Journal of Fish Biology
Article In Press
Acceptation date : July 2023
https://doi.org/10.1111/jfb.15507
https://archimer.ifremer.fr/doc/00847/95906/

Archimer
https://archimer.ifremer.fr

A Novel Protocol For Rapid Deployment Of Heart Rate Data Storage Tags In Atlantic Bluefin Tuna Thunnus Thynnus Reveals Cardiac Responses To Temperature And Feeding

Rouyer Tristan [1, *], Bonhommeau Sylvain [2], Bernard S. [3], Kerzerho V. [3], Derridj Olivier [1], Bjarnason Á. [4], Allal H. [5], Steffensen J. F. [6], Deguara S. [7], Wendling B. [8], Bal G. [9], Thambithurai Davide [10], McKenzie D. J. [10]

[1] MARBEC Univ Montpellier, CNRS, IFREMER, IRD Sète, France
[2] IFREMER DOI, rue Jean Bertho, 97822 Le Port, La Réunion
[3] LIRMM, Univ. Montpellier, CNRS Montpellier, France
[4] Star-Oddi Ltd. Garðabær, Iceland
[5] University Hospital of Montpellier Montpellier, France
[6] Marine Biological Section University of Copenhagen, Strandpromenaden 5, 3000 Elsinore ,Denmark
[7] AquaBioTech Group, 'Central Complex', Naggar Street, Targa Gap, Mosta MST 1761, MALTA
[8] SATHOAN, 29, promenade J.B. Marty, 34200 Sète ,France
[9] UMS PatriNat (OFB-CNRS-MNHN), 4 rue du Petit Château, 91800 Brunoy,France
1 [0] MARBEC Univ Montpellier, CNRS, IFREMER, IRD Sète, France

* Corresponding author : Tristan Rouyer, email address : tristan.rouyer@ifremer.fr

Abstract :

The Atlantic bluefin tuna (ABFT) is a highly prized species of large pelagic fish. Studies of their environmental physiology may improve understanding and management of their populations, but this is difficult for mature adults because of their large size. Biologging of heart rate holds promise in investigating physiological responses to environmental conditions in free-swimming fishes but it is very challenging to anaesthetise large ABFT for invasive surgery to place a tag in the body cavity near to the heart. We describe a novel method for rapid deployment of a commercially available heart rate tag (HR-tag) on ABFT, using an atraumatic trocar to implant it in the musculature associated with the cleithrum. We performed three sequential experiments to show that the tagging method 1) is consistently repeatable and reliable; 2) can be used successfully on commercial fishing boats and does not seem to affect fish survival, and 3) is effective for long-term deployments. In experiment 3, a tag logged heart rate over 80 days on a 60-kg ABFT held in a farm cage. The logged data showed that heart rate was sensitive to prevailing seasonal temperature and feeding events. At low temperatures, there were clear responses to feeding but these all disappeared above a threshold temperature of 25.5 °C. Overall, the results show that our method is simple, rapid and repeatable, and can be used for long term experiments to investigate physiological responses by large ABFT to environmental conditions.

Keywords : Heart Rate, Atlantic Bluefin Tuna, Tagging, Protocol, Longliner, Physiology

Please note that this is an author-produced PDF of an article accepted for publication following peer review. The definitive publisher-authenticated version is available on the publisher Web site.

Accepted

INTRODUCTION

The Atlantic bluefin tuna (*Thunnus thynnus*, hereafter ABFT) is a large and highly migratory pelagic species that supports a valuable international fishery (Fromentin and Powers, 2005). For ABFT, understanding the interplay between environmental conditions and migrations has important implications in terms of the species' exploitation and conservation in a context of global change (Rooker et al., 2007; Fromentin et al., 2014b, 2014a; Failletaz et al., 2019). Studies of tuna environmental physiology may provide insights into drivers of migratory movements (Block et al., 2011, 2001; Brill, 1994; Clark et al., 2013; Fry, 1971; Horodysky et al., 2016; Whitlock et al., 2015). Studying the in-vivo physiology of mature adult ABFT is, however, logistically very challenging and costly, especially if it involves invasive techniques, due to their size, highly active lifestyle with obligate ram ventilation of the gills, and sensitivity to handling. Such challenges largely explain why physiological studies on bluefin tuna species are scarce and generally involve

/onlineLibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Accepted Article

experiments on small individuals (Blank et al., 2007a, 2007b; Block et al., 2005, 2001; Clark et al., 2013).

For large animals, one option is to work with partners in the private sector, fishermen and fish farmers, and use techniques such as biologging to gain physiological information on animals under field conditions (Rouyer et al., 2019). Electronic data storage tags can log heart rate from the electrocardiogram (ECG) and have been used to record cardiac responses to environmental conditions by free-swimming fishes including a bluefin tuna species (Brijs et al., 2019; Clark et al., 2008; Gamperl et al., 2021; Mignucci et al., 2021). These previous studies all worked on relatively small fishes and placed the tags in the peritoneal cavity (Brijs et al., 2019; Clark et al., 2008; Gamperl et al., 2021; Mignucci et al., 2021). Such a surgical intervention on large ABFT would be extremely difficult, especially if it is from the deck of a commercial vessel, with a risk of harming the fish and obtaining little or no meaningful data.

Here, we propose a novel method for implantation of a HR-tag that is rapid, easy and relatively non-invasive, which can simplify tagging of ABFT under field conditions, such as during commercial fishing or farm husbandry operations. The HR-tag is inserted by trocar into the musculature associated with the cleithrum, where this membrane bone runs below the operculum and in close proximity to the heart. We describe three sequential experiments on live ABFT to validate the methodology. The first experiment tested the feasibility of the HR-tag deployment and the quality of the signals obtained on freshly-captured tuna on the deck of a commercial longliner. The second experiment assessed the fate of fish implanted on the deck of a longliner and then released with survival tags. The third experiment tested whether the technique was suitable for long-term deployment by implanting ABFT tuna on a fish farming barge and then releasing them into a rearing cage for several months. The HR data collected in the third experiment was analyzed to explore whether temperature and the amount of food provided was associated with variations in cardiac activity. Our findings are discussed in terms of the usefulness of the technique to study ABFT physiology.

MATERIALS AND METHODS

Ethical approval

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Accepted Article

Experimental procedures were approved by the ethics committee for animal experimentation n° 036 of the French Ministère de l'Enseignement Superieur, de la Recherche et de l'Innovation, with reference number APAFIS #32610-2021062115252354 v7.

Tagging protocol

Tagging was performed on conscious fish on the deck of a vessel, with fish placed on a large plastic covered mattress, their eyes covered with a cloth and gills force-ventilated with a flow of seawater (see below). ABFT shows tonic immobility when air-exposed and placed on their side, facilitating tagging procedures. The site of tagging was the fleshy area below the operculum, into muscles associated with the cleithrum that, in ABFT, is in close proximity to the heart. It is rich in fat and thick enough to hold an implanted tag (Fig. 1 panel A). Tag placement was by trocar (Patel et al., 2019) with a cannula that had an internal diameter similar to the tag diameter. We used a disposable 15x150mm atraumatic trocar that allows wound healing without sutures (Kii Fios First Entry Trocar, Applied Medical). First, a small incision was made in the skin (10 mm diameter, 5 mm deep) a couple of centimeters under the point of maximum curvature of the operculum (Fig. 1 panels A-B). The trocar was sterilized in a bath of chlorhexidine and then inserted into the incision and advanced parallel to the lower edge of the operculum, where it followed a groove in the cleithrum, within the thickness of the flesh (Fig. 1, panel B). The depth of insertion has to be carefully considered depending on the size of the fish, to ensure that the trocar remains within the muscle and does not risk damaging or traversing the membranous cleithrum, which may also lead to damage of underlying blood vessels or the heart in smaller individuals. As a rule of thumb the depth of insertion was at least 2 cm, to allow the flesh to close back together completely as the trocar was withdrawn, which it was hoped would promote rapid healing. The obturator of the trocar was then removed and the cylindrical HR-tag (Star-Oddi® Centi-HRT-ACT) inserted into the open cannula (Fig. 1 panels C-D), then the obturator is used to advance the tag gently into the tissue. The whole trocar was then removed; the flesh closed completely behind the trocar and no suture was used to close the point of entry, as this would increase handling time with potential negative effects on fish recovery.

