To scale or not to scale
a perspective on describing fish energy budgeting
Svendsen, Morten Bo Søndergaard; Christensen, Emil Aputsiaq Flindt; Steffensen, John Fleng

Published in:
Conservation Physiology

DOI:
10.1093/conphys/cox056

Publication date:
2017

Document version
Publisher's PDF, also known as Version of record

Document license:
CC BY

Citation for published version (APA):
To scale or not to scale: a perspective on describing fish energy budgeting

Morten Bo S. Svendsen*, Emil A. F. Christensen and John F. Steffensen

Department of Biology, University of Copenhagen, Helsingør DK 3000, Denmark

*Corresponding author: Tel: +45 23235265; Email: mortenbosvendsen@gmail.com

Conventionally, dynamic energy budget (DEB) models operate with animals that have maintenance rates scaling with their body volume, and assimilation rates scaling with body surface area. However, when applying such criteria for the individual in a population level model, the emergent behaviour of the conventional model apparently only reflects juveniles and not adult animals. This paper discusses the relevance of what level assumptions are made on, and the subsequent impact on interpreting the animal (top-down or bottom-up). The alternative DEB model has maintenance scaling with body area, and assimilation with body volume—the opposite of the conventional energy budget animal. Likewise, scaling of organism function to body mass is emphasized to take into account the different challenges organisms face when growing in size. It is emphasized that homoeostasis and its challenges are continuously changing, and cannot be assumed constant. The perspective is finalized by a discussion on perceiving animals as machines, and how it can maybe serve as a lingua franca for physiologists and modellers alike.

Key words: Aerobic scope, dynamic energy budgeting, efficiency, fishes, gills, homoeostasis

Introduction

Assessing effects of perturbations (e.g. fisheries) on ecosystems requires a mechanistic approach in determining cause and effect relationships (Horodysky et al., 2015; McKenzie et al., 2016). For this purpose, organismal physiology has been suggested as a viable tool, as the environment, and the physiology of organisms continually interact (Clarke, 1993). Furthermore, since the dawn of physiology as a research topic, the field has expanded widely, leading Wieser (1973) to formulate a need for analytical approaches for the progression of the area.

'Since the purely descriptive phases in the former sciences [biochemistry and physiology] have largely passed it is the application of strictly analytical methods that will lead to the formulation of the questions that are to occupy biochemists and physiologists of the future.'—W. Wieser, 1973

When an analytical model of any system is being coined, it is of importance how the system is perceived. In trying to describe an animal as a system, in words or via a mathematical model, from which perspective one perceives the animal will affect how one describes it. One fundamental difference in describing complex systems is whether one attempts to describe the system from a bottom-up or a top-down point of view (Pezzulo and Levin, 2016) (Fig. 1). A Bottom-up approach tries to describe the animal by its specific components and their responses, and as components are added complexity ensues. On the other hand, in a top-down approach, all the individual processes integrated as one, yielding a generalized response. Some 90 years ago, Krogh (1929) described that the physiology as ‘growing unwieldy,” making it impossible for one person to be familiar with all branches, illustrating the complexity of physiology already at that time. When trying to
describe a system bottom-up, one has to make assumptions, in a way that sets the rules of life for the given description or model. The set of assumptions of a model de
sets the rules of life for the given description or model. In the paper, ‘A paradox in individual-based models of populations’ by van der Meer (2016), the author highlights a paradox in the application of assumptions in conventional dynamic energy budget (DEB) models. The paradox is that in contrast to conventional DEB models, the desired behaviour of an alternative DEB model, created by van der Meer (2016) requires the creation of a ‘weird animal’ where maintenance scales with body area and assimilation rate scales with body volume.

In this perspective, the importance whole organism function and homoeostasis are emphasized when analytically describing physiology. Exemplified by highlighting what the authors perceive as an oddity in the assigning of functional scaling to a specific organismal dimension, rather than to assign it to a specific need or challenge. Finalized by a discussion on the usefulness as perceiving organisms as machines.

