales and for all the TBSs studied: 15-, 30-, and 60-min. Nevertheless, the prediction power of Depth was rather poor and fluctuated between 22 and 33% in the conditions explored: it was higher for the short scale and for the largest bin sizes (30- and 60-min; Table 4 and Figure 6). At the long-term, the prediction power of Depth decreased considerably, and ranged between 6 and 9% (fixed predictor). Differently, the models containing Unique and Total number of detections as fixed predictors had less statistical support than the null model. The explanatory power of those variables was always below 2.5%. These results were consistent at both temporal scales and for different TBSs (Table 4 and Figure 7). The inclusion of fish ID as a random effect (random intercept and slope) improved significantly model fit (Table 4).

Discussion

To our knowledge, this is the first study in which high-frequency tri-axial acceleration data were used to assess the performance of acoustic telemetry aimed to estimate activity in free-ranging fishes. Conclusions can be beneficial for studying many aquatic animals as most of them, like the dusky grouper, use different habitats in which the receivers' array cover a variety of marine environments with different physical properties, which may condition the propagation of the signals and, therefore, the type and quality of the data obtained. The limitations considered here for acoustic telemetry, both technical and operational, are common to any study using this technology. This work was conducted in an acoustically complex system with numerous interferences to sound propagation (e.g. physical barriers, thermoclines, marine currents, and so on) that in turn vary according to the microhabitat (caves, seabed, water column, and so on), and hence it is useful not only for the dusky grouper but to study any aquatic species whose behaviour changes in space and time.

Goal 1: performance of internal acceleration transmitters

The raw activity estimates provided by the acceleration transmitters approached well those from the loggers in logarithmic scale, despite the occurrence of among-individuals differences in the position and stability of the V13AP tags [see Wilson *et al.* (2019) for further discussion on this issue]. Also, the relationship between the activity values from the loggers and the acceleration transmitters departed from a straight line for a few low-activity values. This might be due to errors introduced during the successive transformations of continuous RMS values into discrete units before transmission. Indeed, the magnitude of the errors introduced between the initial and final (i.e. stored) RMS values may reach 100% for low activity

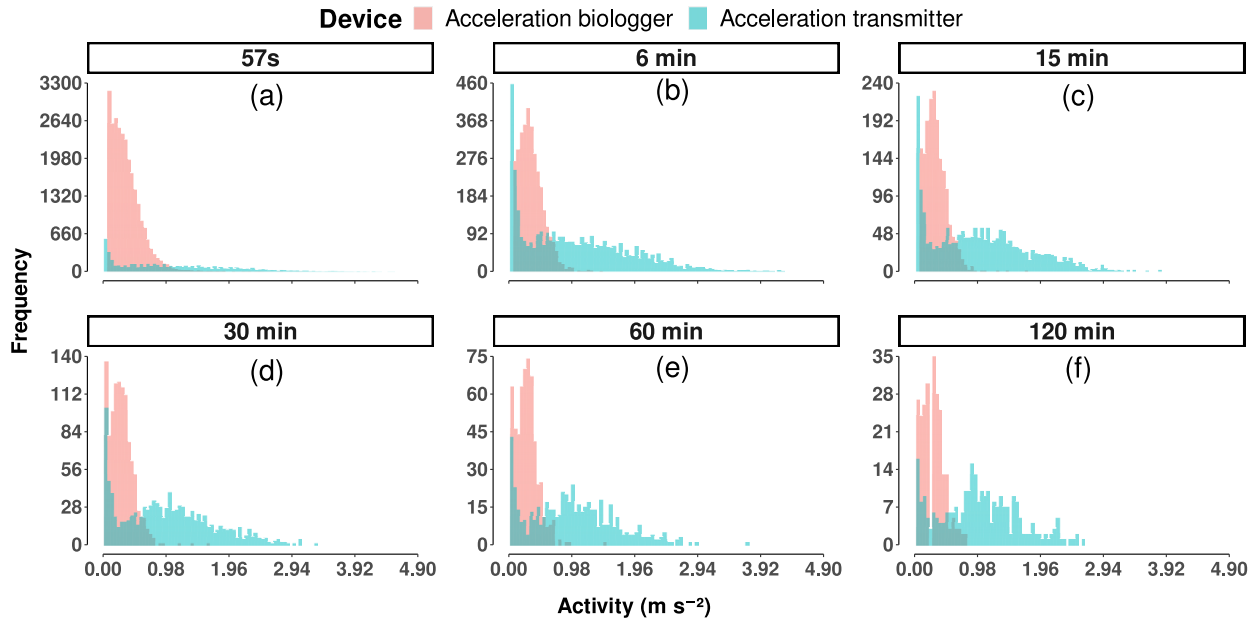


Figure 3. Histograms showing the frequency distributions of activity from acceleration biologgers and transmitters at time-intervals of 57 s (a), 6 min (b), 15 min (c), 30 min (d), 60 min (e), and 120 min (f). Note that the activity values from the acceleration transmitters at SWS of 57 s are raw activity values (i.e. retrieved from the receivers).

