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David Mckenzie

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BOOK REVIEW

“Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Aquatic Animals” by Daniel Pauly

This is the 2nd edition of Daniel Pauly’s book entitled ‘Gasping Fish and Panting Squids Oxygen, Temperature and the Growth of Aquatic Animals’. Dr Pauly is a highly-cited researcher, a major figure of global renown in the field of fisheries biology. This book is about a model to explain how the respiratory physiology of water-breathing animals, notably fishes, affects their physiological energetics to cause asymptotic growth. This is the phenomenon whereby most fish species show a growth curve with an initial period of rapid increase in mass, up until sexual maturity, after which growth rate slows – becomes asymptotic. Understanding the mechanisms that underly patterns of growth is obviously of major interest to fisheries biologists. Fishes use gills to obtain oxygen for metabolism and a core element of Dr Pauly’s proposed model is the fact that gill surface area declines hypo-allometrically with increasing body mass within fish species: as individuals grow their gill surface area declines in relation to their body volume. It is argued that this phenomenon occurs because fish gills are two-dimensional structures and their surface area just cannot grow at the same rate as their body mass and volume. Consequently, a fish would risk eventually growing to a mass where its gills were only able to meet the oxygen demands of simple maintenance - they could only provide tissue mitochondria with enough oxygen to simply keep ticking over and staying alive - they could not sustain any metabolic activities beyond this. Therefore, fishes stop growing and switch to reproducing before this limitation occurs, and this is what defines a species’ asymptotic adult mass. In this second edition of the book, this paradigm is called the Gill Oxygen Limitation Theory (GOLT).

A major explanatory component of the GOLT model is the ‘P-diagram’. It is not explained what the ‘P’ refers to. The P-diagram has body mass on the abscissa and ‘oxygen supply per body weight’ on the ordinate. It then plots two physiological variables. Firstly, how capacity for oxygen supply, which is assumed to be equivalent to gill surface area, would decline allometrically with increasing mass following a negative power function. Then, how oxygen demands for maintenance are assumed to remain constant with increasing mass, a horizontal line parallel to the abscissa. The mass at which a fish would become oxygen-limited is given by the point of intersection where the curvilinear decline in capacity for oxygen supply meets the demands of maintenance. It is argued that the GOLT is a universal principle for water-breathing animals, and the P-Diagram is used to explain various phenomena in fish populations. For example, the fact that many female fishes reach larger adult sizes than males would be because females are ‘less active’ and therefore have lower maintenance, so they can grow to a larger

mass before their gill surface area would become limiting.

I think that all biologists support the search for universal physiological principles that can explain patterns in nature and, in this era of alarming global change, that can predict how animals will be affected. There is no doubt that gill surface area could be a limiting factor for oxygen uptake in fishes, in deep aquatic hypoxia or at maximum metabolic activity during, for example, intense aerobic exercise. The GOLT, however, is not a universal physiological paradigm. I agreed to write this book review because I think it is important that readers of this journal are aware of the major concerns that have been raised about the GOLT (Lefevre et al., 2017, 2018; Marshall & White, 2019). Although I have many comments about the book itself, these are essentially moot because the underlying paradigm is fundamentally flawed. For the sake of brevity, therefore, I will focus on why the model and the P-diagram cannot tell us anything useful about how the respiratory physiology of fishes influences their growth. First and foremost, the core element of the GOLT is that fish gill surface area cannot grow as fast as body volume, because gills are two-dimensional structures. This is simply not true, fish gills are folded three-dimensional surfaces, the folding allows them to overcome the constraints of simple surface to volume relationships (Lefevre et al., 2017). The reason that gill relative surface area declines with increasing body mass in fishes is because area matches metabolic oxygen demand over a species' size range (Lefevre et al., 2017; Marshall & White, 2019). This can be explained further by a critique of the P-diagram.

The two variables in the P-diagram bear no clear relationship to real traits of respiratory metabolism in fishes. The 'maintenance' variable is never properly defined, early on it is explained in terms of the costs of protein metabolism but, when discussing why females grow to larger adult sizes than males, activity level becomes a component of maintenance. This is at odds with the correct physiological definition of maintenance metabolism. The standard metabolic rate (SMR) of ectothermic animals, which might seem to be what Dr Pauly refers to as maintenance, is the amount of oxygen needed to meet the energy demands of basic life processes - staying alive - at the prevailing acclimation temperature. These processes include protein metabolism but also maintaining ion gradients across membranes, cardiac pumping, gill ventilation, among others. The SMR has no component of activity, whether that be swimming or digesting and assimilating food. Then, there is the curve describing how 'oxygen supply per body weight' would decline with mass. This is also not defined in relation to a real trait of fish respiratory metabolism. For fish respiratory physiologists, the maximum capacity for oxygen supply (or uptake) is known as maximum metabolic rate (MMR) and it is measured under defined conditions, for example at peak aerobic swimming exercise in an active species. The difference between MMR and SMR is considered an ecologically important trait in fishes, known as aerobic metabolic scope

(AS). The AS represents the capacity to increase supply of oxygen above simple maintenance, to meet the energy demands of critical activities such as swimming or growing. The GOLT does not contemplate AS but the P-diagram and the underlying concepts of the GOLT clearly predict that AS should decline profoundly as a fish grows, becoming very low in mature adults. Experimental evidence in multiple species demonstrates that this is not the case (Lefevre et al., 2017). The notion that adult sexually mature fishes are critically constrained in their ability to provide oxygen to perform any activities - have low AS - is difficult to reconcile with, for example, the spawning migrations of salmonids.

Meanwhile, back in the P-diagram, maintenance is considered to be constant as mass increases. In the real world, SMR actually declines allometrically with mass as a fish grows. The mechanism for this decline in SMR with increasing mass is not fully understood, but it means that larger fish can reduce their relative gill surface area while still maintaining the same AS as a smaller fish. Dr Pauly acknowledges that gills are expensive organs, a large area of delicate epithelium that brings liabilities in terms of maintaining internal homeostasis or as a site of attack by parasites or pathogens. That is, as mentioned above, gill surface area in a fish species is matched to metabolic demand for oxygen over its size range (Lefevre et al., 2017; Marshall & White, 2019).

Dr Pauly argues that the strength of the GOLT is that it is parsimonious, it can be used to explain various phenomena. This is no guarantee that it has a sound theoretical basis. Various celestial phenomena can be explained by assuming that the sun and stars orbit the earth.

David J. McKenzie

UMR Marbec, Université de Montpellier, CNRS, IRD, Ifremer.

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Correspondence

David McKenzie, UMR Marbec, Place Eugène Bataillon cc093, Université de Montpellier, 34095 Montpellier cedex 5, France.

david.mckenzie@cnrs.fr