**Different perceptions of fish energy budgeting**

The cornerstone of physiology, both in the field and in the laboratory, is the concept of homoeostasis; that animals maintain an inner environment optimal for processes of life (Cannon, 1935; Costa and Sinervo, 2004; Cooper, 2008). The concept of homoeostasis is a general top-down perception in physiology, with the only rule being the active maintenance of organismal homoeostasis to ensure organismal function. A bottom-up approach to how the ‘environment’ affects behaviour and distribution of animals is whole animal physiology and behaviour. Fry (1947, 1971) proposed a framework that relates environmental effects on whole animal metabolism to animal activities, such as growth and habitat selection, both of which will have a consequence for lifetime fitness. The determinant of habitat choice and growth potential have often, due to the works by Fry, been interpreted as the aerobic scope (AS), that is, the capacity of the animal to increase its oxygen consumption from resting level (Fry, 1971). As of present, however, there is an ongoing discussion of the practical applicability of the AS as a bottom-up approach to higher order analyses (Pörtner and Knust, 2007; Pörtner and Farrell, 2008; Clark et al., 2013; Gräns et al., 2014; Norin et al., 2014; Brijs et al. 2015; Farrell, 2016).

Dynamic energy budget model theory: A potential gathering theory is the maximum power principle described by Lotka (1922a, 1922b) which suggests that natural selection acts on maximum available energy (Sciubba, 2011). In this context, it makes sense that animals can balance the different costs and gains attributable to an environment via metabolic resource allocation (Priede, 1985; Korsmeyer et al., 1996; Holt and Jørgensen, 2015; Sandblom et al. 2016). This sub-organismal level of allocating energy (Kooijman, 1986) is closely related to the theory of DEB (Kooijman, 1986; van der Meer, 2006; 2016; Sousa et al., 2008), and can at the same time explain the physical theory that underlies the Fry paradigm.

**Homoeostasis**

A general top-down perception in physiology is the centering on homoeostasis, with the only rule being that organismal homoeostasis is maintained for organismal function. However, investigating parts of organisms and focusing on those parts’ responses to challenges has been a general practice and is, in essence, a bottom-up approach: homoeostasis is about keeping the mitochondria well-functioning. Simplified, this allows...
thinking of animals open systems (Fig. 2), where different transport phenomena interact in maintaining homeostasis. Transport phenomena have been argued to be the cause of allometric scaling in biology (West et al., 1997; Savage et al., 2007). Oxidative phosphorylation that forms the core reactions of metabolism requires both substrate (food) and oxygen to take place. Respiration:

\[ \text{Food} + \text{oxygen} \rightarrow \text{carbon dioxide} + \text{water} + \text{energy} + \text{heat} \]

Oxygen is not a substrate that can be converted to a reserve; it needs to be taken up and utilized directly in metabolism. Therefore, oxygen homoeostasis should be regarded as a primary organismal function; insufficient oxygen uptake will lead to anaerobiosis that in turn will be detrimental to all other homoeostatic functions (Pörtner and Grieshaber, 1993). As a result, it seems fair to assume that the first costs to pay would be the most immediate for whole organism function, the ones associated with oxygen uptake, which is ventilation and cardiac oxygen transport (external and internal oxygen transport, respectively).

Any energetic part of organismal homeostasis would be included in what is known as the standard oxygen consumption (Beamish, 1964) often described as Standard Metabolic Rate, SMR, as oxygen consumption is a proxy for metabolic rate when studying fishes (Fry, 1971; Nelson, 2016). The standard metabolic rate would be the average maintenance cost of living for a resting fish (Beamish and Mookherjii, 1964; Beamish, 1964), and both energetic cost of ventilation and osmoregulation, therefore, are examples of homoeostatic processes that must be considered a part of SMR (Fry, 1971). The metabolic cost of ventilation varies from 4 to 43% but is most likely in the vicinity of 10% in normoxia (Jones et al., 1970; Jones, 1971; Jones and Schwarzfeld, 1974; Kramer, 1983; Steffensen and Lomholt, 1983). The cost of internal (cardiac) oxygen transport (Hughes, 1973), has as such not been assessed but suggested to equal that of ventilation (Jones, 1971; Farrell and Steffensen, 1987). However, considering the volumes of internal and external oxygen medium need to transport to maintain a fixed oxygen consumption, ventilation of water requires much larger volumes to be moved compared to that of blood (Piiper et al., 1971; Piiper and Scheid, 1984), why it logically could be assigned as the most costly.

A second abiotic factor affecting maintenance costs via the gills would be the cost of osmoregulation. Osmoregulation has been reported from in the order of a few percent, over 12–16% (Febry and Lutz, 1987) to as high as 50% (Febry and Lutz, 1987; Boeuf and Payan, 2001). However, the cost of osmoregulation seems to interact with temperature (Christensen et al., 2017), why it is difficult to assign a single percentage. Summing up these two factors directly attributable to surface area, expected maintenance cost of the fish would range from a minimum of 20–30% to at least 60% of measurable maintenance metabolism (SMR). Both oxygen uptake and osmoregulation are challenges included in the whole organism homeostasis, and the gills are the major functional organ for both (Evans et al., 2005).