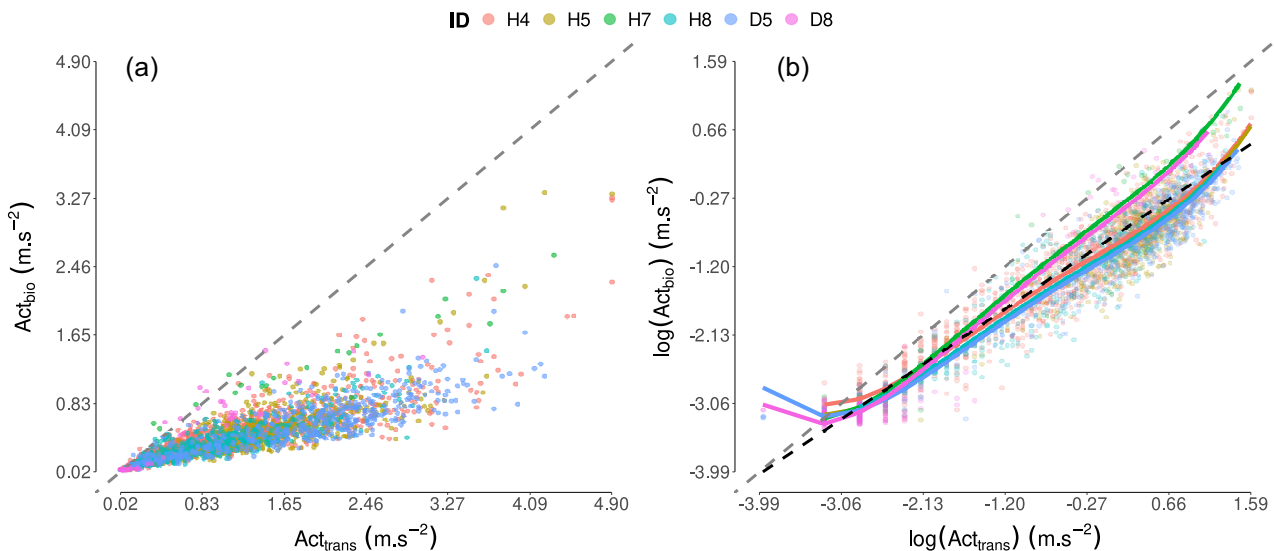


Figure 4. Scatterplots showing the relationship between the activity (in m.s^{-2}) measured by the acceleration biologgers (Act_{bio}) and by the acceleration transmitters ($\text{Act}_{\text{trans}}$), with 57-s SWS, in their natural scale (a) and after log-transformation (b). Different individuals are identified with different colours. The grey dashed line in both panels represent 1:1 relationship between both variables. The solid lines (b) show the fit of the selected LME model (4th degree polynomial) per individual, while the black dashed line shows the global fit of the linear (1st degree polynomial) model.

values (see Online Resource 8). This issue could be of particular concern for species with low mobility (where a greater frequency of low-activity values would be expected), especially when the acceleration transmitters are configured to detect high activities, as it diminishes the resolution. It is notable that activity estimates for the acceleration transmitter were consistently higher than those from the acceleration biologger. This, along with the individual effect included in the models, could be a consequence of bearing non-fixed accelerometer transmitters. The lack of a fixed position and varying stability of the surgically implanted accelerometers might increase both

the recorded activity and individual differences in prediction accuracy (Wilson *et al.*, 2019). This issue, however, has been scarcely considered in the literature, being a common practice to place the acoustic accelerometers internally (e.g. Kneebone *et al.*, 2018) due to other advantages (Brownscombe *et al.*, 2019).

A loss in the accuracy of the activity estimates from the acceleration transmitters was also evident as the activity level increased. This may be caused by (1) the lower recording frequency of the acoustic transmitters compared to the acceleration biologgers, (2) the narrower acceleration measurement

Table 1. Results of the linear mixed effects models for activity (RMS) measured by acceleration biologgers (Act_{bio}), with a 57-s sampling-window size (Goal 1). Model structure, model coefficients, explained variances, degrees of freedom, ΔAIC, and ΔBIC values are shown. Due to space limitations in the Table, model structure specified following the “nlme” notation refers to the general model of the form $Y_{ij} = \beta_0 + \beta_1 x_{ij} + b_{0j} + b_{1j} x_{ij} + e_{ij}$, with $\begin{pmatrix} b_{0j} \\ b_{1j} \end{pmatrix} \sim N\left(\begin{pmatrix} \mu_0 \\ \mu_1 \end{pmatrix}, \begin{pmatrix} \sigma_0^2 & \sigma_{01} \\ 0 & \sigma_1^2 \end{pmatrix}\right)$ and $e_{ij} \sim N(0, \sigma^2)$. Act_{trans}: activity (RMS) measured by acceleration transmitters; r²m: marginal goodness-of-fit; r²c: conditional goodness-of-fit; ΔAIC₁: difference in AIC between the GLS model (without random term) and the LME model with random intercept; and ΔAIC₂: difference in AIC between the GLS model and the LME model with random intercept and slope. The selected model and random effect are shown in bold.