Experiment 1: Efficacy of the method

The tagging protocol was tested on three live ABFT caught during a French commercial longliner set in the Gulf of Lions (Rouyer et al., 2021). Longliners operate on short sets and numerous

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Accepted Article

ABFT are still alive when hauled onboard, providing the opportunity to perform rapid and brief tag deployments. The ABFT fishery is strictly regulated, fish are killed immediately after they have been hauled onboard.

The fish handling protocol has been described in detail previously (Rouyer et al., 2020, 2019). Three Centi-HR-ACT tags were programmed using Mercury software 5.99 (Star-Oddi, Iceland) to continuously record HR every other minute. Three fish were implanted, the first (HR-tag1, 120 cm SFL) had just been killed by the Ike Jime technique (Pérez-Lloréns, 2019) but was not bled, to maximize the chances that the heart would still be beating. The other two (HR-tag2 126 cm and HR-tag3 152 cm) were implanted alive. The tags were left in the fish for about three minutes then animals were killed and/or bled by the fishermen, and tags retrieved. Data were immediately downloaded and the quality of ECG signals visually inspected using Star-Oddi Pattern Finder software.

Experiment 2: Survival of tagged fish

The potential effect of HR-tag deployment on mortality was tested on three ABFT (138 cm, 149 cm and 116 cm) fitted with survival tags (Spat, Wildlife Computers), during the same fishing operation as for Experiment 1. The Spat tags were deployed as described previously (Rouyer et al., 2020, 2019). The third fish was also implanted by trocar with a non-functional Centi-HR-tag, to compare survival of implanted and non-implanted fish. Death of the animal causes tag release and they were set to release after 50 days, which would indicate survival until at least that time. Information about the area of release was received via the Argos system. The time out of the water was below 2 minutes for all fish, which were then immediately released back into the wild.

Experiment 3: Long-term deployment of HR-tag

To test suitability of the tagging protocol for longer deployments studies, we implanted three fish in a fattening cage in Malta with custom-made Star-Oddi DST centi-HRT ACT G2 (70 mm long, 15 mm diameter, 26.5 g weight in air), and placed a spaghetti tag on the dorsal fin, for visual identification. The fish spent less than 3 minutes out of the water and were then released back into the cage.

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Accepted Article

The tags were custom-made to allow more memory and a larger battery. They were programmed so that each 10 minutes they recorded the ECG for 7.5 s at 200 Hz; tri-axial acceleration for one minute at base frequency 25 Hz, and temperature. On-board algorithms within the tags calculated heart rate and an associated quality index (QI), and various statistical variables for external acceleration (EA) every ten minutes. EA is the recorded 3-axis acceleration above standard gravity defined with static calibration, normalized, and calculated as the vectorial sum in mg. The approach is similar to both the calculation of vectoral sum of body acceleration (VeDBA) (Qasem et al., 2012; Shepard et al., 2008) and minimum specific acceleration (MSA) (Simon et al., 2012). We report the average activity values (AvgEA). Raw data for ECG and acceleration was stored once every 30 minutes.

The quality of the ECG traces used to calculate HR was verified using HRT-Analyzer software (v. 1.1.0, Star-Oddi) as the QI, which ranged from QI=0 (Excellent) to QI=3 (Poor), with visual inspection of ECG traces to confirm the HR values returned by the algorithm. HR measurements with QI=3 and 2 were eliminated as well as heart rates above 120 bpm or below 8 bpm, this latter being the lower theoretical limit of HR measurable over a 7-s interval. See electronic supplementary material.

Data for each variable were then summarized over each day as the median for heart rate (HRm), peripheral body temperature (TPm) and acceleration (ACm), and the variability in temperature over each day was measured through its interquartile range (TPiq). The daily total food fed to the cage was recovered from the fish farm to further interpret daily variations in HR.

The variations in HRm in relation to total food given to the cage (TF), TPm, TPiq and ACm were investigated using a model selection approach with a set of nested linear models. The set of models that we considered, to assess whether the variables had a statistically significant impact on HRm can be summarized as follows :

$$\begin{cases} HRm_t \sim Poisson(\mu_t) \quad (1) \\ \mu_t \sim \alpha + \beta_i \times X_{i,t} \end{cases}$$

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Where X_i denotes the i^{th} variable included and β_i is the parameter linking it linearly to HRm.
The use of a Poisson over a Gamma error model was decided after some preliminary analyses and for the sake of parsimony as it allows for one parameter less (details not shown). Temperature has profound physiological effects on fishes that are often not linear (Fry, 1971; Schulte et al., 2011), so we decided to test for temperature thresholds associated with a change in the intensity and/or polarity of the link between HRm and the variable considered. To do so, for each given temperature variable TX, we refined the second line of equation set (1) as such:

$$\mu_t \sim \alpha + \beta_{TX} \times TX_t$$
$$with \beta_{TX} =$$

Here we considered all the possible combinations of the variables TF, TPm, TPiq and ACm but limited the complexity to only one threshold. We developed this nested modeling in a Bayesian framework because it provided i) a formal and flexible framework to estimate threshold effects, and ii) estimates of parameter uncertainties in a fully probabilistic framework. The nested models were compared using two criteria. The first was Deviance Information Criterion (Spiegelhalter et al., 2002), whose rationale is comparable to that of AIC in that it allows the comparison of goodness of fit while penalizing complexity. The smaller the DIC the better and a five points reduction is usually considered as indicative of a significant improvement. Second, we reinforced the selection of significant variables by looking at the percentage of variance explained by each model through their R^2.

Models were implemented with JAGS software (Plummer, 2003) through the library Rjags in R (R Development Core Team, 2022). Specifically, we ran three MCMC in parallel for each model fit. We kept 10000 draws for each one after an initial burning period of 10000 draws. All the parameters used were given non-informative priors. MCMC mixing and convergence were established by visual inspection of the chains' histories and by means of Brooks-Gelman-Rubin statistics (Brooks and Gelman, 1998). The code and data are available upon request to the authors.

RESULTS

Accepted Article

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Accepted Article

Experiments 1 and 2

The tag implantation only caused limited hemorrhaging and the briefly recorded data displayed a high signal to noise ratio. HR-tag1 displayed a signal identifiable as an ECG (Fig. 2). HR-tag2 and HR-tag3 recorded some signals that were identifiable as ECGs (Fig 2) although, overall, the data were not uniform and less clear than HR-tag1. Two of the three survival tags reported after 50 days, one off to the Southeast of Majorca from the fish implanted with the HR-tag, the other near the Western coast of Sardinia (Fig 3).

Experiment 3

This experiment confirmed that implanted ABFT do not show subsequent mortality as two were slaughtered during farming operations and the last one is currently still alive in the cage. The tag was retrieved successfully from ABFT5, HR-tag5 (mass 60kg), at slaughter 80 days after deployment. Of 11368 measurements collected, 9680 passed quality control, representing 85%. These data showed a very clear signal with repeated waveforms and elements that are discernable as PQRST components (Fig. 3). The waveform was generally well-preserved across measurements samples and variations in the ECG are clearly visible among the 7 second recordings. The data were generally much less noisy than those obtained in experiment 1, with less noise and clearer ECGs.

