Peer Community In
Ecology

Extreme weight loss: when accelerometer could reveal reproductive investment in a semelparous fish species

Francois-Xavier Dechaume-Moncharmont based on reviews by Aidan Jonathan Mark Hewison, Loïc Teulier and 1 anonymous reviewer

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A recommendation of:

Cédric Tentelier, Colin Bouchard, Anaïs Bernardin, Amandine Tauzin, Jean-Christophe Aymes, Frédéric Lange, Charlotte Recapet, Jacques Rives. **The dynamics of spawning acts by a semelparous fish and its associated energetic costs** *(2020), bioRxiv, 436295, ver. 7 peer-reviewed and recommended by Peer Community in Ecology.* https://doi.org/10.1101/436295

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Continuous observation of animal behaviour could be quite a challenge in the field, and the situation becomes even more complicated with aquatic species mostly active at night. In such cases, biologging techniques are real game changers in ecology, behavioural ecology or eco-physiology. An accelerating number of methodological applications of these tools in natural condition are thus published each year [1]. Biologging is not limited to movement ecology. For instance, fine grain information about energy expenditure can be inferred from body acceleration [2], and accelerometers has already proven useful in monitoring reproductive costs in some fish species [3,4]. The first part of the study by Tentelier et al. [5] is in line with this growing literature. It describes measurements of energy expenditure during reproduction in a fish species, Allis shad (Alosa Alosa), based on tail beat frequency and occurrence of spawning acts. The study has been convincingly conducted, and the results are important for fish biologists. But this is not the whole story: the authors added to this otherwise classical study a very original and insightful analysis which deserves closer interest.

Tentelier et al. propose to use static accelerometer to monitor change in body roundness through the reproductive season. These semelparous fish first mature and built up reserves in the Atlantic Ocean and migrate into fresh water to reproduce. Contrary to iteroparous species, female shads do not have to strategically preserve energy for future reproduction. The females die few days after spawning having exhausted their energetic reserves: they typically lose almost half of their body mass during the spawning season.

The beautiful idea in this study was to track down information about this dramatic slimming in the accelerometer data. Indeed, the accelerometer was attached on the side of the fish (close to the dorsal fin). A change in its angle with the vertical plane could be correlated with the change in roundness, the angle declining with the female thinning. Accelerometers have already been used to record body posture [6] but, in the present study, the novelty was to monitor the change in body shape.

Unfortunately, the data by Tentelier et al. are inconclusive so far. Broadly speaking, the accelerometer angle recorded declined through the spawning season, indicating an average slimming of the females, but there was no correlation between the change in angle and the mass loss at the individual level. This was partly due to the fact that the dorsal position of the accelerometer was not optimized to measures egg laying whose effects are mostly observable on ventral side.

Yet, this nice idea deserves more scrutiny. The method seems to be sensitive enough to detect inflation of swim bladder, the gas-filled organ helping the fish to control their position in the water column, as the accelerometer angle increased when the fish stayed close to the water surface. Additional works and proper calibration are certainly needed to validate the use of accelerometer angle as a proxy for body roundness. The actual data were not strong enough to justify a standalone publication on the subject, but it would have been shame to lose traces of such analysis and keep it in the file drawer. This is why I strongly support its report as a side question in a broader study. Science progresses not only with neat conclusive studies but also when unexpected (apparently anecdotal) observations stimulate new researches.

References

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[4] Sakaji H, Hamada K, Naito Y. 2018 Identifying spawning events of greater amberjack using accelerometers. Mar. Biol. Res. 14, 637–641. 10.1080/17451000.2018.1492140
[5] Tentelier C, Bouchard C, Bernardin A, Tauzin A, Aymes J-C, Lange F, Récapet C, Rives J (2020) The dynamics of spawning acts by a semelparous fish and its associated energetic costs. bioRxiv, 436295. doi: 10.1101/436295 ver. 7 peer-reviewed and recommended by PCI Ecology. 10.1101/436295
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Revision round #2