Model structure	Model coefficients					r ² m	r ² c	df	ΔAIC	ΔBIC	Selection of random effect	
	Intercept	a	b	c	d						e	ΔAIC ₁
Act _{bio} 5 ~ poly(Act _{trans} , 5) + Act _{trans} ID	-1.18*	60.43*	3.52*	-1.20*	3.36*	0.54	0.936	10	0	5	109	212
Act_{bio} 4 ~ poly(Act_{trans}, 4) + Act_{trans} ID	-1.18*	60.43*	3.49*	-1.16*	3.36*	-	0.884	9	1	0	121	258
Act _{bio} 3 ~ poly(Act _{trans} , 3) + Act _{trans} ID	-1.19*	60.40*	3.48*	-1.13*	-	-	0.881	8	142	136	123	270
Act _{bio} 2 ~ poly(Act _{trans} , 2) + Act _{trans} ID	-1.19*	60.34*	3.32*	-	-	-	0.883	7	152	140	125	280
Act_{bio} 1 ~ Act_{trans} + Act_{trans} ID	-0.81*	-	-	-	-	-	0.880	6	262	236	122	280

*p < 0.05.

range of the acceleration transmitters compared to acceleration biologgers, (3) the lack of a fixed attachment of the acceleration transmitters within the fish body, and (4) a combination of all these factors. Lower recording frequencies may cause drops in the detection of sporadic, high activity behaviours (Broell *et al.*, 2013) and narrower acceleration measurement ranges may cause acceleration transmitters saturate. That, together with the possible magnification of the acceleration records due to the absence of stability and a fixed attachment of the acceleration transmitters within the coelomic cavity of fish, might cause an increase of the variance in the activity estimates from acceleration transmitters. Nevertheless, and similar to what was observed in previous studies (Murchie *et al.*, 2011; Kneebone *et al.*, 2018; Hori *et al.*, 2019), the predominance (otherwise expected, see Priede, 1977) of low activity values may have minimized the problem, which could be of greater concern in more active species.

Goal 2: effects of binning activity from acceleration transmitters

The density functions showed a lower proportion of activity estimates near zero from the acceleration transmitters as the TBS increases. This was expected as the fish are less likely to remain immobile for time periods of increasing duration. Also, the number of detections on its own or integrating the interaction term was always included in the selected models, pointing to the relevance of this variable. However, according to the results, the importance of n_{det} for the predictions enlarges as the TBS increases, which is likely related to the strongest association of n_{det} with the activity of the fish as the TBS increases. For small time bins (e.g. 6 min), it seems reasonable that a low (e.g. 1) or high (e.g. 3) n_{det} is less dependent on the activity level of the fish, being related, simply, to the random recording and transmission of acoustic transmitters. However, as TBS increases, the correlation of n_{det} with fish activity is expected to increase, especially for low values of n_{det}, since a low n_{det} at large bin sizes is impossible to be due to randomness in the recording and transmission of the acoustic transmitters, but rather to an individual strongly associated with its refuge, where activity usually is weak (i.e. resting) and the probabilities for acoustic signals to be propagated is lower. This would explain why the weight of n_{det} in predictions increases as the TBS increases or why the activity estimates from the acceleration transmitters were less accurate at the shorter time bins, particularly for low activity values: the larger the TBS, the less likely that a low number of detections occurred when the animal was indeed very active for the whole time bin.

When the use of time intervals is needed in the context of the study design, the selection of an appropriate TBS appears as a trade-off between a time bin small enough to capture the complexities of a dynamic activity pattern, at the expenses of a slightly loss in accuracy, and a time bin long enough to get more robust activity estimates, which implies losing resolution. For large time bins (i.e. > 30 min), it would be advisable to establish a threshold for the number of detections (e.g. n_{det} ≥ 2), below which activity estimates might be discarded. Different TBSs have been used in the literature: for example, Taylor *et al.* (2013) used 15-min, Runde *et al.* (2020) 30-min, and Udyawer *et al.* (2017) 60-min bins. The selection of an adequate TBS or of a threshold number of detections should take into account the objectives of the study and its design, as well as previous knowledge, at least qualitative, on the behaviour of the species targeted.

Table 2. Results of the linear mixed effects models for activity measured by the acceleration biologgers (Act_{bio}) with different TBSS.

