



Aerobic scope in fishes with different lifestyles and across habitats: Trade-offs among hypoxia tolerance, swimming performance and digestion

Shi-Jian Fu^{a,*}, Yun-Wei Dong^b, Shaun S. Killen^c

^a Laboratory of Evolutionary Physiology and Behavior, College of Life Sciences, Chongqing Normal University, Chongqing 400047, China

^b Fisheries College, Ocean University of China, Qingdao 266100, China.

^c Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK.

ARTICLE INFO

Edited by Michael Hedrick

Keywords:

Fish
Aerobic scope
Anaerobic capacity
Adaptation
Hypoxia tolerance
Habitat
Metabolic type
Metabolic priority mode

ABSTRACT

Exercise and aerobic scope in fishes have attracted scientists' attention for several decades. While it has been suggested that aerobic scope may limit behavioral expression and tolerance to environmental stressors in fishes, the exact importance of aerobic scope in an ecological context remains poorly understood. In this review, we examine the ecological relevance of aerobic scope by reconsidering and reanalyzing the existing literature on Chinese freshwater fishes across a wide-range of habitats and lifestyles. The available evidence suggests that natural selection in fast-flowing aquatic habitats may favor species with a high aerobic scope and anaerobic capacity for locomotion, whereas in relatively slow-flowing habitats, hypoxia tolerance may be favored at the cost of reduced locomotor capacity. In addition, while physical activity can usually cause fishes from fast-flowing habitats to reach their aerobic metabolic ceiling (i.e., maximum metabolic rate), possibly due to selection pressure on locomotion, most species from slow-flowing habitats can only reach their metabolic ceiling during digestion, either alone or in combination with physical activity. Overall, we suggest that fish exhibit a continuum of metabolic types, from a 'visceral metabolic type' with a higher digestive performance to a 'locomotion metabolic type' which appears to have reduced capacity for digestion but enhanced locomotor performance. Generally, locomotor-type species can either satisfy the demands of their high swimming capacity with a high oxygen uptake capacity or sacrifice digestion while swimming. In contrast, most visceral-type species show a pronounced decrease in swimming performance while digesting, probably owing to conflicts within their aerobic scope. In conclusion, the ecological relevance of aerobic scope and the consequent effects on other physiological functions are closely related to habitat and the lifestyle of a given species. These results suggest that swimming performance, digestion and hypoxia tolerance might coevolve due to dependence on metabolic traits such as aerobic scope.

1. Introduction

Fish locomotor physiology has been investigated for several decades due to its ecological relevance and potential applications in an aquaculture context. Since the early description by Fry (1947), the concept of metabolic scope has been widely adopted for investigations of bioenergetics, evolution of swimming performance, behavioral and physiological ecology, aquatic ecotoxicology, and fisheries and aquaculture. Renewed interest in aerobic scope has been generated by the concept of 'oxygen- and capacity-limited thermal tolerance' (OCLTT) and other frameworks regarding how aerobic scope may influence the ability of

ectotherms to respond to environmental change (e.g., oxygen- and temperature-limited metabolic niche) (Pörtner and Knust, 2007; Ern, 2019). In this review, we outline how hypoxia tolerance, digestion, and their trade-offs with locomotion in fishes lie at the root of conflicts within an animal's available aerobic scope. We first provide a brief introduction to exercise physiology, aerobic scope, and the measurement of key metabolic traits. Then, we mainly discuss: (1) the trade-off between hypoxia tolerance and swimming performance of freshwater fishes as a possible consequence of coevolution with aerobic scope; and (2) the trade-off between digestion and locomotion, i.e., the partitioning of aerobic scope between these two physiological functions.

* Corresponding author at: Laboratory of Evolutionary Physiology and Behavior, College of Life Sciences, Chongqing Normal University, Chongqing 400047, China.

E-mail address: shijianfu9@cqu.edu.cn (S.-J. Fu).