All variables monitored during the experiment showed variations but also trends. Heart rate ranged between 8 and 109 beats per minute (bpm) but 90% of the data were between 29 and 70 bpm, with a median of 50 bpm. Figure S1 in Supplementary Material shows a frequency distribution of HR measures, indicating a bimodal distribution with two peaks at 35-40 bpm and 55-60 bpm. There was a general downward trend in HRm over time (Fig. 4), but clear daily variations could be seen over certain time periods (Fig. 5). Meanwhile, the TF also displayed strong variations, ranging from 0 kg up to 20 tons. Over the deployment period, the TPm decreased from about 28°C to 20°C, with variation that was less marked than for the other factors. The ACm had a rather noisy signal, with a slightly increasing trend.

The variations in HR at different time scales, daily or over longer periods, seemed to be associated with different processes. Over some periods, for example, clear daily patterns in AC and HR appeared, with sudden increases in activity followed by a sharp increase in HR that progressively

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

decreased until another peak of activity occurred (Fig. 5). When the cage was fasted for more than two days, there was an increased variability of AC and TP (e.g. in late October Fig. 5).

Daily median values for each variable displayed clear patterns (Fig. 6). HRm was stable until the beginning of October, when it started to become more variable, with a decreasing trend. It decreased from about 60 bpm to about 35 bpm over the study period, while TPm decreased from 27.5°C to 19°C and there was increasing daily variability. The ACm seemed to increase slightly over the period whereas the TF displayed fluctuations that were very similar to those of HR, but without displaying a similar decreasing long-term trend.

The nested modeling approach indicated that TF and TPm were explanatory variables for HRm. The best model DIC included a threshold effect of TPm on TF and a linear effect of TPm on HRm (Table 1). All models with this threshold effect of TPm on TF had significantly lower DIC and higher R^2 than the others. The TPm threshold in the best model was estimated to be 25.4°C [24.1-26.2] and the effect of food on HRm was not significantly different from 0 when the temperature was above that threshold, but was significantly positive below the threshold (Table 2). The effect of TPm on HRm was significantly positive as well.

The best model explained 81% of variance and its predictions captured most of the substantial variations in HRm while still being quite parsimonious (Fig. 7).

DISCUSSION

The rapid sub-opercular deployment technique for HR-tags, using a trocar, seems very promising in terms of consistent logging of good quality ECGs and HR data, and animal survival. The quality of data collection cannot be monitored during logging so it is essential to have a technique that yields meaningful information. The technique allows the HR-tag to be placed very close to the heart, consistent with the literature on optimal locations for collecting good ECG signals (Brijs et al., 2018). The entry point for the trocar is easy to identify in relation to the operculum, which allows deployments to be repeated accurately and consistently. Furthermore, because the tag is advanced deep into the tissue it is presumably less likely to move; in experiment 3 the tag remained in place for 80 days, despite an absence of stitches at the point of entry. Inspection showed that this entry point healed very well. As a consequence, good quality data was obtained over the entire experiment. The whole tagging procedure only required a few seconds and, since

Accepted Article

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

the deployment was intramuscular, the placement was relatively easy to control. This should ensure that the technique is reproducible and causes limited bleeding, being significantly less invasive than internal deployments in the body cavity, which require incisions and sutures, may cause injury to other organs, and have a risk of post-surgery complications such as infections. Therefore, this tagging technique is also less likely to affect fish health and behavior. Finally, the rapid sub-opercular technique allows easy deployment of HR-tags on very large individuals (e.g. the 280 kg tuna in experiment 3) for which more complex surgical interventions are logistically challenging.

The first and second experiments were conducted on the same day, to reveal that the technique could be applied on living ABFT, that it provided useful ECG signals, and that ABFT survived following implantation. The ECGs that were recorded during experiment 1 were, however, more noisy than in Experiment 3. This may have been partially because these were the first ever attempts at using this technique, but also because they were acute measurements on ABFT that were either brain dead (HR-tag1) or moribund (HR-tag2 and HR-tag3), and air-exposed on the deck of the ship. Experiment 2 had a very small sample size, constrained by the number of survival tags we possessed, which does not permit very firm conclusions about the effect of the technique on survival and behavior. Nonetheless, the tag implantation did not cause premature death and the distances subsequently traveled by implanted and non-implanted fish were similar. Experiment 3 confirmed that implanted ABFT did not show premature mortality.

The HR and ECG data in experiment 3 were much less noisy than those collected in experiment 1 (Fig. 3). This could be because the tag in Experiment 3 was custom-made for ABFT with longer distance between the electrodes, which may improve the overall quality of the signal by increasing the signal-to-noise ratio. The fish was also alive and able to recover from handling stress and heal any tissue wounding during implantation. Our analysis of the data from experiment 3 was not aimed at answering a specific ecological or physiological question. The objective was to illustrate the type of data that can be collected, its quality, and that it contained signals that could be interpreted in light of environmental conditions, notably temperature and feeding.

The variations in HR, ranging between 8 and 120 bpm, with 90% of the data between 28 and 70 bpm, is consistent with heart data obtained on smaller individuals (all below 21kg) of other bluefin tuna species (Blank et al., 2004; Clark et al., 2013, 2008). The data clearly showed an overall positive association of HR with temperature but work on more individuals is needed to understand

Accepted Article

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Accepted Article

the validity and the basis of a threshold around 25 °C, above which daily variations in heart rate linked to feeding were not visible. As the temperature decreased progressively over the 80 days, it was at experimental outset that the fish showed no daily fluctuations in heart rate. The fact that these became visible about three weeks later could also indicate recovery of normal cardiac activity after implantation. However, a 25-day recovery time seems unlikely because, in other teleost species, HR recovers from highly invasive surgical tag implantation in days rather than weeks (Brijs et al., 2019; Campbell, 2004; Gamperl et al., 2021; Mignucci et al., 2021). In Pacific bluefin tuna *Thunnus orientalis*, animals resume feeding within a matter of days after surgical implantation of temperature loggers in the visceral cavity (Gleiss et al., 2019), which is an indication of effective recovery.

The threshold around 25 °C may, instead, be linked to an aspect of ABFT thermal physiology. This temperature is at the warm end of the waters that adult ABFT are reported to occupy in the wild, although they will inhabit waters up to 30°C during the breeding season (Block et al., 2001; Fromentin and Powers, 2005). Wild animals can, however, use dives below the thermocline to cool off (Block et al., 2001), something that caged fish cannot do. The threshold may have occurred in the caged fish because, above this temperature, it had high oxygen demand that required constant swimming activity to ram ventilate the gills. This may have obscured any variation in daily median heart rate associated with, notably, total food. Feeding is expected to raise heart rate because of the specific dynamic action (SDA) response, the metabolic cost of feeding, digestion and assimilation that is a major component of the energy budget of fishes (Dupont-Prinet et al., 2009; Fitzgibbon et al., 2007; McCue, 2006), with heart rate responses to feeding potentially more pronounced in bluefin tuna if they also swim faster to increase ram ventilation of the gills (Clark et al., 2008; Fitzgibbon et al., 2007; Gleiss et al., 2019). At the same time, the absence of variation in daily median heart rate above 25.5 °C could also indicate that the animals were not feeding at all, because they were physiologically constrained in their ability to meet the combined oxygen demands of warmth and specific dynamic activity (Whitlock et al., 2015).

The close association of daily median heart rate with total food, below the threshold value of 25.5 °C, presumably reflects SDA responses. The SDA can itself raise heart rate due to increased metabolic oxygen demand (Dupont-Prinet et al., 2009; Iversen et al., 2010) but the close association with total food may also reflect increased swimming activity to increase rates of gill ventilation (Clark et al., 2008; Fitzgibbon et al., 2007; Gleiss et al., 2019). This is because the

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

swimming has a cost itself, which will also require increased HR and thereby enhance an association of HR to feeding in bluefin tuna species. Interestingly, although the ACm displayed some daily peaks that corresponded to increases in HRm, there was no overall and clear association between these two variables and average activity was not retained in the best model. In our data, the link between total food and average activity was somewhat at odds; in late October a period with no feeding at all was associated with an increase in average activity. A period of no feeding together with variability in temperature may explain increased average activity, if the animals were searching for food rather than just schooling at some routine speed. Although all of this is speculation at this stage, the data do indicate the kind of insights that monitoring heart rate can provide, in terms of revealing how environmental factors can influence physiology and behaviour, including the identification of thermal thresholds.