2020-09-17
Dear Cédric Tentelier,

Both reviewers and myself agree that your preprint deserves recommendation by PCI Ecology. I carefully read through it and I agree that most (but not all) of the referees' previous concerns were satisfactorily addressed. I think that this new version has greatly improved the paper's clarity, and I am ready to recommend it for PCI Ecology. Yet, the final comments by Mark Hewison must first be properly addressed. Could you please modify your MS in line with his comments? In addition, I think that previous uses of accelerometer to monitor spawning behaviour in fish species (e.g. Tsuda et al. 2006, Sakaji et al. 2018) deserve to be cited and commented in the main text. It will help the reader to assess the novelty of your study. Finally, PCI Ecology does not copy-edit the preprints. You should pay particular attention to typographical and other minor issues. For instance, in the abstract (line 56) one should read “complementary” instead of “complimentary”. Please, carefully edit the new version of your preprint prior resubmission.

Pr François-Xavier Dechaume-Moncharmont University of Lyon, France

References - Sakaji, H., Hamada, K., & Naito, Y. (2018). Identifying spawning events of greater amberjack using accelerometers. Marine Biology Research, 14(6), 637 641. https://doi.org/10.1080/17451000.2018.1492140 - Tsuda, Y., Kawabe, R., Tanaka, H., Mitsunaga, Y., Hiraishi, T., Yamamoto, K., & Nashimoto, K. (2006). Monitoring the spawning behaviour of chum salmon with an acceleration data logger. Ecology of Freshwater Fish, 15(3), 264 274. https://doi.org/10.1111/j.1600-0633.2006.00147.x

Preprint DOI: https://www.biorxiv.org/content/10.1101/436295v4

Reviewed by Loïc Teulier, 2020-09-16 14:22

I would like to thank the authors for their reply.
All of my major concerns were now addressed by revising the text and providing further explanations in the responses.
Concerning the issue of EE calibration, I did not want to be too focused on swim tunnel and in vivo metabolism measure, but to my knowledge, it is likely the best reliable system to measure energy expenditure in fish. I fully understand that the authors did not perform that kind of experiment, due to the expensive cost of this very specific material.
They added a whole paragraph about that limitation, and the cautiousness needed for the interpretation of their results. This is fine for me.
I totally agree that these results should not be “thrown away” and that they should be kept as a first step of a really nice experimental setup to get some interesting parameters, and especially the roundness of fish under field conditions through a time period, and therefore to follow the temporal variation of the fish body condition in their natural environment.

Reviewed by Aidan Jonathan Mark Hewison, 2020-08-26 16:02

This manuscript presents empirical data issued from accelerometers born by female Allis shad to detect spawning events and infer associated energetic expenditure. The authors seek to link behaviour to energy expenditure and loss of body condition over the reproductive season. The empirical data indicated that female shad exhausted their energetic stock faster than their egg stock. The authors conclude that this approach using accelerometers is promising for monitoring behaviour-dependent energy expenditure in the wild.
This is something of a pilot study that investigates how high technology sensors can be employed in the wild to measure important physiological parameters such as energy expenditure and infer behaviours that are otherwise impossible to observe. As such, the sample size is small (N = 8), partly due to protocol failure that was beyond the control of the authors, and the monitoring quite short (1 month). However, the feasibility of this kind of study will be of interest to behavioural ecologists across a wide range of cryptic species. Furthermore, the monitoring of energy expenditure, the raw currency of evolution, is an exciting and promising technological advance.

Comments on the revision:
This is a revised version of a manuscript I previously refereed. Overall, the authors have done a good job of taking into account the main points that I highlighted on the previous version. However, I still have a couple of outstanding queries:
Comment 25: I still do not understand the match between Fig. 4B and the text that describes it. The authors

write: “the observed mass loss was on average 1.5 times more than predicted (479 g difference on average)”, but in the Figure observed mass loss varies between around 530g and 780g, while the predicted mass loss varies between around 50 and 250g. I cannot see how this generates the ratio of 1.5 that the authors state. This discrepancy is what I was referring to as “wrong” in my original comment. Comment 27: while R2 values provide an estimation of the proportion of observed variation explained by a model, they do not provide information on differences in means, which is what I was referring to here. Indeed, now that the authors have also provided the latter (note that standard errors should also be included), it becomes apparent that some of the reported effect sizes are in fact very low (e.g. higher probability of spawning on warmer nights, higher TBF and energy expenditure at night vs day, etc.). This may or may not be a problem, but at least the reader can now better assess the support for the stated interpretations.
Finally, although the manuscript is globally well-written, there is still further scope for minor language improvement.