TBSS	Model structure	Coefficients				r ² m	r ² c	df	ΔAIC	Selection of random effect	
		Intercept	Act _{trans}	n _{det}	Act _{trans} × n _{det}					ΔAIC ₁	ΔAIC ₂
6	Act _{bio} ~ Act _{trans} + Act _{trans} ID	-1.24*	0.57*	-	-	0.723	0.761	6	36	21	94
	Act _{bio} ~ Act _{trans} + n _{det} + Act _{trans} ID	-1.23*	0.57*	-0.05*	-	0.723	0.762	7	38	23	95
	Act _{bio} ~ Act _{trans} + Act _{trans} × n _{det} + Act _{trans} ID	-1.24*	0.55*	-	0.11*	0.728	0.765	7	0	24	85
	Act _{bio} ~ Act _{trans} + n _{det} + Act _{trans} × n _{det} + Act _{trans} ID	-1.24*	0.55*	-0.00	0.11*	0.728	0.765	8	8	24	85
15	Act _{bio} ~ Act _{trans} + Act _{trans} ID	-1.29*	0.55*	-	-	0.715	0.774	6	64	14	102
	Act _{bio} ~ Act _{trans} + n _{det} + Act _{trans} ID	-1.26*	0.55*	-0.03	-	0.715	0.775	7	69	17	105
	Act _{bio} ~ Act _{trans} + Act _{trans} × n _{det} + Act _{trans} ID	-1.29*	0.47*	-	0.12*	0.741	0.786	7	0	24	63
	Act _{bio} ~ Act _{trans} + n _{det} + Act _{trans} × n _{det} + Act _{trans} ID	-1.32*	0.46*	0.04*	0.14*	0.744	0.786	8	4	16	49
30	Act _{bio} ~ Act _{trans} + Act _{trans} ID	-1.27*	0.58*	-	-	0.757	0.796	6	40	4	39
	Act _{bio} ~ Act _{trans} + n _{det} + Act _{trans} ID	-1.33*	0.58*	0.04*	-	0.757	0.796	7	45	2	39
	Act _{bio} ~ Act _{trans} + Act _{trans} × n _{det} + Act _{trans} ID	-1.27*	0.48*	-	0.09*	0.776	0.805	7	15	13	21
	Act _{bio} ~ Act _{trans} + n _{det} + Act _{trans} × n _{det} + Act _{trans} ID	-1.45*	0.41*	0.13*	0.13*	0.786	0.808	8	0	0	5
60	Act _{bio} ~ Act _{trans} + Act _{trans} ID	-1.29*	0.58*	-	-	0.733	0.760	6	99	3	11
	Act _{bio} ~ Act _{trans} + n _{det} + Act _{trans} ID	-1.34*	0.58*	0.03	-	0.734	0.759	7	106	0	9
	Act _{bio} ~ Act _{trans} + Act _{trans} × n _{det} + Act _{trans} ID	-1.28*	0.29*	-	0.17*	0.774	0.800	7	40	13	15
	Act _{bio} ~ Act _{trans} + n _{det} + Act _{trans} × n _{det} + Act _{trans} ID	-1.75*	0.12*	0.23*	0.24*	0.806	0.814	8	0	-2	-1
120	Act _{bio} ~ Act _{trans} + 1 ID	-1.27*	0.63*	-	-	0.756	0.763	6	68	1	0
	Act _{bio} ~ Act _{trans} + n _{det} + 1 ID	-1.82*	0.61*	0.20*	-	0.784	0.784	7	41	-2	-5
	Act _{bio} ~ Act _{trans} + Act _{trans} × n _{det} + 1 ID	-1.27*	0.23	-	0.15*	0.771	0.785	7	52	5	6
	Act _{bio} ~ Act _{trans} + n _{det} + Act _{trans} × n _{det} + 1 ID	-2.00*	0.06	0.26*	0.21*	0.816	0.816	8	0	-2	-4

*p < 0.05. The TBSS in minutes, model structure, model coefficients, variance explained, degrees of freedom, and ΔAIC values are shown. Due to space limitations in the Table, model structure was specified following the “lme” notation, with the same distributional assumptions for the random effects as those specified in Table 1. Act_{trans}: activity (RMS) measured by acceleration transmitters; n_{det}: number of detections; r²m: marginal goodness-of-fit; r²c: conditional goodness-of-fit; ΔAIC₁: difference in AIC between the GLS model (without random term) and the LME model with random intercept; and ΔAIC₂: difference in AIC between the GLS model and the LME model with random intercept and slope. The selected models and random effects are shown in bold.