In conclusion, the proposed technique allows HR-tag to be implanted rapidly in large ABFT using a technique which is significantly simpler than the more invasive and time-consuming surgical deployments in the body cavity (Clark et al., 2008). This technique does not allow data on internal temperature to be obtained but it has the advantages that it is rapid, minimally invasive and provides high-quality ECG data over extended periods of time. The technique might be specific to ABFT because it takes advantage of the species' skeletal anatomy and its size, which allow it to withstand implantation of relatively large tags by trocar. Therefore, this specific sub-opercular technique would need to be tested on other tuna species. Nonetheless, rapid implantation by trocar of archival tags may be a useful approach for many large pelagics under field conditions, with the actual procedure of tag placement requiring validation for a given species.

ACKNOWLEDGEMENTS

This study is part of the PROMPT project funded by France Filière Pêche. We thank the crew of the "LES TROIS FRÈRES II" longliner from the SATHOAN association, whose help and support allowed Experiment 1 and 2 to happen. We also thank Malta Fish Farming and its crew, whose unique skills and continuous help and support allowed Experiment 3.

REFERENCES

Accepted Article

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Accepted Article

Blank, J.M., Farwell, C.J., Morrissette, J.M., Schallert, R.J., Block, B.A., 2007a. Influence of Swimming Speed on Metabolic Rates of Juvenile Pacific Bluefin Tuna and Yellowfin Tuna. Physiol. Biochem. Zool. 80, 167–77. https://doi.org/10.1086/510637

Blank, J.M., Morrissette, J.M., Farwell, C.J., Price, M., Schallert, R.J., Block, B.A., 2007b. Temperature effects on metabolic rate of juvenile Pacific bluefin tuna Thunnus orientalis. J. Exp. Biol. 210, 4254–4261. https://doi.org/10.1242/jeb.005835

Blank, J.M., Morrissette, J.M., Landeira-Fernandez, A.M., Blackwell, S.B., Williams, T.D., Block, B.A., 2004. In situ cardiac performance of Pacific bluefin tuna hearts in response to acute temperature change. J. Exp. Biol. 207, 881–890. https://doi.org/10.1242/jeb.00820

Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., Boustany, A., Teo, S.L., Seitz, A., Walli, A., 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. Science 293, 1310–1314.

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.-L., Ganong, J.E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W., Costa, D.P., 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475, 86–90. https://doi.org/10.1038/nature10082

Block, B.A., Teo, S.L.H., Walli, A., Boustany, A., Stokesbury, M.J.W., Farwell, C.J., Weng, K.C., Dewar, H., Williams, T.D., 2005. Electronic tagging and population structure of Atlantic bluefin tuna. Nature 434, 1121–1127. https://doi.org/10.1038/nature03463

Brijs, J., Sandblom, E., Axelsson, M., Sundell, K., Sundh, H., Huyben, D., Broström, R., Kiessling, A., Berg, C., Gräns, A., 2018. The final countdown: Continuous physiological welfare evaluation of farmed fish during common aquaculture practices before and during harvest. Aquaculture 495, 903–911. https://doi.org/10.1016/j.aquaculture.2018.06.081

Brijs, J., Sandblom, E., Axelsson, M., Sundell, K., Sundh, H., Kiessling, A., Berg, C., Gräns, A., 2019. Remote physiological monitoring provides unique insights on the cardiovascular performance and stress responses of freely swimming rainbow trout in aquaculture. Sci. Rep. 9, 9090. https://doi.org/10.1038/s41598-019-45657-3

Brill, R.W., 1994. A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. Fish. Oceanogr. 3, 204–216. https://doi.org/10.1111/j.1365-2419.1994.tb00098.x

Brooks, S.P., Gelman, A., 1998. General Methods for Monitoring Convergence of Iterative

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Simulations. J. Comput. Graph. Stat. 7, 434–455. https://doi.org/10.1080/10618600.1998.10474787

Campbell, H. a., 2004. The use of power spectral analysis to determine cardiorespiratory control in the short-horned sculpin Myoxocephalus scorpius. J. Exp. Biol. 207, 1969–1976. https://doi.org/10.1242/jeb.00972

Clark, T.D., Farwell, C.J., Rodriguez, L.E., Brandt, W.T., Block, B.A., 2013. Heart rate responses to temperature in free-swimming Pacific bluefin tuna (Thunnus orientalis). J. Exp. Biol. 216, 3208–3214. https://doi.org/10.1242/jeb.086546

Clark, T.D., Taylor, B.D., Seymour, R.S., Ellis, D., Buchanan, J., Fitzgibbon, Q.P., Frappell, P.B., 2008. Moving with the beat: heart rate and visceral temperature of free-swimming and feeding bluefin tuna. Proc. R. Soc. B Biol. Sci. 275, 2841–2850.

Dupont-Prinet, A., Claireaux, G., McKenzie, D.J., 2009. Effects of feeding and hypoxia on cardiac performance and gastrointestinal blood flow during critical speed swimming in the sea bass Dicentrarchus labrax. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 154, 233–40. https://doi.org/10.1016/j.cbpa.2009.06.015

Fitzgibbon, Q.P., Seymour, R.S., Ellis, D., Buchanan, J., 2007. The energetic consequence of specific dynamic action in southern bluefin tuna Thunnus maccoyii. J. Exp. Biol. 210, 290–298. https://doi.org/10.1242/jeb.02641

Fromentin, J.-M., Bonhommeau, S., Arrizabalaga, H., Kell, L.T., 2014a. The spectre of uncertainty in management of exploited fish stocks: The illustrative case of Atlantic bluefin tuna. Mar. Policy 47, 8–14. https://doi.org/10.1016/j.marpol.2014.01.018

Fromentin, J.M., Powers, J.E., 2005. Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. Fish Fish. 6, 281–306.

Fromentin, J.-M., Reygondeau, G., Bonhommeau, S., Beaugrand, G., 2014b. Oceanographic changes and exploitation drive the spatio-temporal dynamics of Atlantic bluefin tuna (Thunnus thynnus). Fish. Oceanogr. 23, 147–156. https://doi.org/10.1111/fog.12050

Fry, F.E.J., 1971. 1 - The Effect of Environmental Factors on the Physiology of Fish, in: Hoar, W.S., Randall, D.J. (Eds.), Fish Physiology, Environmental Relations and Behavior. Academic Press, pp. 1–98. https://doi.org/10.1016/S1546-5098(08)60146-6

Gamperl, A.K., Zrini, Z.A., Sandrelli, R.M., 2021. Atlantic Salmon (Salmo salar) Cage-Site Distribution, Behavior, and Physiology During a Newfoundland Heat Wave. Front. Physiol. 12, 719594. https://doi.org/10.3389/fphys.2021.719594

Gleiss, A.C., Dale, J.J., Klinger, D.H., Estess, E.E., Gardner, L.D., Machado, B., Norton, A.G., Farwell, C., Block, B.A., 2019. Temperature dependent pre- and postprandial activity in

Accepted Article

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Accepted Article

Pacific bluefin tuna (Thunnus orientalis). Comp. Biochem. Physiol. -Part Mol. Integr. Physiol. 231, 131–139. https://doi.org/10.1016/j.cbpa.2019.01.025

Horodysky, A.Z., Cooke, S.J., Graves, J., Brill, R., 2016. Themed Issue Article: Conservation Physiology of Marine Fishes Fisheries conservation on the high seas: linking conservation physiology and fisheries ecology for the management of large pelagic fishes. Conserv. Physiol. 4.https://doi.org/ 10.1093/conphys/cov059

Iversen, N.K., Dupont-Prinet, A., Findorf, I., McKenzie, D.J., Wang, T., 2010. Autonomic regulation of the heart during digestion and aerobic swimming in the European sea bass (Dicentrarchus labrax). Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 156, 463–8. https://doi.org/10.1016/j.cbpa.2010.03.026

McCue, M.D., 2006. Specific dynamic action: a century of investigation. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 144, 381–94. https://doi.org/10.1016/j.cbpa.2006.03.011

McKenzie, D., 2011. The energetics of Fish Swimming. pp. 1075–1080.