**Scaling**

In the contemporary paper by Lefèvre et al. (2017), gill surface-to-volume is argued to scale with an exponent of 1 with body mass. The arguments in Lefèvre et al. (2017) claims against the gill scaling assumptions of Pauly et al., yet in predictions of future size ranges of fishes, however, Lefèvre et al. (2017) do not deny the many functions occurring in connection with the gills. Figure 3 illustrates that scaling of physiological entities with body size is largely dependent on the unit used to quantify them. The two top panels show SMR values from the dataset in Lefèvre et al. (2017), as a function of body mass. Whole animal oxygen consumption, \( \text{MO}_2 \) (mg·min\(^{-1}\)) scales with an exponent of \(-1.2\), indicating that it increases faster than body mass alone. However, using mass-specific oxygen uptake (mg·min\(^{-1}\)·kg\(^{-1}\)) to remove the effect of mass, then the scaling exponent becomes negative (\(\approx -0.13\)), indicating fewer costs per unit of mass for larger animals. Lastly, when correcting for temperature (\(Q_{10} = 2, 20^\circ\text{C}\)) the effect of body mass on oxygen consumption decrease to \(\approx -0.042\) (Table 1). Just as well as oxygen uptake is an approximation on metabolism (Fry, 1971; Nelson, 2016), one could argue that ventilation is a
proxy for oxygen uptake. By correcting the oxygen uptake for the oxygen content of the ventilation medium, oxygen consumption can be expressed as ventilation volume, $V_G$ (L·min⁻¹·kg⁻¹). In doing this, the scaling exponent of ventilation with body mass becomes $-0.009$, that is, practically constant.

In conclusion, the most determining factors in the order of impact for scaling of oxygen uptake in fishes are body mass, temperature and ventilation volume. Depending on the units used to express metabolism (maintenance) the observed allometric scaling changes from positive, to negative, to almost zero. Thus, instead of considering whether maintenance or similar scales with a surface or volume, efforts should be put in establishing the actual currency, or unit, for the specific functions. The challenges faced in different environments goes back to either thermodynamic effects on metabolism (temperature), or homoeostatic (maintenance) challenges attributable to the gill surface area (oxygen, salinity) (Evans et al., 2005). Suggesting that the body surface that relates to maintenance cost in fishes is the gill surface, as also stated by Pauly (1981). That the gill surface also represents the largest working surface of the fish is additional support for this (Byczkowska-Smyk, 1957). Due to the large water transport in connection with oxygen uptake occurring over the gills, the gill surface inflicts homoeostatic challenges on fishes (Evans et al., 2005). As a consequence, maintenance costs scale to the metabolic rate and physical size of the organism. Scaling of maintenance via ventilatory volume sets an environmental dependency of homoeostasis via the gills. If metabolic demand for oxygen is high, supply is low, or a combination, gills (surface) and heart (ventricular mass)

Figure 3: Top left: Oxygen consumption (MO2) at standard metabolic rate of different fishes and conditions ($n = 218$) vs body mass in kg on the x-axis (data from Lefever et al. (2017)). Demonstrates different scaling of MO2 vs the mass of the animals, using either mass-specific [mg·min⁻¹·kg⁻¹] ($b = 0.154$) or whole animal oxygen consumption rates [mg·min⁻¹] ($b = 1.196$), the dashed line represent a temperature correction of mass-specific scaling ($b = -0.042$). Top right: pane is similar to the top left, except oxygen consumption has been converted to ventilation [L·min⁻¹·kg⁻¹] ($b = -0.0125$; temperature corrected $b = -0.0099$) and [L·min⁻¹] ($b = 1.172$). Bottom left: panel depict calculations of oxygen transport limitation of size in organisms relying on aquatic respiration, as per Krogh (1941). The x-axis with the units the units of mass in gram, assuming a sphere shape organism with mass scaling with $b = 1$ to volume. The intersection of the coloured lines with the horizontal black line, signifies where metabolism starts being limited by oxygen transport (0.21 atm) (red: diffusion only, blue: with convection/ventilation) (Krogh, 1941). Bottom right: depicts the fitted equation of metabolic rate reported in Lefever et al. (2017), converted to whole animal oxygen consumption (—). The magenta graph represents a fixed metabolic rate (maintenance at body mass approximating 0 g) the difference between the two lines ( ) and a vertical line ( ) highlighting where the difference between fixed maintenance (magenta) and scaled maintenance ( — ) are the largest ($M_b ~0.32$ g). The dotted line in the bottom left represents the same point, e.g. maximum difference between the fitted equation from Lefever et al. (2017) and that of fixed maintenance. For a body mass larger than the found $M_b ~0.32$ g, respiration of an aquatic organism requires further measures than convective oxygen transport only, e.g. haemoglobin, to increase the gradient across the gas exchanger (Krogh, 1941; Schmidt-Nielsen, 1984).
acclimates to the conditions (Hughes, 1966). As organismal functions scale with the challenges faced, the focus should be put on the physical environment, and the specific challenges (and equations) it brings as scaling exponents differ depending on the level of correction of the data.