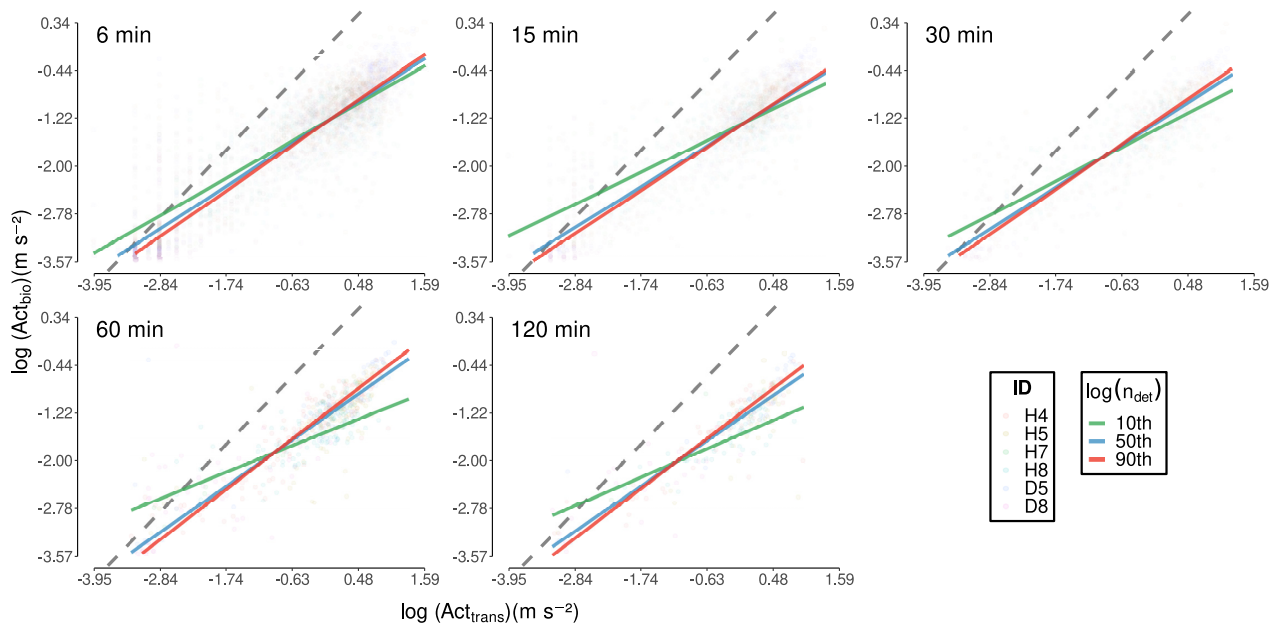


Figure 5. Scatterplots showing the relationship between activity estimates obtained with the acceleration biologgers (Act_{bio}) and transmitters (Act_{trans}), averaged by time bins of differing sizes. The continuous lines represent model predictions from the fixed linear predictor when the 10th (green), 50th (blue), and 90th (red) percentile of activity detections (n_{det}) was considered. The dashed line represents 1:1 fit between both variables.

Table 3. Descriptive statistics and results for the unpaired two-sample Wilcoxon test (UWT) of the differences in activity between “reference” and “detection” windows.

Fish ID	Act_{Ref}	Act_{Det}	r	$p_{Two-sided}$	$p_{One-tailed}$	n_{Ref}	n_{Det}
H4	0.250	0.353	0.106	< 0.001*	< 0.001*	18 704	1 761
H5	0.040	0.040	0.011	0.7061	0.353	1 096	102
H7	0.226	0.245	0.021	< 0.001*	< 0.001*	29 646	3 879
H8	0.167	0.224	0.057	< 0.001*	< 0.001*	26 050	1 998
D5	0.343	0.340	0.001	0.9368	0.5316	11 396	1 655
D8	0.033	0.033	0.022	< 0.05*	< 0.05*	8 398	773

* $p < 0.05$. Act_{Ref} and Act_{Det} : median activity for “reference” and “detection” windows, respectively; r : effect size; $p_{Two-sided}$ and $p_{One-tailed}$: p -values for both tests; n_{Ref} and n_{Det} : sample-size for “reference” and “detection” windows, respectively.

Goal 3: assessment of potential sampling-bias in data acquisition

The present study has highlighted a trend towards greater activity in the detection than in the reference windows, despite important individual differences, a pattern explainable by the sheltering behaviour of the dusky grouper, so that they would be less audible for the receivers during low-activity periods within their crevices. Furthermore, the individual variability detected supports recent claims about individual behaviour as a source of sampling bias (Frair *et al.*, 2010; Stuber *et al.*, 2013; Caravaggi *et al.*, 2020), so that not only differences between species, but also between individuals, should be evaluated when studying activity patterns with acoustic telemetry technology (Killen *et al.*, 2016; Villegas-Ríos *et al.*, 2017).

Although there was evidence of biases in the data collected by acceleration transmitters, it was consistently small for all tagged fish, suggesting no marked differences in activity among habitats with distinct capacities for acoustic signals propagation. Hence, it can be considered that in this system, acceleration transmitters provided an adequate overall estimation of the activity level for the population studied although mean or median activity estimates would likely be inflated.