Mignucci, A., Bourjea, J., Forget, F., Allal, H., Dutto, G., Gasset, E., Mckenzie, D.J., 2021. Cardiac and behavioural responses to hypoxia and warming in free-swimming gilthead seabream Sparus aurata. bioRxiv 2021.02.05.429945. https://doi.org/10.1101/2021.02.05.429945

Patel, E., Lea, J., Clarke, C., 2019. Inner space: translating advances in human medicine to minimise the invasiveness of marine tagging procedures. Anim. Biotelemetry 7, 3. https://doi.org/10.1186/s40317-019-0165-7

Pérez-Lloréns, J.L., 2019. Bluefin tuna and Cádiz: A pinch of history and gastronomy. Int. J. Gastron. Food Sci. 17, 100170. https://doi.org/10.1016/j.ijgfs.2019.100170

Plummer, M., 2003. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling.

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L.G., Shepard, E.L.C., Gleiss, A.C., Wilson, R., 2012. Tri-Axial Dynamic Acceleration as a Proxy for Animal Energy Expenditure; Should We Be Summing Values or Calculating the Vector? PLOS ONE 7, e31187. https://doi.org/10.1371/journal.pone.0031187

R Development Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ravier, C., Fromentin, J.M., 2004. Are the long-term fluctuations in Atlantic bluefin tuna (Thunnus thynnus) population related to environmental changes ? Fish Ocean. 13, 145–160.

Rooker, J.R., Bremer, J.R.A., Block, B.A., Dewar, H., Metrio, G. de, Corriero, A., Kraus, R.T.,

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Prince, E.D., Rodríguez-Marín, E., Secor, D.H., 2007. Life History and Stock Structure of Atlantic Bluefin Tuna (Thunnus thynnus). Rev. Fish. Sci. 15, 265–310. https://doi.org/10.1080/10641260701484135

Rouyer, T., Bonhommeau, S., Bal, G., Derridj, O., Fromentin, J.-M., 2021. The environment drives Atlantic bluefin tuna availability in the Gulf of Lions. Fish. Oceanogr. 30. https://doi.org/10.1111/fog.12532

Rouyer, T., Bonhommeau, S., Giordano, N., Ellul, S., Ellul, G., Deguara, S., Wendling, B., Belhaj, M.M., Kerzerho, V., Bernard, S., 2019. Tagging Atlantic bluefin tuna from a farming cage: An attempt to reduce handling times for large scale deployments. Fish. Res. 211, 27–31. https://doi.org/10.1016/j.fishres.2018.10.025

Rouyer, T., Bonhommeau, S., Giordano, N., Giordano, F., Ellul, S., Ellul, G., Deguara, S., Wendling, B., Bernard, S., Kerzerho, V., 2020. Tagging Atlantic bluefin tuna from a Mediterranean spawning ground using a purse seiner. Fish. Res. 226, 105522. https://doi.org/10.1016/j.fishres.2020.105522

Schulte, P.M., Healy, T.M., Fangue, N.A., 2011. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. Integr. Comp. Biol. 51, 691–702. https://doi.org/10.1093/icb/icr097

Shepard, E.L.C., Wilson, R.P., Halsey, L.G., Quintana, F., Laich, A.G., Gleiss, A.C., Liebsch, N., Myers, A.E., Norman, B., 2008. Derivation of body motion via appropriate smoothing of acceleration data. Aquat. Biol. 4, 235–241. https://doi.org/10.3354/ab00104

Simon, M., Johnson, M., Madsen, P.T., 2012. Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. J. Exp. Biol. 215, 3786–3798. https://doi.org/10.1242/jeb.071092

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., Van Der Linde, A., 2002. Bayesian measures of model complexity and fit. J. R. Stat. Soc. Ser. B Stat. Methodol. 64, 583–639. https://doi.org/10.1111/1467-9868.00353

Whitlock, R.E., Hazen, E.L., Walli, A., Farwell, C., Bograd, S.J., Foley, D.G., Castleton, M., Block, B.A., 2015. Direct quantification of energy intake in an apex marine predator suggests physiology is a key driver of migrations. Sci. Adv. 1, e1400270–e1400270. https://doi.org/10.1126/sciadv.1400270

TABLES

Accepted Article

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Accepted Article

Table 1: Model structure, effective number of parameters (pD), Deviance Information Criterion deviation (ΔDIC) compared to best model and R^2 for each of the model tested

model	pD	ΔDIC	R2
α + TF:thresh + TPm	5.6	0	0.815
α + TF:thresh + TPm + TPiq	5.9	1	0.812
α + TF:thresh + TPm + TPiq + ACm	7.2	3	0.808
α + TPiq:thresh + TF + TPm + ACm	4.4	13	0.725
α + ACm:thresh + TF + TPm	4.5	13	0.725
α + TF + TPm	5.5	14	0.723
α + TF + TPm + TPiq	3.6	14	0.711
α + TF + TPm + TPiq + ACm	3.4	14	0.708
α + TPiq:thresh + TF + TPm	5.2	14	0.722
α + TPm:thresh + TF	5.9	14	0.731
α + TPm:thresh + TF + TPiq + ACm	5.7	15	0.721
α + TPm:thresh + TF + TPiq	3.8	15	0.708
α + ACm:thresh + TF + TPm + TPiq	5.5	15	0.719
α + ACm:thresh + TF	6.1	25	0.664
α + TF:thresh	4.2	36	0.587
α + TF	2.1	52	0.51
α + TPiq:thresh + TF	3.6	53	0.512
α + TPm:thresh	8.5	72	0.429
α + ACm:thresh	4.9	87	0.323
α	1.3	141	-0.007

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/fbi.13507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

α + TPiq:thresh	5.2	141	0.017

Table 2. Parameters estimated for the best model.

Parameter	Estimate	SD	2.5%	97.5%
α	50.188	0.838	48.507	51.772
β^{+}_{TF}	0.313	0.338	-0.364	0.967
β^{-}_{TF}	1.831	0.211	1.432	2.237
β_{TP}	2.137	0.346	1.462	2.810
threshold	25.462	0.546	24.080	26.206

FIGURES

Figure 1. Material used for implanting HR-tags (panel A), description of a HR-tag deployment in a live ABFT (panels B-G) and dissection of a dead ABFT implanted with a HR-tag (panel H). Panel A shows the atraumatic trocar that was used for the implantation, with the removable obturator, which is then used to push the HR-tag into the fish. The entry point for the trocar is below the point of maximum curvature of the operculum, into muscles associated with the cleithrum, a membranous bone (B). Once the trocar is inserted and advanced forward in the fatty flesh, the obturator is removed (C) and the tag placed into the outer cannula (D), and advanced with the obturator (E), into the tissue (F). The trocar is then removed (G), and the fish is released back into the water. In panel H, a dead tuna was implanted with a tag following this protocol, then dissected ventrally to show the tag location in close proximity to the heart.

Figure 2: One minute of HR data acquired from experiment 1. The 3 rows represent HR-tag1 (top), HR-tag2 (middle) and HR-tag3 (bottom), respectively. The box identifies the chunk of data presented in detail in the right-hand column, which depicts individual ECG waveforms identified within the signal.

Accepted Article

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Figure 3: A sample electrocardiogram (ECGs) of 7 second duration, corresponding to 43 bpm, recorded on a 60 kg fish tagged and released into a rearing cage.