**Ontogenetic dependency of homeostasis-specific thresholds**

A primary assumption of DEB theory is the ‘assumption of strong homeostasis’, meaning that homeostasis is always maintained. Further assumptions are ontogenetic shifts in feeding and reproduction of animals (Sousa et al., 2008). Ontogenetic shifts determine preferred habitats for fish in nature (Félix-Hackradt et al., 2014); likely because the characteristic sizes of animals determine many of the challenges animals face (Andersen et al., 2016). Accordingly, assimilation and maintenance are likely to shift from being either surface or volume related, to the other, during the life history of a fish.

An example of the difficulty in assigning performance to a volume or surface could be the physical movement of the animal. Locomotion sets the scene for both assimilation (feeding) and maintenance (i.e. behavioural thermoregulation and escaping predators) in ectothermic fishes. During the growth of fish, they will experience changes in what forces (inertial or viscous) that govern their ability to move (McHenry and Lauder, 2005). In larger fishes, governed by inertial forces, sustained swimming performance is related to the oxygen uptake capability of the fish (gills) (Brett, 1965; 1972). On the other hand, it is anaerobic burst swimming that limits the fish top-speed via propulsive power (white muscle) (Wardle, 1975). In contrast, for the largest of fishes, top-speed is again limited by a surface, this time due to destructive cavitation to tissue requiring increased maintenance (Iosilevskii and Weihs, 2008). The performance of the white muscle has then been suggested to be constrained via evolution to avoid this incurrence of increased maintenance (Svendsen et al., 2016). Again, the weird animal paradox of van der Meer (2016) may not lie as much in the specific assumptions, as in the assignment of traits to specific volumes or surfaces. The swimming examples should highlight, that in doing so in modelling, one is bound to miss the exceptions; the boundary conditions.

Homoeostasis and its related maintenance costs cannot be assumed constant; a similar argument is formulated in Lefevre et al. (2017). It should be evident that homoeostasis is dependent on the oxygen supply in fishes, but onset of ontogenetic shifts are also hypothesized to be determined by oxygen supply relations (Pauly, 1984). Though the last topic is questioned by Lefevre et al. (2017), it seems to be a causality dilemma; is metabolism constrained by oxygen transport, or is oxygen transport adapting to the metabolic needs? The general need for aquatic ventilation, that is, the onset of a ventilatory requirement, occurs at a body size of 1 mm (sphere) (Krogh, 1941). Thus, if the body size of a fish, either embryo or larvae, increases above 1 mm, the homoeostatic challenge of obtaining oxygen is altered; diffusion will no longer suffice. The bottom part (left) of Fig. 3 illustrates the calculations by Krogh (1941), the lower right pane illustrates calculations of relationships between oxygen consumption and body mass. By assuming a default oxygen uptake, indicative of no constraints on metabolism, the difference to the observed average scaling can be calculated (SMR = 158 mg·min⁻¹·kg⁻¹, a body mass of 1 g, using the best-fit equation from Lefevre et al. (2017): 158 · M⁻⁰.¹¹). This difference would be above zero for body sizes where the metabolism is larger than the expected default metabolism—i.e. body sizes that allow for more than an average metabolic

