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The GOLT as a theory of optimization

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The impact of global warming and deoxygenation on fishes and their growth is currently the topic of heated debates between fisheries scientists, physiologists, and ecologists. The most comprehensive theoretical framework that seeks to explain the widely observed phenomenon of “shrinking fish” is the Gill-Oxygen Limitation Theory (GOLT), which figures at the center of this debate. The GOLT explains final size reductions in fishes and other water-breathing animals as a consequence of oxygen limitation that is experienced in warmer waters due to higher maintenance costs. If these maintenance costs rise but respiratory surfaces do not allow for more significant increase in oxygen uptake, less energy is available for further growth. Critics of the theory maintain that it would be evolutionary implausible to argue for intrinsic physiological limitations on resource uptake that could not be overcome through regulatory upscaling mechanisms. Alternatively, recent theoretical proposals have suggested to move away from constraint-based to optimization-based models and to explain final size reductions as a result of different energy allocation strategies at higher temperatures. This paper evaluates these current debates and examines the role of evolutionary optimization in the architectural framework of the GOLT. Contrary to the view that the GOLT neglects the role of evolutionary optimization, I make the case that its central tenets are in fact based on adaptive mechanisms, which is illustrated by its reformulation of the Pütter/von Bertalanffy equation with flexible scaling exponents whose values result from specific growth and life-history strategies. As I argue, current adaptationist frameworks tend to overlook the relationship between physiological constraints and optimizations. The GOLT conceives of evolutionary optimizations as intrinsically constraint-dependent – in other words: optimization is only a meaningful concept in relation to a given constraint on which it can act. Discussing the most prominent recent critiques of the GOLT, I highlight the importance of distinguishing between intraspecific (ontogenetic) and interspecific (evolutionary) scaling patterns. As I show, this distinction is often blurred in the current



debate about the GOLT, which results in a flawed understanding of the role of limitations and constraints and the optimization of their respective physiological traits.