Figure 4: Time series of the raw data for HR (in bpm, top panel), total feed provided to the cage (TF in tons, second panel), peripheral body temperature logged on the tag (TP in °C, third panel) and average activity values (AC in mg, bottom panel). The different days are separated by vertical black lines. A smoother was added in red to the time series of HR, TF and AC to help visualize trends.

Figure 5: Time series of raw heart rate data (HR in bpm, top panel), activity (AC in mg, second panel), temperature (TP in °C, third panel) and total food (TF in tons, bottom panel) over 13 consecutive days. Colors indicate different days separated by vertical black lines.

Figure 6: Time series of daily median values of Heart Rate (HRm, top panel), daily median values of peripheral body temperature (TPm, second panel), daily interquartile range of temperature (TPiq, third panel), daily median values of activity (ACm, fourth panel) and total food (TF, fifth panel). The bottom panel displays rescaled data of HRm and TF overlaid on top of each other.

Figure 7: Predicted HRm values obtained from the best model (red) and observed HRm values (black). The pink area represents the 95% confidence interval.

Accepted Article

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

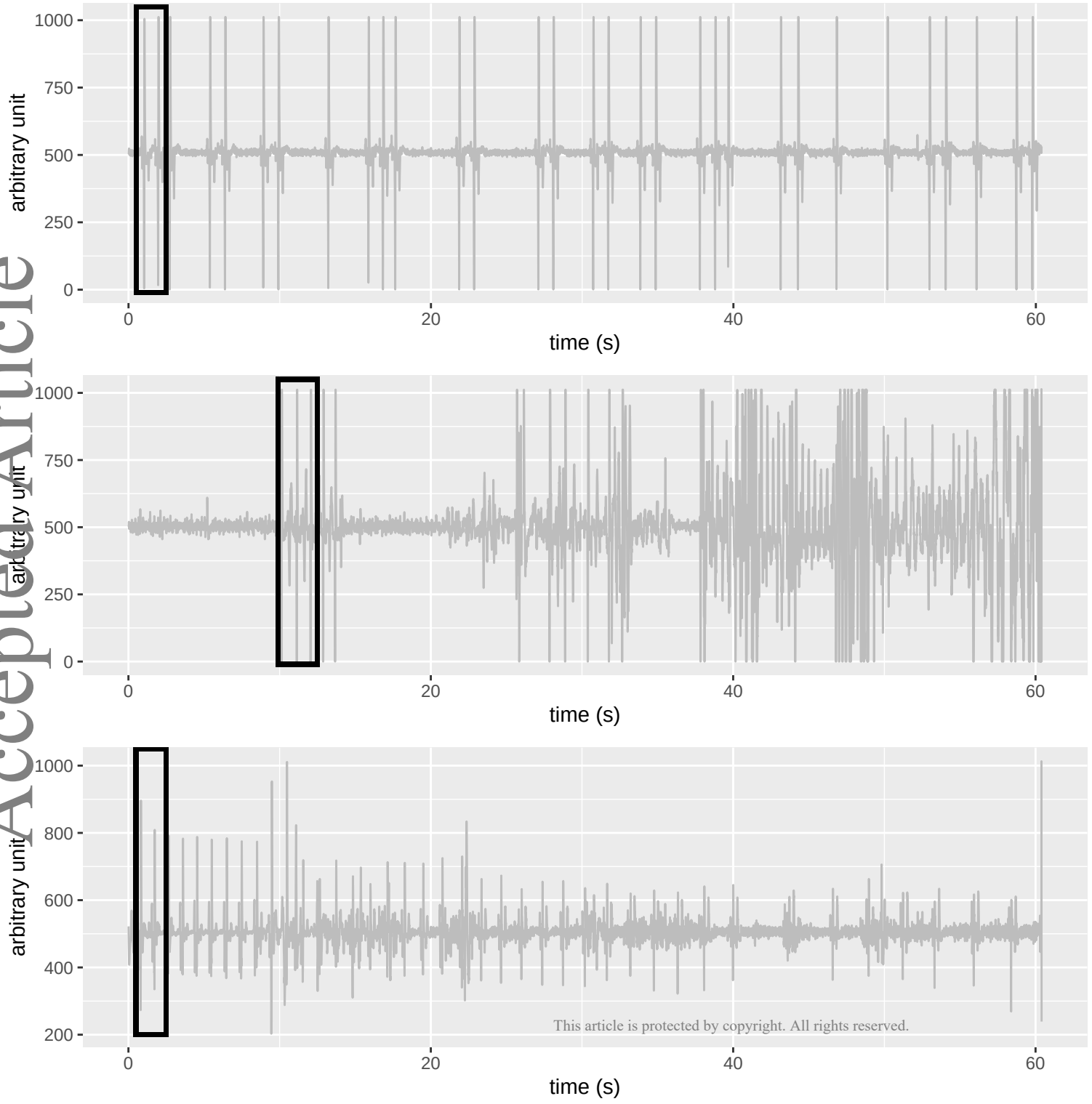
Figure

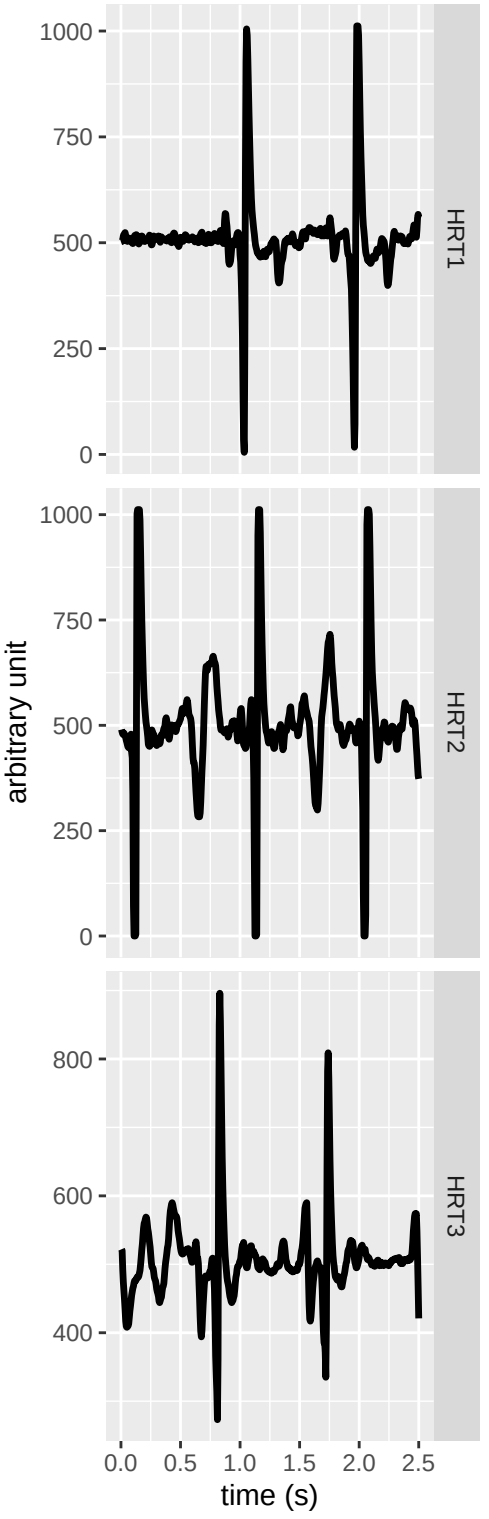
Accepted Article

This article is protected by copyright. All rights reserved.