Mark Hewison

Author's reply:

Dear Recommender and reviewers,

We thank you for pointing at the issues remaining in this revision. We addressed them as follows:
- We added references to Tsuda et. al (2006) and Sakaji et al. (2018), at line 113.
- The discrepancy between Fig. 4B and the text referring to it was just a mistake in the ratio between the observed and predicted mass loss. It is 3.7 and not 1.5. We changed it in the text.
- For the differences between morning, afternoon and night, we added standard errors and qualify our discussion of these results (L593): " Although differences between mornings, afternoons and nights were tenuous…". - We also checked the whole manuscript for residual language errors and corrected as many as we could spot.

We are pleased to submit this revised version and excited to see it soon recommended in PCI Ecology.
Yours,
On behalf of the authors, Cédric Tentelier

Revision round #1

2020-07-07
The present manuscript is a methodological study assessing the potential use of accelerometer for estimating spawning activity in a fish species. Despite the limited sample size, the idea is original, appealing and, if its reliability is confirmed, possibly very useful in field works. It could therefore be a valuable contribution to the field and it could be recommended by PCI-Ecology provided some clarifications and developments.

In its present form, one of the major weaknesses of the manuscript lies in the lack of argumentation about the chosen equations and metrics: how were they calibrated? How appropriate were they to estimate the energy consumption? Two referees expressed serious concerns about the calibration of the measures. I understand that it will not be possible to perform additional experiments. Yet, complementary statistical analysis may be presented. At the very least, if relevant information is not accessible any more, these caveats and limitations should be extensively discussed in the MS as a warning for the reader. The referees also pointed out that utmost care must be taken to justify the measurement as a proxy for energy expenditure. I strongly advise the authors to carefully take into account their suggestions.

Finally, I share one referee's opinion about the structure of the manuscript. The end of the Introduction section is too abrupt. By contrast, a great deal of information presented in the Material and Methods section (p.8) concern hypotheses and predictions and should be moved at the end of the Introduction section. Similarly, some details about the statistical analysis (around line 270) should be moved down to the Statistics section. This latter section should be carefully edited. In its present form, it contains many details which are more related with experimental procedure than statistical analysis.

Additional requirements of the managing board:
As indicated in the 'How does it work?' section and in the code of conduct, please make sure that:
-Data are available to readers, either in the text or through an open data repository such as Zenodo (free), Dryad or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data.
-Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) are available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused.
-Details on experimental procedures are available to readers in the text or as appendices.
-Authors have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this preprint declare that they have no financial conflict of interest with the content of this article." If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: “XXX is one of the PCI XXX recommenders.”

Preprint DOI: https://www.biorxiv.org/content/10.1101/436295v3

Reviewed by Aidan Jonathan Mark Hewison, 2020-06-22 17:13

The dynamics of spawning acts by a semelparous fish and its associated energetic expenses
This manuscript presents empirical data issued from accelerometers born by female Allis shad to detect spawning events and infer associated energetic expenditure. The authors seek to link behaviour to energy expenditure and loss of body condition over the reproductive season. The empirical data indicated that female shad exhausted their energetic stock faster than their egg stock. The authors conclude that this approach using accelerometers is promising for monitoring behaviour-dependent energy expenditure in the wild.
This is something of a pilot study that investigates how high technology sensors can be employed in the wild to measure important physiological parameters such as energy expenditure and infer behaviours that are otherwise impossible to observe. As such, the sample size is small (N = 8), partly due to protocol failure that was beyond the control of the authors, and the monitoring quite short (1 month). However, the feasibility of this kind of study will be of interest to behavioural ecologists across a wide range of cryptic species. Furthermore, the monitoring of energy expenditure, the raw currency of evolution, is an exciting and promising technological advance. The manuscript is globally well-written, although there is scope for minor language improvement (particularly the abstract, see below), the analyses appear sound, and there is a lot of novel information here (although I am no specialist of the literature on this system). Below I list the some points that the authors might like to consider:

Major comments:
1. Lines 120-21: it is a bit of a shame to just put this at the end of the introduction, it reads like a throw away; while earlier the authors nicely set up the context around optimality of coincidence between gamete exhaustion and energetic exhaustion (Lines 72-78). Why not translate this into a hypothesis about what to expect in terms of mismatch, for example, in relation to water temperature, as they appear to do in the Abstract (although this needs to be more explicit, see below).
2. Hypotheses (end of Introduction): indeed, following on from the previous comment, it would be nice to have explicit hypotheses rather than just description at this point in the manuscript. What are the

expectations for the link between temperature and spawning schedule? And how should this translate into energy expenditure? Much of the required contextual information for this actually appears in the first part of the methods, describing the study system and the predictions, which is unusual to say the least. I would much prefer to see much of this information in the Introduction leading to clear predictions. Please try to re-work the text to improve this aspect, providing enough contextual information on the study system to generate predictions in the Introduction, while keeping accessory detail (e.g. life cycle) in the Methods.
3. Calibration: The use of accelerometer data to estimate roundness is an interesting and novel application which the authors have calibrated against a traditional measure of body condition. However, I do feel that behavioural calibration for Tail Beat Frequency would also be useful, but there is no information provided. What information is available about the reliability of estimating tail beat frequency with accelerometer data? For spawning events, the authors did indeed do a calibration experiment, which is convincing, although it was based on a single couple. Could there be any inter-individual heterogeneity (see point 5) in the signal which might lead to faulty inference? This might be worth discussing.
4. Analysis: eg Line 325: what is considered night vs. day changes very fast across the spring. If activity is linked to daylight cycles, then it might be worthwhile considering a moving window for what is actually night-time determined by the times of sunrise and sunset. This could provide better precision when contrasting behaviour and energy expenditure across the 24h cycle.
5. Inter-individual heterogeneity: while I appreciate that the sample size is small, it would still be nice to discuss the inter-individual variability that the authors observed. For example, Line 545 there is a total energetic expenditure that varies by a factor of 2, which is considerable. Could this be linked to reproductive phenology? behaviour (eg swimming depth)? or reproductive allocation (eg spawning events)? This discussion (eg following on from line 566) would be of course a little speculative given the sample size, but an interesting perspective.

Minor comments:
1. Title: “costs” not “expenses” (also Line 589)
2. Abstract – this is the first time I have seen the expression “gametic budget”, and it is not immediately clear what that means. Consider modifying.
3. Line 45: synchronised among individuals? This needs to be clearer throughout.
4. Line 45-47: this sentence is not clear; perhaps “When daytime temperature was higher, they remained at greater depths, and spent more energy on nights when they swam at faster pace”.
5. Line 53-54: this is not easy to understand, can you help the reader interpret this prediction?
6. Line 77: “steep” is a bit strange here, “pronounced”?
7. Lines 78-80: not explicit enough ‘eg “social factors” is very vague, what do you mean by that? This sentence reads like an add-on which needs a mini-paragraph in itself.
8. Line 84: not “supervision”, “recording”?
9. lines 96-105: I am no expert here, but I was surprised that the authors did not refer to the use of dynamic body acceleration to index energy expenditure (e.g. in the Introduction,), reviewed in Wilson et al. 2019 J Anim Ecol (https://doi.org/10.1111/1365-2656.13040
10. Line 109: add “pattern”.
11. Line 117: “vertical plane” (and throughout the text)
12. Line 118 (and throughout): “thinning” is a bit strange, I would suggest “weight loss” or “loss of body condition”, but I acknowledge its not quite the same thing.
13. Line 132: although I understand the link, capital breeding is not necessarily associated with fasting. It is strictly related to the fact that energy for offsetting increased needs during reproduction are sourced from stored reserves, rather than from current intake (see Jonsson 1997 Oikos 78).
14. Line 149: replace “with a regular delay” by “by a consistent time elapse”
15. L163: “deviate” not “depart”
16. Line 181-3: not clear
17. Line 292: do you mean “compared with” ?
18. Line 319: this is fine, but be careful to be clear throughout the text that the synchronisation you wish to look for is “among” not “within” individuals.
19. Line 341: it’s a bit odd to come back to predictions at this stage of the manuscript. These aims/predictions