<https://doi.org/10.1016/j.cbpa.2022.111277>

Received 11 January 2022; Received in revised form 16 July 2022; Accepted 18 July 2022

Available online 21 July 2022

1095-6433/© 2022 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Throughout, we review what is known about the ecological importance and interpretation of aerobic scope in fish species of different lifestyles (sit-and-wait predators vs. active foragers; fast-lifestyle vs. slow-lifestyle) and consider whether correlations among traits vary with habitats. We mainly focus on Chinese freshwater fish species for which there is an extremely wide ecological and physiological diversity, but that have in general been overlooked with regard to synthesizing knowledge of the broad ecological relevance of fish bioenergetics and locomotor performance.

2. Swimming performance as a cornerstone of aerobic scope-related compromises

Locomotor activity is fundamental to the ability of fishes, and animals in general, to capture food, avoid predators, associate with conspecifics, and perform reproductive activities. It is therefore not unreasonable to expect that many aspects of fish physiology, morphology, and behaviour are affected by adaptations and plasticity in the context of trade-offs with swimming capacity and performance. As such, researchers have long been interested in understanding how natural selection shapes phenotypic variation in swimming both among and within species (Langerhans, 2009; Marras et al., 2010; Ouffiero et al., 2011; Fu et al., 2013; Yan et al., 2013; Pang et al., 2020; DeWitt et al., 2022). Swimming gait generally changes with speed and can generally be broken down into three categories: sustained, prolonged and burst-type swimming (Beamish, 1978; Kieffer, 2010). The critical swimming speed (U_{crit} , i.e., maximum sustained swimming speed), measured with a progressively increasing speed in stepwise increments within a swimming flume, is the most popular benchmark to assess aerobic swimming capacity in fish species, although an anaerobic component is recruited to some extent during measurement (Brett, 1964). On the other hand, intensive burst swimming depends mainly on anaerobic metabolism and lasts for a short period, usually less than 20 s. Furthermore, fast-start escape swimming and the maximum swimming speed (V_{max}), which is fueled exclusively anaerobically and lasts less than 1 s, occurs mainly during predator-prey interactions and has attracted considerable research attention in the last two decades (Domenici and Kapoor, 2010; Yan et al., 2015). In addition to these indicators of swimming performance, the exhaustive exercise and recovery processes that follow also are very important ecologically because they determine the frequency at which energy-demanding activities can be performed in a repeated manner (Lee et al., 2003; Hedrick et al., 2015).

3. Aerobic scope

3.1. Definition and development

The aerobic metabolic scope, calculated as the difference or ratio between metabolic ceiling and metabolic floor, was formulated by Fry and colleagues (Fry, 1947; Fry and Hart, 1948) and is a touchstone to bridge the environment, metabolism, physiological function and population dynamics in fishes (see Priede, 1985; Claireaux and Lefrançois, 2007; Eliason et al., 2011; Claireaux and Chabot, 2016). The maximum oxygen consumption rate a fish can achieve during high-performance swimming activities can be used as a proxy to determine the metabolic ceiling, or the maximum (aerobic) metabolic rate (MMR) (Norin and Clark, 2016). The metabolic floor, i.e., the standard metabolic rate (SMR), is the maintenance energy expenditure below which physiological performance is impaired and survival is compromised (Priede, 1985; Chabot et al., 2016). Metabolic scope can be expressed as either the difference (i.e. absolute metabolic scope) or ratio (factorial metabolic scope) between MMR and SMR. Fry proposed that the effect of environmental factors on an organism's physiological performance occurs primarily via effects on aerobic scope. Thus, aerobic scope has been widely used as a bioindicator in studies related to ecotoxicology (Kulesza et al., 2020; Milinkovitch et al., 2020), aquaculture production

(Fu et al., 2008; Wegner et al., 2018) and as a key phenotypic trait in the investigation of various eco-evolutionary questions (e.g. the evolution of endothermy, Nespolo et al., 2017). Among environmental factors, water temperature and oxygen partial pressure are among the main controlling and limiting factors of aerobic scope and hence swimming activity, and have been most frequently investigated (Claireaux et al., 2000; Lowe and Davison, 2006).