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Figure



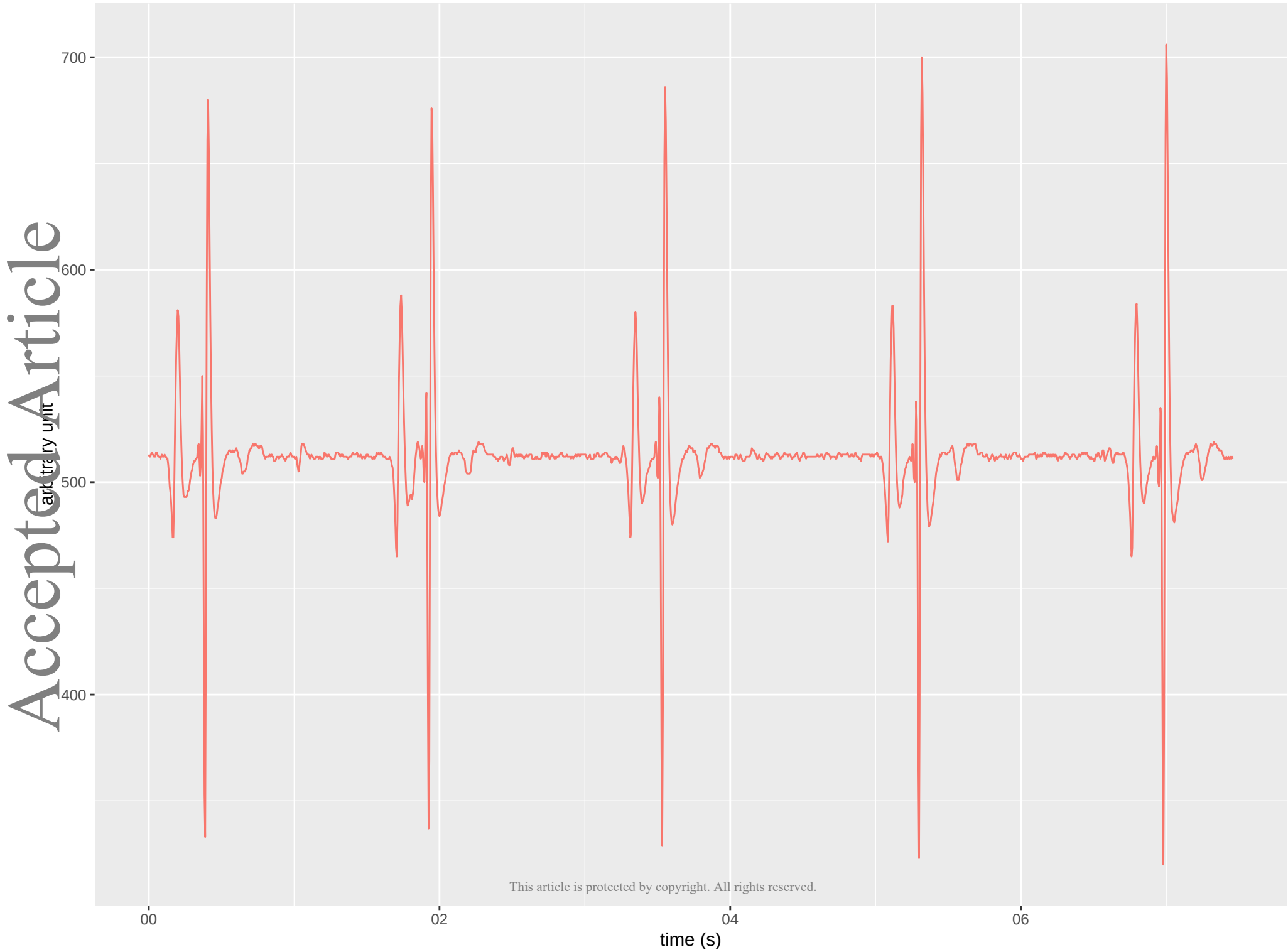


Accepted Article

This article is protected by copyright. All rights reserved.

10958648), ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Figure

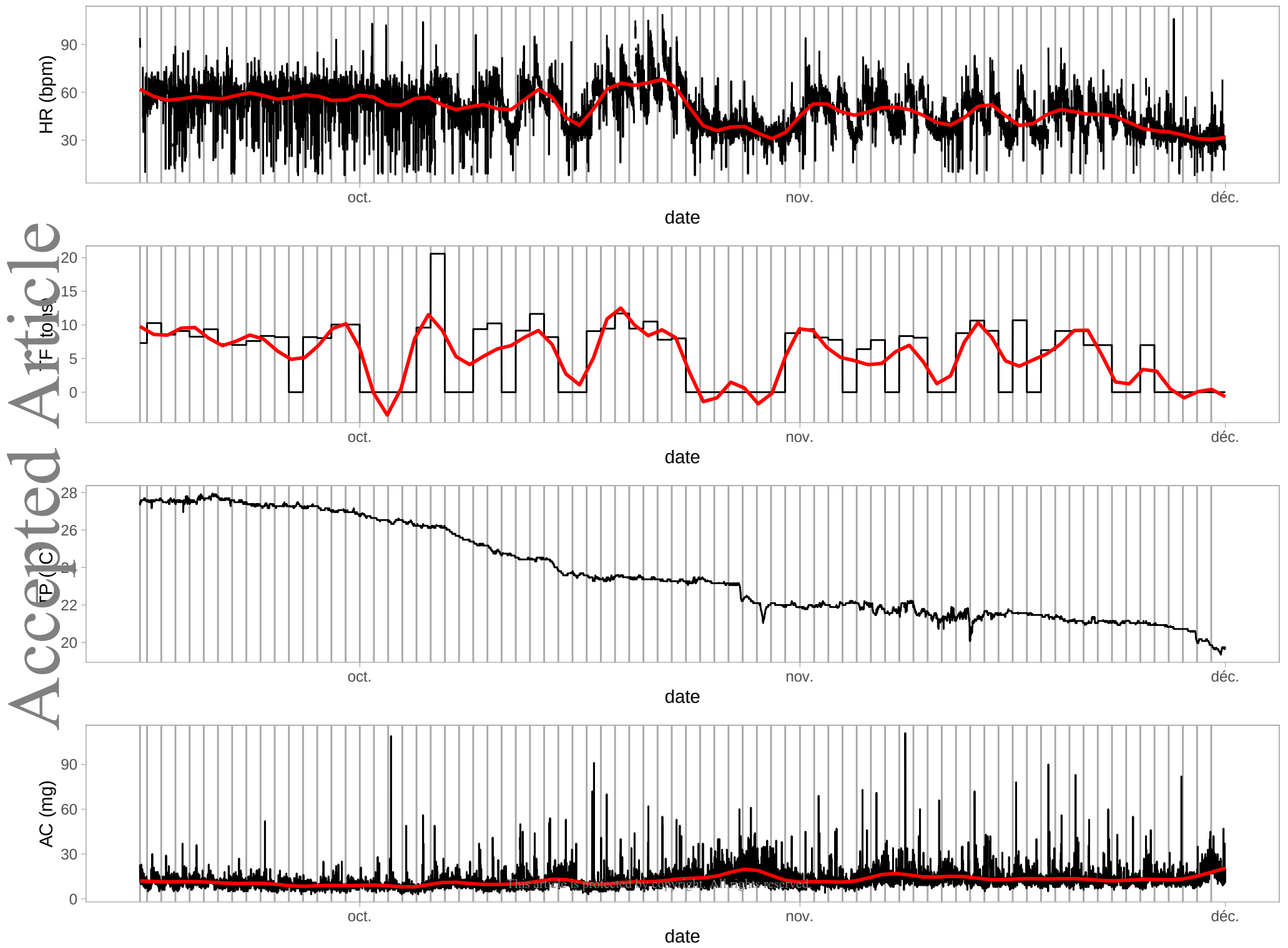


Accepted Article

This article is protected by copyright. All rights reserved.