Goal 4: performance of three common proxies for activity

The results clearly point to the proxies “Number of Total detections” and “Number of Unique detections” as very poor predictors of activity. In the case of “Depth range”, although the results suggest it is a better predictor of activity, it is still far below the prediction power of the acceleration transmitters (33 vs. 81%), both compared at time bins of 1 h. The consistency of the results at different TBSs (15-, 30-, and 60- min) and at both temporal scales for the three proxies of activity evaluated, strengthens the conclusions of our analyses.

Assumptions on the use of the number of detections as proxies for activity strongly rely on effective displacements. In this sense, a low number of detections would relate to an individual hidden most of the time and, therefore, less active, which would go at least partially unnoticed by the receivers (Koeck *et al.*, 2014), establishing a relationship between the number of detections and the activity level. This is quite possible for rocky-reef fish species such as the dusky grouper, which spend significant periods of their time resting or moving slowly around their refuge. However, fish may be outside

Table 4. Results of the linear mixed-effects models for assessing the performance of the number of unique (Unique) and total (Total) detections, and the depth range (Depth) as proxies for activity in dusky grouper.

Temporal scale	Proxy	TBS	Model structure	r^2_m	r^2_c	df	ΔAIC	Selection of random effect	
								ΔAIC_1	ΔAIC_2
Short	Depth range	15	Act_{bio} ~ Intercept	0.000	0.559	5	6.1	–	–
			Act_{bio} ~ Depth + Depth ID	0.223	0.533	6	0	413	532
		30	Act_{bio} ~ Intercept	0.000	0.643	5	6.3	–	–
			Act_{bio} ~ Depth + Depth ID	0.331	0.645	6	0	296	401
		60	Act_{bio} ~ Intercept	0.000	0.702	5	7.8	–	–
			Act_{bio} ~ Depth + Depth ID	0.325	0.675	6	0	144	186
	Total detections	15	Act_{bio} ~ Intercept	0.000	0.292	5	0	–	–
			Act_{bio} ~ Total + Total ID	0.025	0.273	6	9.8	125	162
		30	Act_{bio} ~ Intercept	0.000	0.341	5	0	–	–
			Act_{bio} ~ Total + Total ID	0.024	0.329	6	11.3	58	81
		60	Act_{bio} ~ Intercept	0.000	0.341	5	0	–	–
			Act_{bio} ~ Total + Total ID	0.011	0.362	6	13.1	22	33
Unique detections	15	Act_{bio} ~ Intercept	0.000	0.288	5	0	–	–	
		Act_{bio} ~ Unique + Unique ID	0.008	0.293	6	8.8	201	265	
	30	Act_{bio} ~ Intercept	0.000	0.328	5	0	–	–	
		Act_{bio} ~ Unique + Unique ID	0.015	0.335	6	9.5	100	140	
	60	Act_{bio} ~ Intercept	0.000	0.337	5	0	–	–	
		Act_{bio} ~ Unique + Unique ID	0.005	0.363	6	11.2	45	68	
Long	Depth range	15	Act_{bio} ~ Intercept	0.000	0.126	5	23.7	–	–
			Act_{bio} ~ Depth + Depth ID	0.063	0.117	6	0	8 073	9 064
		30	Act_{bio} ~ Intercept	0.000	0.167	5	25.6	–	–
			Act_{bio} ~ Depth + Depth ID	0.084	0.159	6	0	7 003	7 794
		60	Act_{bio} ~ Intercept	0.000	0.195	5	25.3	–	–
			Act_{bio} ~ Depth + Depth ID	0.091	0.190	6	0	5 006	5 621
	Total detections	15	Act_{bio} ~ Intercept	0.000	0.081	5	0	–	–
			Act_{bio} ~ Total + Total ID	0.007	0.071	6	4.6	9 888	11 400
		30	Act_{bio} ~ Intercept	0.000	0.112	5	0	–	–
			Act_{bio} ~ Total + Total ID	0.009	0.099	6	6.1	7 475	8 685
		60	Act_{bio} ~ Intercept	0.000	0.146	5	0	–	–
			Act_{bio} ~ Total + Total ID	0.011	0.130	6	7.9	5 131	5 922
Unique detections	15	Act_{bio} ~ Intercept	0.000	0.053	5	0	–	–	
		Act_{bio} ~ Unique + Unique ID	0.000	0.054	6	9.7	8 162	8 978	
	30	Act_{bio} ~ Intercept	0.000	0.076	5	0	–	–	
		Act_{bio} ~ Unique + Unique ID	0.000	0.075	6	1.8	6 085	6 928	
	60	Act_{bio} ~ Intercept	0.000	0.110	5	0	–	–	
		Act_{bio} ~ Unique + Unique ID	0.000	0.113	6	11.3	4 186	4 763	