3.2. Measurement of MMR and SMR affecting the reliability of aerobic scope estimation

To properly examine trade-offs within an animal or species' aerobic scope, we first need to consider possible methodological biases or confounds that may related to the factors we are interested in studying, namely species lifestyle and ecology. The calculation of aerobic scope is entirely dependent on the reliability of the estimates for SMR and MMR (Chabot et al., 2016; Clark et al., 2013; Norin and Clark, 2016; Halsey et al., 2018). The calculation of SMR from a single value or a few low values in an entire dataset might underestimate true maintenance requirements due to aberrant measurements or hypometabolism following disturbance (Clark et al., 2013). On the other hand, stress due to handling or confinement in a respirometer may cause an overestimation of SMR (see detailed in Chabot et al., 2016), particularly for species that do not acclimate well to the laboratory and associated handling. For example, increased cortisol levels during respirometry may suggest an elevation of oxygen uptake due to stress and an overestimation of SMR (Murray et al., 2017). To combat these issues, various methods have been proposed for statistically estimating SMR from large datasets of repeated measures of oxygen uptake on the same individual animals (Chabot et al., 2016). Interestingly, even without disturbance, the irregular operculum movements of fish species, such as southern catfish (*Silurus meridionalis*), for which only one side of the operculum is sometimes involved in respiration (personal observation), suggest that fluctuation in oxygen uptake may be quite normal in a natural setting, at least for some fish species.

The method used to determine MMR for animals also can be complicated in multiple ways, and as pointed out by Hedrick et al. (2015): 'in many cases, the maximal available values may not represent the actual VO_{2max} (i.e., metabolic ceiling)'. In fish species, the maximum oxygen consumption during U_{crit} testing has long been used as a proxy for metabolic ceiling. However, it is clearly not proper for species that show weak or even no willingness to swim against a water current (Norin and Clark, 2016). The protocol can also be difficult to apply to some species, such as *Pseudogyrincheilus procheilus* and *Garra pingi*, that have suckers that might adhere to the flume during U_{crit} measurement. An alternative method for estimated MMR is the so-called chase protocol, which is also commonly used in animals other than fishes (see details in Hedrick et al., 2015), during which the animal is manually chased to exhaustion and then measured for oxygen uptake during the recovery period. A key concern in the estimation of MMR is whether the choice of protocol is appropriate for a given study species, as it has been suggested that the most suitable protocol may depend on factors such as species lifestyle (for example, sedentary versus active swimmers). A meta-analysis recently found that, although the values elicited by the chasing protocol were slightly lower than those obtained by the U_{crit} protocol, there was no significant difference when comparing these two protocols based on published data from 121 species. Species lifestyle (benthic vs. pelagic) also seemed to have little effect on the difference between the two protocols. When looking at individual species, however, there may be important differences between the two methods (Norin and Clark, 2016). For example, MMR of Atlantic salmon (*Salmo salar*) was 52% higher during a swim-tunnel protocol as compared to a chase protocol (Hvas and Oppedal, 2019). Conversely, for Atlantic cod (*Gadus morhua*), MMR elicited by the chase protocol is perhaps higher than MMR estimated during swim-flume respirometry (Bushnell et al., 1994; Schurmann and Steffensen, 1997). Generally, benthic species or

ambush predators may be more appropriate for application of the chase protocol to elicit MMR, whereas fish that readily swim in flumes may reach higher MMR during a U_{crit} or U_{burst} test (Clark et al., 2013). Nevertheless, minimizing the variability of both SMR and MMR is important for obtaining robust aerobic scope estimates (Halsey et al., 2018).

Finally, it is worth considering whether exercise alone, using any protocol, is sufficient for eliciting MMR for a given species. While this is usually the default assumption, studies in at least six fishes to date have found that neither the chasing protocol nor U_{crit} can account for all aerobic scope in fasting fish, especially when fish are held and measured toward the lower end of their ecologically relevant temperature range (see details later, Altimiras et al., 2008; Dupont-Prinet et al., 2009; Fu et al., 2009a, 2009b; Zhang et al., 2012; Li et al., 2010a, 2010b; Pang et al., 2011; Nie et al., 2017; Nie and Fu, 2017). For these species, it appears that MMR can only be achieved after feeding, while experiencing the metabolic costs of digestion and assimilation, referred to as specific-dynamic action (SDA). Importantly, very few fish species have actually been tested to determine whether MMR during digestion is actually higher than that which is measured during or after exhaustive swimming. Therefore, not only may there be many species for which MMR is currently underestimated in the published literature, but we also lack general knowledge of how these two key physiological functions (digestion and locomotion) may trade-off within an animal's available aerobic scope.