10958648, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Figure

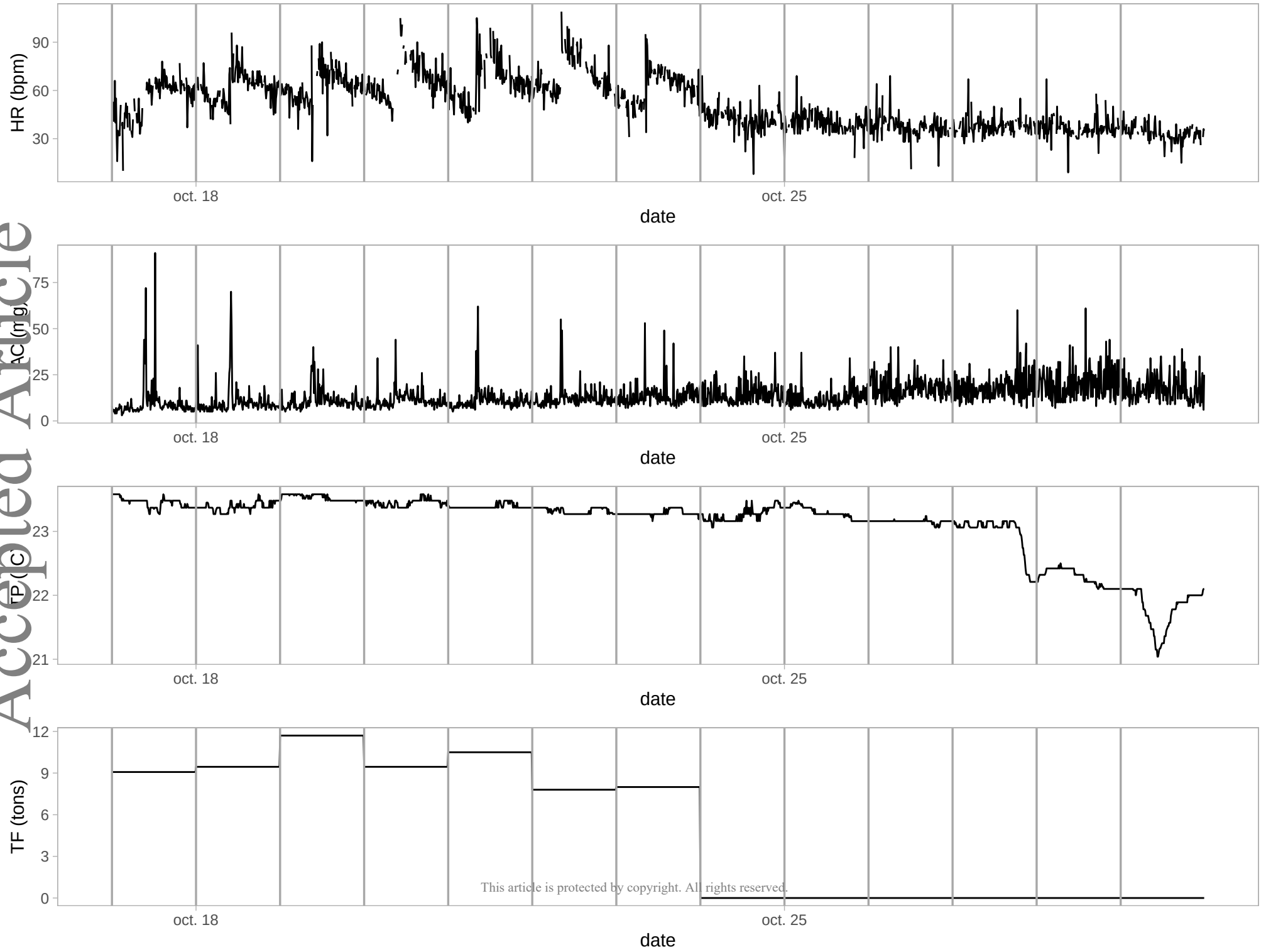


Accepted Article

This article is protected by copyright. All rights reserved.

10958648), ja. Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Figure

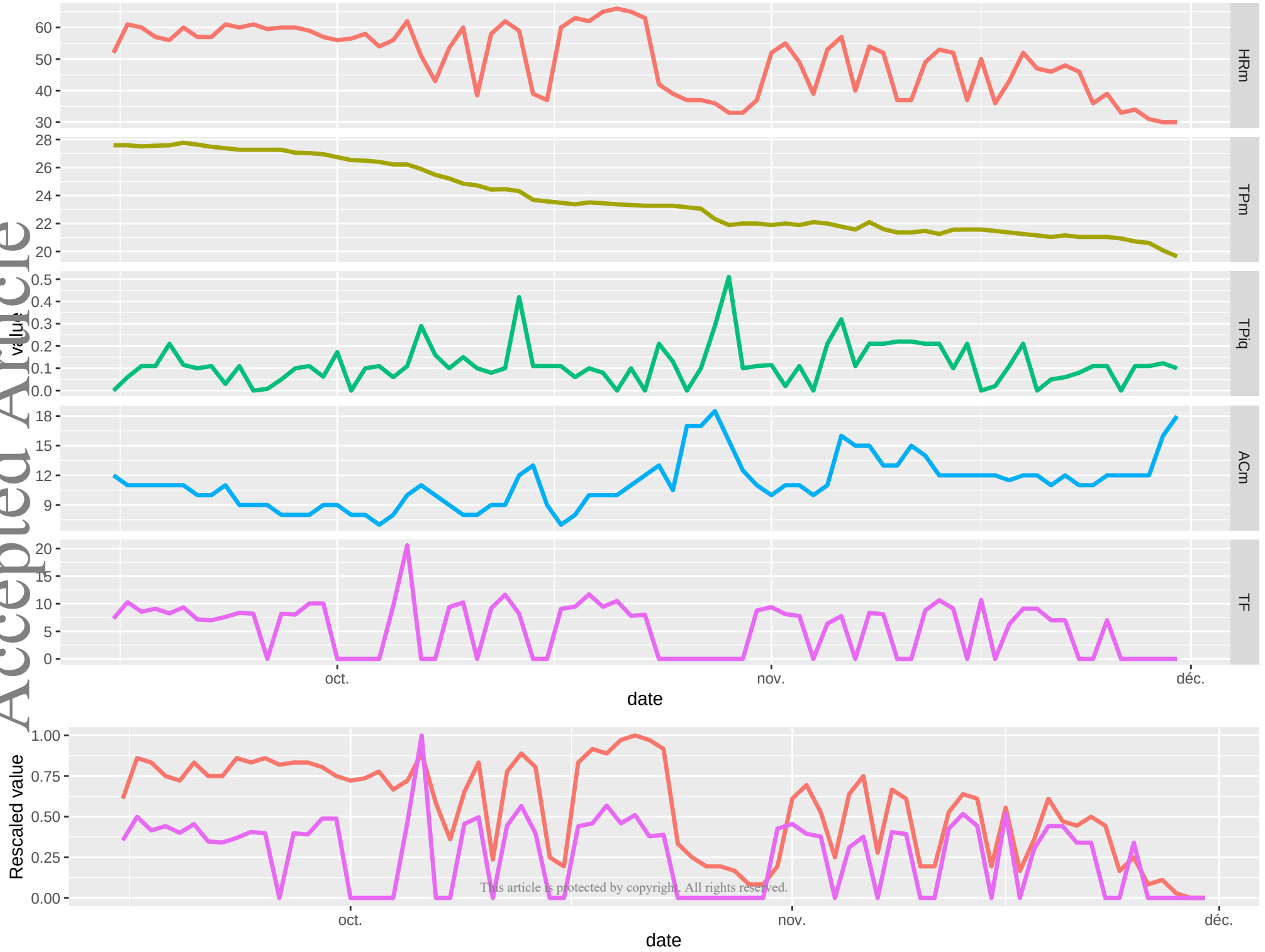


Accepted Article

This article is protected by copyright. All rights reserved.

10958648, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Figure



Accepted Article

This article is protected by copyright. All rights reserved.

10958649, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Figure

Accepted Article

This article is protected by copyright. All rights reserved.

10958648, ja, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15507 by IFREMER Centre Bretagne BLP, Wiley Online Library on [25/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License