Act_{bio} and Act_{trans} were the dependent variables for the short- and long-scale models, respectively. The TBS in minutes, model structure, variance explained, degrees of freedom, and ΔAIC values are shown. Due to space limitations in the Table, model structure was specified following the “nlme” notation, with the same distributional assumptions for the random effects as those specified in Table 1. r^2_m : marginal goodness-of-fit; r^2_c : conditional goodness-of-fit, ΔAIC_1 : difference in AIC between the GLS model (without random term) and the LME model with random intercept; and ΔAIC_2 : difference in AIC between the GLS model and the LME model with random intercept and slope. The selected model and random effect for each TBS are shown in bold.

their shelters, and hence be detectable, but still stay stationary. Therefore, it seems that there is no robust rationale for establishing a relationship between the number of detections and activity, something supported by our results, which evidence the almost negligible prediction power of the number of detections of the activity estimates made by accelerometers (both from the biologist and the transmitter).

Similarly to the number of detections, the use of changes in depth as a proxy of activity is based on the assumption of its close relationship with movement (e.g. Brazo *et al.*, 2021). This rationale seems more logical than using the number of detections as a proxy of activity, as although “Depth range” only relates to vertical movements, it is somehow related to

the movement of animals. However, it should not be ignored that fishes can also be very active at a certain depth, such as occurs, for example, in nesting or territorial species, which would worsen the predictive power of the “Depth range” of the activity estimates made by accelerometers (both from the biologist and the transmitter). In this regard, although our results show that the “Depth range” is a substantially better predictor of activity than the number of detections, it is still well below the prediction power of acceleration transmitters. This, together with the differences in the predictive power of “Depth range” found between the short and the long-term scales, suggests that conclusions derived from the use of this proxy should be cautious, as its utility may vary over time,

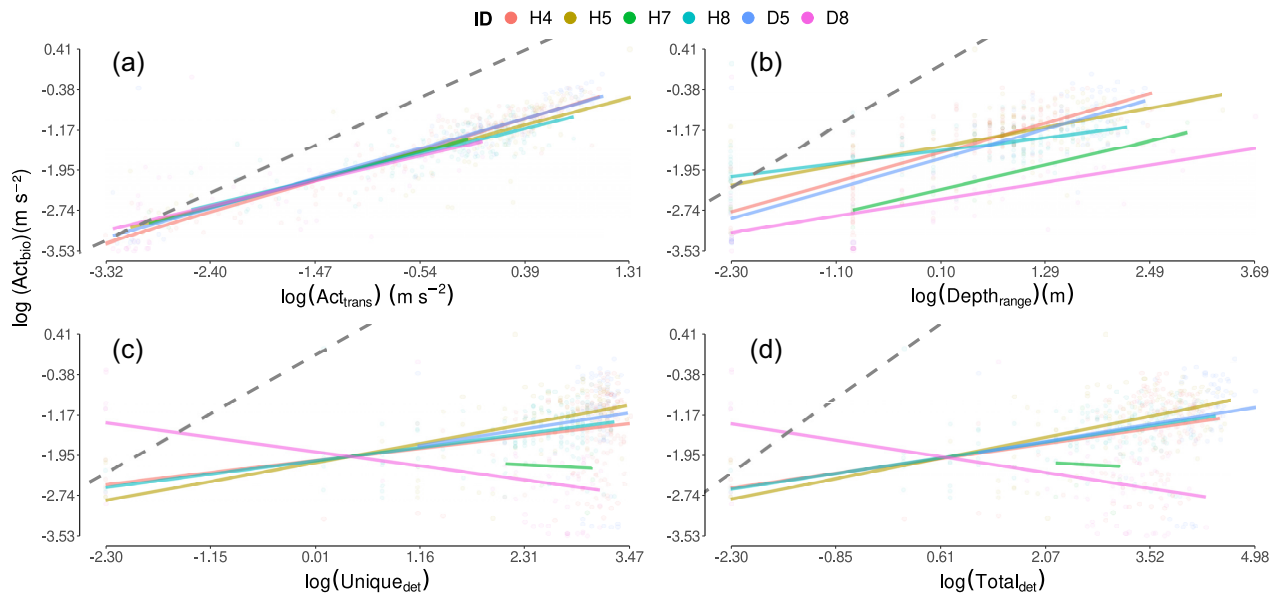


Figure 6. Scatterplots showing the relationship between activity estimates obtained with the acceleration biologgers (Act_{bio}) and the averaged activity estimates obtained with the acceleration transmitters (Act_{trans}) (a), depth-range (Depth) (b), number of unique detections (Unique) (c), and number of total detections (Total) (d), at the short-term scale (\sim days). All the variables were calculated at 1-h TBSs and log-transformed. Different fish are identified with different colours. In each panel, solid regression lines show model predictions for each fish. The dashed line represents a 1:1 fit between both variables.