should be clearer earlier (see above).
20. Fig 2: you do not have a measure of “longevity”. I presume this is supposed to be the number of days between capture and death, which may be related to longevity, but not necessarily. Please modify label.
21. Results: while the relationships are not strong, this is likely due to a lack of statistical power; it is notable however that the number of spawning acts seems to be negatively correlated with all the size/condition parameters, which is surprising to me, who knows nothing about this particular model. Worth discussing (eg Line 515)?
22. Line 418: “total energy expenditure” not “energy expenditure cumulated”
23. Line 421: “representing” not “making”
24. Fig 4 legend: spell out what TBF is in the legend
25. Line 426-7: unless I have misunderstood something, this seems to be wrong. The authors say “the predicted weight loss was on average 1.5 times less than the actual loss”, but the Fig 4 indicates that real weight loss was much higher than predicted, by up to 4 fold! Also, it would be more usual to turn the thing around, to say “observed weight loss was XX times more than predicted…”
26. Line 439: “experienced” not “underwent”
27. Lines 437-445: I would like to see the effect sizes for each of these also in the text, as they are not easy to judge in the Fig 5.
28. Fig 6B: this figure is the wrong way round, it would be more logical to show a decrease in condition over time from initial release until death
29. Line 468-73: it would be nice to have the full table of AIC values for all tested models as a Table in the Supplementary materials.
30. Lines 473-5: I do not really understand what this result means (or indeed why the period of the day is included in the model). Does this mean that the fish get fatter at night then thinner again during the day? Is body shape expected to vary at this temporal scale, within a 24h cycle?
31. Line 489: delete “individual”
32. Line 493: give effect size, by how much?
33. Line 494: “too high to allow shad to spawn all their eggs” is not clear, please clarify (females could not spawn all eggs prior to death due to energetic exhaustion? Or something like that).
34. Line 494: “novel”, not “original”
35. Line 496: for what? Be explicit as to the use of this approach
36. Line 529: “are reminiscent” not “remind”
37. Line 540: “end” not “final”
38. Line 541: “occurred in” not “struck”
39. Line 543 “with” not “to”
40. Line 557: “by” not “of”
41. Line 591: “fish have to conserve protein” not “fishes have to spare proteins”
42. Line 607: “wiped away” – this is not clear.
43. Line 633: while this is true, it is difficult to conclude that the two are not related; from Fig 6B, it seems that there is some degree of consistency in the two measures with the exception of the individual represented by the green line which has a much steeper slope than the others

Mark Hewison

Reviewed by [Loïc Teulier](), 2020-07-03 08:28

This study deals with a really great idea to improve the protocols of non-invasive technics, to accurately estimate the energy expenditure of fish in the wild. Throughout the introduction, the authors explain the central role of studying energy allocation in the ecological context of spawning periods, using a highly relevant model, the anadromous Allis shad, which is a semelparous fish. This latter point is of interest, because the cost of reproduction corresponds almost to the total energy expenditure of the spawning period. And as a capital breeder, no food supply is expected. As stated line 81-82, the energy budget estimation of wild fish is really challenging. And with this study, the authors give some new tools for measuring some proxies. For example, using the accelerometers for evaluating the roundness of fishes is really interesting, but as highlighted by the authors, this method needs further investigation to be improved.