3.3. Physiological limitations and adaptation

As fish are water-breathing animals, oxygen uptake capacity in gills and subsequent distribution by the cardiocirculatory system is usually assumed to be the most important limiting factor for MMR and hence aerobic scope. Thus, fish should adaptively optimize their cardiorespiratory system to meet oxygen-demanding situations, and the respiratory surface area of the gill and thus the capacity for oxygen extraction might be the primary limitation of the MMR (Fu et al., 2014; Norin and Clark, 2016). Some cyprinid fish species keep their gill respiratory area to a minimum but exhibit extraordinary flexibility and increase their respiratory surface area under energy-demanding situations such as during exposure to hypoxia, warming, or while performing physical activity (Sollid et al., 2003; Brauner et al., 2011; Fu et al., 2014; Chen et al., 2019). While most species that have been studied experience a decrease in MMR during exposure to environmental hypoxia, mainly due to a reduction in oxygen uptake at the gills, some fish species do not decrease MMR and/or U_{crit} under moderate hypoxia, e.g., 50% air saturation in southern catfish and Chinese crucian carp (*Carassius auratus*) (Zhang et al., 2010; Penghan et al., 2014). It has been suggested that the maximal oxygen flux appears to be dependent on cardiovascular O_2 transport rather than pulmonary/gill and tissue diffusing capacity among vertebrates (Hedrick et al., 2015).

Fish may be more adapted to their habitat oxygen tension regime (both average and variation), and those species living under low oxygen tension might have evolved specific morphological, physiological, biochemical, and behavioral mechanisms that buffer their response to changes in oxygen tension. The critical oxygen tension (P_{crit}) is defined as the threshold tension where metabolic rate transitions from being independent to dependent on the environmental oxygen tension (Pörtner and Grieshaber, 1993). P_{crit} may be related to the habitat and lifestyle of the organism and be shaped during evolution, alongside various morphological, physiochemical or behavioral strategies for altering hypoxia tolerance (Fu et al., 2014; Sollid et al., 2003; Dhillon et al., 2013, 2018). Such mechanisms also underlie the profound plasticity exhibited by some fish species, which allow them to persist well when environmental oxygen tension shifts. In contrast, other species, including species in fast-flowing aquatic habitats that seldom experience hypoxia, do not appear to possess this capacity (Fu et al., 2014).

4. Anaerobic capacity and its ecological relevance

In addition to aerobic scope, anaerobic capacity is likely critical in determining the impacts of environmental change on aquatic animals (Sørensen et al., 2014). As noted several decades ago, 'metabolic processes must be within the limits specified by the metabolic scope, whereas the capacity for anaerobic metabolism therefore represents a buffer permitting the upper limit of metabolic scope to be temporarily exceeded' (Priede, 1985). The 'buffering' effect of anaerobic capacity may allow individuals or species to temporarily compensate for a reduction in their aerobic scope, being especially important for species living in an environment with high spatial or temporal heterogeneity in oxygen tension and temperature. This seems to include coral reef fish, which experience periods of nocturnal hypoxia (Nilsson and Östlund-Nilsson, 2004), and Chinese cyprinid and Amazonian fish species living in small, temporally isolated pools. Thus, it is important to take anaerobic metabolism into account when assessing tradeoffs within an animal or species' aerobic scope, as well as the effects of environmental change on aerobic scope and physiological performance (Ejbye-Ernst et al., 2016; Nilsson and Renshaw, 2004; Dhillon et al., 2018; Behrens et al., 2018).