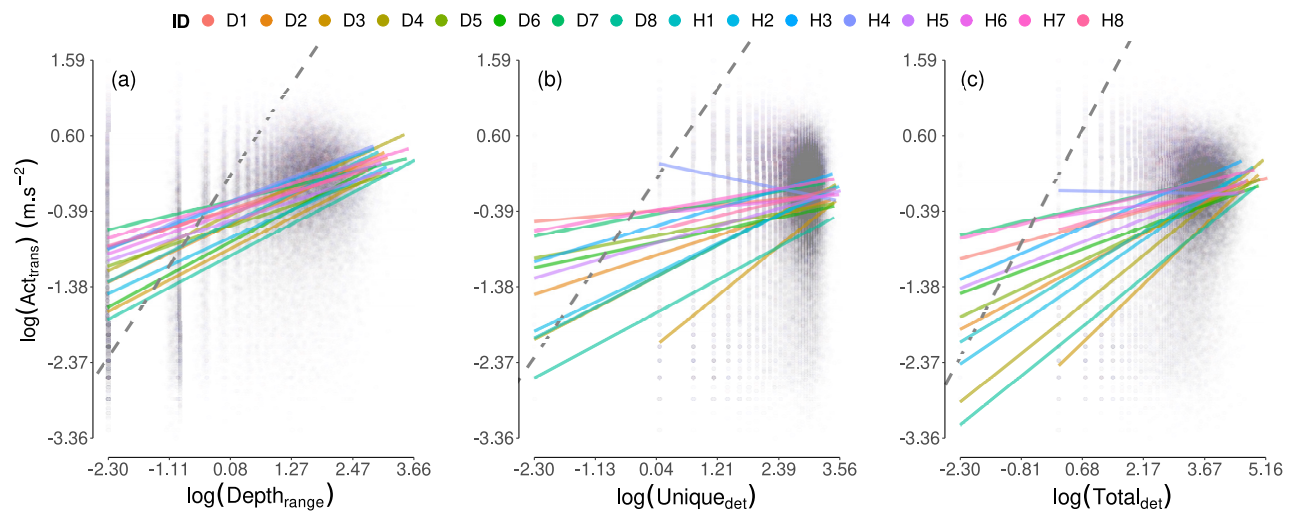


Figure 7. Scatterplots showing the relationship between averaged activity estimates obtained with the acceleration transmitters (Act_{trans}) and the depth-range (Depth) (a), number of unique detections (Unique) (b), and number of total detections (Total) (c), at the long-term scale (\sim months). All the variables were calculated at 1-h TBSs and log-transformed. Different fish are identified with different colours. In each panel, solid regression lines show model predictions for each fish. The dashed line represents a 1:1 fit

probably linked with the behavioural characteristics of the species under study.

Conclusions

The interpretation of the data obtained with acoustic telemetry is complex due to the influence of multiple factors, ranging from environmental conditions to technical and operational constraints that can introduce variability and biases (Murchie *et al.*, 2011; Huvneers *et al.*, 2016). In the dusky grouper, the number of unique and total detections were very poor predic-

tors of the activity level estimated with accelerometers, which detect movement that not necessarily imply displacement. Although depth range performed better than the number of detections and predicted more closely the variation in activity determined by accelerometry, its predictive power was still low and varied considerably between time scales. Based on the results presented in this study, the use of non-acceleration-derived proxies, an approach widely applied in the context of acoustic telemetry for species differing in ecology and behaviour (e.g. Koeck *et al.*, 2014; Gandra *et al.*, 2018; Brazo *et al.*, 2021), should be taken with caution when they have not been appropriately validated.

Regarding the use of acceleration as a proxy of activity, there is a broad consensus about its utility in both the aquatic and terrestrial environments (Wilson *et al.*, 2019). Our results showed that, despite some activity overestimation due to sampling bias, it is small enough to consider that built-in accelerometers included in acoustic transmitters are reliable for describing the overall activity of the dusky grouper. Nevertheless, we also evidenced that the predictive power of activity estimated with acceleration transmitters is constrained, particularly for the most extreme values. Inherent limitations of acoustic transmitters (e.g. intermittency of data recording, among-habitats differences in acoustic signals propagation, and so on) together with operational constraints (e.g. the need to pool activity into time bins) are key aspects to consider for proper study design and the interpretation of the data obtained.

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Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

Data availability statement

Data used in this manuscript are available at <http://hdl.handle.net/10201/124130>.

Author contributions statement

JMP and JAG-C conceived the ideas; JMP designed the methodology; JMP and PJ-M collected the data; JMP; CG-C and LAV analysed the data; and JMP and LAV led the writing of the manuscript. JMP, LAV, CG-C, JEC, DA, PJ-M, and JAG-C contributed critically to the draft and gave final approval for publication.

Conflict of interest statement

The authors declare they have no conflict of interest.

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