---

**Table 1: Scaling exponents of fishes and the effects of unit conversion and transformation**

<table>
<thead>
<tr>
<th>Scaling exponents, b</th>
<th>Oxygen consumption</th>
<th>Ventilation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mg · min⁻¹</td>
<td>mg · min⁻¹ kg⁻¹</td>
</tr>
<tr>
<td>SMR</td>
<td>1.196</td>
<td>−0.154</td>
</tr>
<tr>
<td>SMR (Q10)</td>
<td>1.096</td>
<td>−0.042</td>
</tr>
<tr>
<td>Effects on allometric scaling</td>
<td>Δ(\text{lb})</td>
<td>var % (\text{lb})</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.112</td>
<td>0.076</td>
</tr>
<tr>
<td>Ventilation</td>
<td>0.321</td>
<td>0.263</td>
</tr>
<tr>
<td>Body mass</td>
<td>1.212</td>
<td>0.111</td>
</tr>
<tr>
<td>Effects of unit transformation on observed variance</td>
<td>Coefficient of variation</td>
<td></td>
</tr>
<tr>
<td>mg · min⁻¹</td>
<td></td>
<td>3.88</td>
</tr>
<tr>
<td>mg · min⁻¹ · kg⁻¹</td>
<td></td>
<td>0.96</td>
</tr>
<tr>
<td>L · min⁻¹ · kg⁻¹</td>
<td></td>
<td>0.84</td>
</tr>
<tr>
<td>L · min⁻¹ · kg⁻¹ (Q10)</td>
<td></td>
<td>0.65</td>
</tr>
</tbody>
</table>
turnover. The peak of this difference should indicate the onset of a respiratory constraint, equalling the threshold calculated by Krogh, a body mass from which larger animals starts becoming constrained by oxygen transport. Interestingly, the calculations by Krogh (1941) exactly predict the peak of the difference curve based on data from Lefèvre et al. (2017). As suggested by Krogh (Krogh, 1941) and Pauly (Pauly, 1981; 1984), metabolism may be constrained by oxygen transport. Regardless, as there is an observed allometric scaling of mass-specific metabolic rate (Krogh, 1941; Gillooly et al., 2001; Lefèvre et al., 2017), the fractional allocation of energy to homeostasis must change and cannot be assumed constant (cf. DEB).

**Absence of a lingua franca—assuming homeostasis**

One pivotal point of the progression of conservation physiology of fishes as a scientific field is a collaboration between fish physiologists and ecological modellers (McKenzie et al., 2016). Results (Ern et al., 2014; 2015; Gräns et al., 2014; Norin et al., 2014; Brijs et al., 2015; Raby et al., 2016) questioning a theory of temperature and oxygen uptake capability (Pörtner and Knust, 2007) highlights a divergence among physiologists. The environments providing maximum power for the organism, as per Fry (1971), may not be preferable for certain fishes (Norin et al., 2014). Could long term maximum power output (Lotka, 1922a, 1922b) be determined by something different than the absolute power output (Fry, 1971) as determined by physiological experiments? Answering such questions requires mechanistic approaches (McKenzie et al., 2016), such as the DEB theory. In a review, investigating the applicability of assumptions of the DEB theory and their corresponding evidence in the scientific literature, it is concluded:

‘... we prove that (i) the DEB theory is fully supported by empirical biological patterns and the universal laws of physics and evolution and (ii) it is a theory on metabolic organization that is as formal as physics.’—Sousa et al. (2008)

However promising, it remains unclear to the authors of present paper, being physiologists, how the DEB theory accounts for maintaining homeostasis (van der Meer, 2006; 2006; Sousa et al., 2008). In our opinion, homeostasis and related costs must be the maintenance costs related to living. The introductory DEB literature does not seem fully supported by empirical biological patterns; however applicable DEB models might be in different settings. Does the word maintenance represent the same meaning to a modeller as it does to a physiologist? The most apparent DEB paradox from a physiological point of view is that homeostasis is assumed, and not maintained, a semantic difference that could prove to be of large impact. Environmental tolerances of animals are, in one way or the other, determined by a failure of homeostasis (Fry, 1971). If the mentioned progression should be successful, it should be of importance that a common language is agreed upon. Can the measurements physiologists carry out be utilized directly in a model, or does one part need to adapt?