Thus, for a complete picture of an animal's metabolic capacity, it may be necessary to measure anaerobic capacity and hypoxia tolerance (e.g., P_{crit}), along with their thermal tolerance and aerobic scope (Ern, 2019; Jung et al., 2019; Marcek et al., 2019; Slesinger et al., 2019; Zhou et al., 2019). A key challenge, however, is accurately definition and measurement of anaerobic capacity. Several general approaches have been used in this regard. The first is the use of behavioural or performance-based endpoints, associated with 'the capacity to survive partially or fully on anaerobic metabolism during severely hypoxic conditions' (Sørensen et al., 2014), including the time tolerated in hypoxia (i.e., the time between P_{crit} and loss of equilibrium) or the difference between U_{burst} and U_{gait} (a rapid anaerobic metabolism assumed to start at recruitment) as indicators of anaerobic capacity (Sørensen et al., 2014; Ejbye-Ernst et al., 2016). Excess post-exercise or post-hypoxia oxygen consumption (EPOC_e and EPOC_h) has also long been used as an indicator of anaerobic capacity (Genz et al., 2013; Plambech et al., 2013; Pang et al., 2020). Notably, these two variables measured in the laboratory are not identical to either anaerobic exercise capacity or anaerobic hypoxia capacity, partially because of: (1) facultative metabolic components elicited by increased release of catecholamines and cortisol; and (2) metabolic costs involved in the restoration of substrates (e.g., glycogen) and elimination of end-products, such as lactate, which are usually not easily quantified during short measurement periods (Milligan, 1996; Genz et al., 2013). However, EPOC is usually closely related to anaerobic swimming performance and could be used as general proxy of anaerobic capacity (Svendson et al., 2012; Pang et al., 2020). Additionally, potential biochemical indicators of anaerobic capacity may also be relevant but are generally more invasive and may only be usable under specific circumstances. This includes total lactate production or muscle glycogen content, or lactate dehydrogenase activity (Hedrick et al., 2015).

5. Trade-off between hypoxia tolerance and swimming capacity

Given that aquatic hypoxia can lower the ceiling (MMR) on an animal's aerobic scope, but the ability to buffer these effects morphologically or physiologically appears to vary among species, we aimed to examine whether there is indeed a tradeoff between hypoxia tolerance and swimming capacity among fish species. Furthermore, we sought to examine whether there is any evidence that the extent of this tradeoff may vary among species, in relation to their lifestyle or the frequency with which they are exposed to environmental hypoxia. To investigate these issues, we calculated aerobic scope using data from our previously published studies, and examined correlations among aerobic scope, aerobic an anaerobic swimming capacity, anaerobic capacity and

hypoxia tolerance at both the inter- and intraspecific levels (Yan et al., 2013; Pang et al., 2021; Pang et al., 2020).

5.1. Intraspecific level

The aim of this section is to test whether the relationship between aerobic scope and aerobic swimming performance (U_{crit}) and hypoxia tolerance (LOE) among individuals varies between fish species with different ecological lifestyles. We selected data from Pang et al. (2021), which addressed the intraspecific relationship between metabolism and physiological performances of fish species with different lifestyles based on the associated flow-regime of habitats. While Pang et al. (2021) tested the relationships among SMR (or MMR), U_{crit} (or LOE) and hypoxia tolerance, here we calculated the aerobic scope and conduct regression analysis between aerobic scope and U_{crit} or LOE (Fig. 1).

Interestingly, fast-flowing (i.e. fast-lifestyle) qingbo show a relatively high U_{crit} and greater aerobic scope with less variation in these traits, as compared to slow-flowing crucian carp which exhibit a lower O_2 threshold for LOE with much less variation in this trait (Fig. 1a, b). This suggests that selection may be based more on hypoxia tolerance in slow-flowing crucian carp but acts more strongly on aerobic swimming performance in fast-flowing qingbo, possibly due to relaxed selection (Lahti et al., 2009) occurring in slower-flowing habitats, with the low energy-demand and high food availability, resulting in high phenotypic variance in swimming performance and aerobic scope without a concomitant change for hypoxia tolerance. The positive correlation between U_{crit} and aerobic scope in both species suggests that a greater aerobic scope favors higher aerobic swimming performance for fish in different habitats. However, there was a positive correlation between aerobic scope and LOE value (i.e. negative relationship) in fast-flowing qingbo but not in slow-flowing crucian carp. This suggests a trade-off between aerobic capacity (and hence aerobic swimming performance) and hypoxia tolerance in qingbo at the intraspecies level, possibly because the high energy-demand situation in a fast-flowing habitat results in less room for selection to accommodate both functions simultaneously. Nevertheless, this suggests that the shift in natural selection pressure that varies with habitat might have a profound effect on the ecological consequences of aerobic scope and the possible compromise between aerobic capacity and hypoxia tolerance (Fig. 2). However, whether such relationship is presented across Chinese freshwater species or even among all fish species remained to be tested. More detailed investigation of the relationships between aerobic and anaerobic capacity, aerobic and anaerobic swimming performance, and hypoxia tolerance and comparison among different habitats might provide more interesting results.