I however have some concerns about the other methods, which are described below. - The first concern is about the choice of external tags. Intuitively, I would think that this kind of device would negatively impact the locomotion, and the cost of transport, through an increase of drag force, for example, which is intensively commented in the literature in diving birds (Ropert-Coudert et al. 2000) or in fish (reviewed in Cooke et al. 2012). The authors referred to Breine et al. 2017 for the tagging protocol, and therefore, fish body mass should be higher than 900 g to be in accordance with the limit of 2% cited in Breine. Unfortunately, the morphological characteristics of fish (body mass, body length, width and height) are missing, but seem highly relevant to estimate the effect of tags on fish used in this experiment. I would suggest to add a table with these characteristics.

- As they did for characterizing the spawning act with the accelerometers, I wonder why the authors did not perform any preliminary test (i.e. in swim tunnel, in vivo respirometry) to validate their tagging protocol. A comparison among tagged, sham and control Allis shad would have been great to disentangle the consequences of these external tags in the fish performance. Indeed, some studies show that kind of results: Jepsen et al. (2015) described a list of possible effects of external tag, especially on swimming performance. Tagged fish get exhausted earlier than control ones, which could mean a higher energetic cost of locomotion with external tags. But Breine et al. explained that the effect of such external tag was still unknown in 2017.
- Line 613: “tagging did not seem to impair swimming activity either, as TBF was not lower in the three days following tagging than in the remaining of the season.” Could the authors clarify this sentence: is it the “spawning” season? Therefore, I did not catch the argument that the TBF was not lower in the 3 days after tagging. It would have been great to compare fish locomotion parameters before and after tagging, instead.

- For estimating the energy expenditure (EE) from the Tail Beat Frequency, the authors referred to equations from Leonard et al. (1999) and Castro-santos & Letcher (2010), which were fitted for adult American shad, during migration. In addition, these fish are iteroparous, which is an important point, when dealing with EE. The authors discuss about that very thoroughly in the “methodological considerations” (line 568 and beyond). I therefore wonder about the accuracy of the equations the authors used for EE calculations and if they are correct for Allis fish. Indeed, figure 4 B shows a huge difference between the modelled and the observed “weight” loss. Estimations of energy expenditure from biologgers need to be cautiously taken, due to the several parameters which are playing major roles. For instance, considering the fact that American shad were migrating and that Allis shad were spawning, swimming gaits are likely different and are sustained by two different muscle types, such as red and white fibers. As they are relying to two different metabolic pathways, red and white muscle would need separate equations to estimate EE (Gleiss et al., 2011). Again, preliminary studies in experimental conditions (swim tunnel + respirometry + accelerometers + video) would have been great to validate the EE calculation.

- In line with my last comment, concerning the metabolic fuels: even if carbohydrates only represent a small part of energetic substrates for long-term exercise, glycogen and lactate are commonly used for burst swimming (Moyes and West, 1995; Weber and Haman, 1996), which appears closely related to spawning effort. I do not understand why the authors assumed that shad get 69% of their energy from lipids and 31% of energy from proteins (lines 280-284). They cited the study of Leonard and McCormick (1999), which reports the energy use pattern of migrating American shad. Here, the main goal is about estimating the energy expenditure during spawning period, which is unlikely relying on the same pattern of swimming effort. Indeed, line 586, the authors wrote about recovery after sprint, citing Kieffer 2000.

I also have minor interrogations, Please find them below: - How to discriminate females from males? Is there any specific sexual character? - A picture of the equipped fish could be useful, in addition to the figure 1. - Roundness estimation is a great idea but is the position of the accelerometer accurate enough to generate good data? But I totally agree with the authors, if this new method could be fine-tuned, it will be of great interest for field eco-physiological studies.

- Figure 5.D needed? I did not understand the message, because this graph shows average cumulated EE per 8h. It does not take into account the duration (in contrast with the Fig. 4A) and did not give any further information. It would have been great to get the same graph for each spawning event. For example, what the EE for fish #1 (grey plot), which got 7 or 8 spawning acts the 11/06 (Fig. 3A).
- I am puzzled about using body weight instead of body mass.

Reviewed by anonymous reviewer, 2020-06-28 22:40

Download the review (PDF file)

Author's reply:

Dear recommender, Our reply is attached as a pdf file, with all the initial comments in black and our answer to each in blue. Yours, the authors.

Download author's reply (PDF file)