**The animal as a machine**

Having stated a range of concerns, it is appropriate to suggest a possible solution as well. In the literature, organisms are often described theoretically as engines, that is, thermodynamic systems (Lotka, 1922a, 1922b; Fry, 1947; Von Bertalanffy, 1950). Figure 4 illustrates that for fish, as for engines, there is more to function than power output. In this experiment of thought, the idling of the engine would for fishes be the standard metabolic rate and the maximum turnover around is the maximum metabolic rate, the resulting power output is in this case then the AS (Fry, 1947; 1971). The underlying assumption is that the initial decreasing of maximum metabolic rate at higher temperatures arises from one (Pörtner and Knust, 2007; Farrell, 2016) or a range of homeostatic imbalances (Wang and Overgaard, 2007; Clark et al., 2013; Brijs et al., 2015; Sandblom et al., 2016), leading to inherent inefficiency of the organismal system. The efficiency of a system, in this case across temperature, is by convention described as its power output (AS), divided by its power input (maximum oxygen uptake).

\[
\varepsilon = \frac{AS}{MMR}
\]

Given the efficiency is inherent to the system then an Effective-SMR (output from idling) can be found by multiplication of SMR and the efficiency.

\[
SMR_e = \varepsilon \cdot SMR
\]

An upper ‘turning point’ (pejus) for idling happens when the efficiency drops below 0.5 (Odum and Pinkerton, 1953; Odum, 1983). When transitioning into environments where the efficiency drops below 0.5, an environmental threshold, much like an ontogenetic limit, is encountered. Beyond this point, maintenance will increase dramatically (Figure 4), progressing further into such environments is unfruitful for the organism. Beyond \(\varepsilon = 0.5\), maintenance allocation increases faster, as whole animal efficiency approaches 0. Thinking in the lines of whole animal efficacy, explains why Frisk et al. (2012) suggest their fish to be at a critical acclimation temperature at 28°C (Figure 4), even though the best-fit AS (power output) is at 76% of its maximum (An efficiency of 0.5 is also signified by AS equalling SMR, and thus factorial AS being 2). Similar results of animal functioning deteriorating at high percentages of remaining AS are not uncommon. For six species of animals relying on aquatic respiration, the average AS at maximum acclimation temperature is \(\mu \pm \sigma\) 78% ± 16% with efficiencies of 0.48 ± 0.08 (Frisk et al., 2012; Ern et al., 2014; 2015; Claisson et al., 2016; Jensen et al., 2017).
Likewise, challenging fish by increasing salinity, projecting data from Behrens et al. (2017) indicates a 0% survival at efficiency of 0.55. Thus instead of breaking apart the animal into what specific parts are failing (Brijs et al., 2015; Ern et al., 2015), this simple efficacy analysis of whole animal function, explains, in part or completely, some discrepancies among fish physiologists (Ern et al., 2014, 2015; Claësson et al., 2016; Jensen et al., 2017). Further, whole animal efficiency provides reasoning for why maximum power output, as per absolute AS (Fry, 1971), is not always the determining factor (Norin et al., 2014; Claësson et al., 2016; Raby et al., 2016). Thus impaired performance (Gräs et al., 2014) and change in preference (Norin et al., 2014) is likely due to increased energy allocation to the maintenance of homeostasis. Perceiving fishes in a top-down fashion, in this case, as machines, could provide simpler mechanistic models and serve as a starting point for creating a *lingua franca* for fish physiologists; most of the references in this section are studies that criticize the oxygen carrying capacity for thermal tolerance theory (Pörtner and Knust, 2007) and Fry paradigm, in aquatic breathers. As these differences amongst physiologists can be explained by thinking in terms of efficiency, maybe a bridge between physiologists and modellers is found in using the same terms. Hopefully creating a basis for determining the reaction norm of the effects of the environment on fishes.

**Figure 4:** A fish as a machine. This example is for oxygen uptake rates (\(\text{MO}_2\)) as proxy for metabolic rate in the freshwater fish *Sander lucioperca* from Frisk et al. (2012) (Top part of figure). Lines between the points represent best-fit equations (MMR: Quadratic function, SMR: Exponential). The efficacy analysis (Output/Input; see main text) is seen in the lower plot; a turning point (vertical line), where maintenance will increase radically, happens when the efficiency drops below 0.5 (AS = SMR; Factorial AS = 2). In the lower plot, the points are the calculated efficiencies (AS/MMR) of the measurements in the top plot.

**References**

Beamish FWH (1964) Respiration of fishes with special emphasis on standard oxygen consumption: II. Influence of weight and


Brett JR (1972) The metabolic demand for oxygen in fish, particularly salmonids, and a comparison with other vertebrates. Respir Physiol 14:151–170.


Fry FEJ (1947). Effects of the environment on animal activity. In University of Toronto Studies, (The University of Toronto Press)


Lotka AJ (1922a) Contribution to the energetics of evolution. PNAS 8:147.