5.2. Interspecific level

We also aimed to investigate possible relationships between aerobic scope and swimming performance and hypoxia tolerance across Chinese fish species with different lifestyles based on the associated flow-regime of their respective habitats. To do so, we combined and reanalyzed data from two papers examining: (1) the relationship between energetic metabolic traits (SMR and MMR) and hypoxia tolerance capacity (LOE) and anaerobic capacity (EPOC) among 30 species across typical Chinese aquatic habitats (Pang et al., 2020); and (2) the energetic metabolic traits (SMR and MMR), U_{crit} and V_{max} of 19 Chinese freshwater fish species across habitats with typical flow-regimes (Yan et al., 2013). Again, we calculated the aerobic scope from raw data of MMR and SMR. We determined regressions among aerobic scope and aerobic (or anaerobic) swimming capacity, anaerobic capacity and hypoxia tolerance.

First, we found that aerobic scope was positively correlated with both U_{crit} and V_{max} (Fig. 3a, b). Second, aerobic scope also was positively correlated with anaerobic capacity, as estimated by EPOC_e and EPOC_h (Fig. 3c, d). This suggests that increased aerobic scope favors both aerobic and anaerobic swimming capacity as well as anaerobic capacity at interspecific level.

Using the aforementioned data but removing one airbreathing species, we found that aerobic scope showed no relationship with LOE (Fig. 4a). In Fig. 4a, species with a lower LOE (below $0.5 \text{ mgO}_2 \text{ L}^{-1}$) tend to show a positive relationship with aerobic scope, i.e. hypoxia tolerance and aerobic scope are negatively related among species with a low LOE (Fig. 4a). This might be the result of long-term adaptation to the hypoxia challenge and swimming performance demanding which varies profoundly between slow-flowing and fast-flowing habitats. Fish species in the slowest-flowing habitats (species that tend to have the lowest LOE in Fig. 4a) usually possess relatively low functional performance (e.g., relatively sluggish with poor swimming performance) and hence low aerobic scope but high hypoxia tolerance compared to those of fish species in fast-flowing habitats. However, five fish species (empty circles; Fig. 4) exhibit poor hypoxia tolerance but also low aerobic scope, an observation which opposes this hypothesis. Notably, all of those species, with the exception of one, are distributed only in slow-flowing yet nutrient poor water-bodies with a relatively high oxygen content (Pang et al., 2020). Thus, fish in particular habitats might evolve slow-lifestyles but poor hypoxia tolerance, making the relationship between aerobic scope and hypoxia tolerance complex and non-linear. If analyzed without these species, the aerobic scope would show a positive correlation with LOE.

We anticipated a negative relationship between values of LOE and EPOCs. However, a bell-shaped relationship was found between EPOCs

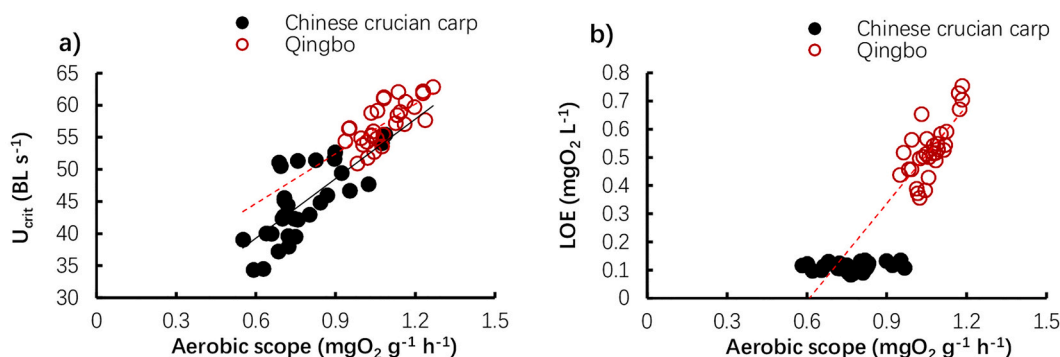


Fig. 1. Intraspecific relationships between aerobic scope and aerobic swimming performance (U_{crit} , a) and hypoxia tolerance (LOE, b) in either slow-lifestyle Chinese crucian carp (*Carassius auratus*) (filled circle) or fast-lifestyle qingbo (*Spinibarbus sinensis*) (empty circle) (data were reanalyzed from Pang et al., 2021). The U_{crit} was positively correlated with aerobic scope in both slow- and fast-lifestyle fish species ($y = 30.932x - 20.711$, $R^2 = 0.525$, $N = 30$, $P < 0.001$ in Chinese crucian carp and $y = 25.838x - 29.174$, $R^2 = 0.499$, $N = 30$, $P < 0.001$ in qingbo), whereas hypoxia tolerance was negatively correlated with aerobic scope (positively correlated with LOE) in only fast-lifestyle fish species ($y = 1.155x - 0.703$, $R^2 = 0.524$, $N = 30$, $P < 0.001$ in qingbo).

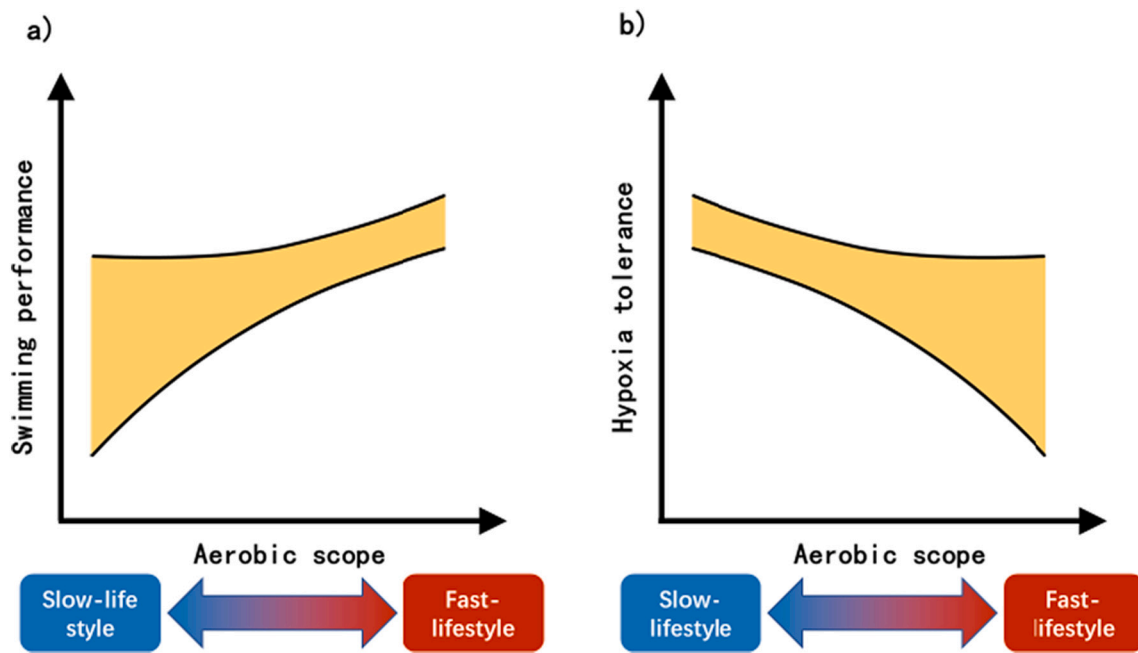


Fig. 2. Possible relationships between aerobic scope and swimming performance (a) and hypoxia tolerance (b) of slow- or fast-lifestyle fish species.

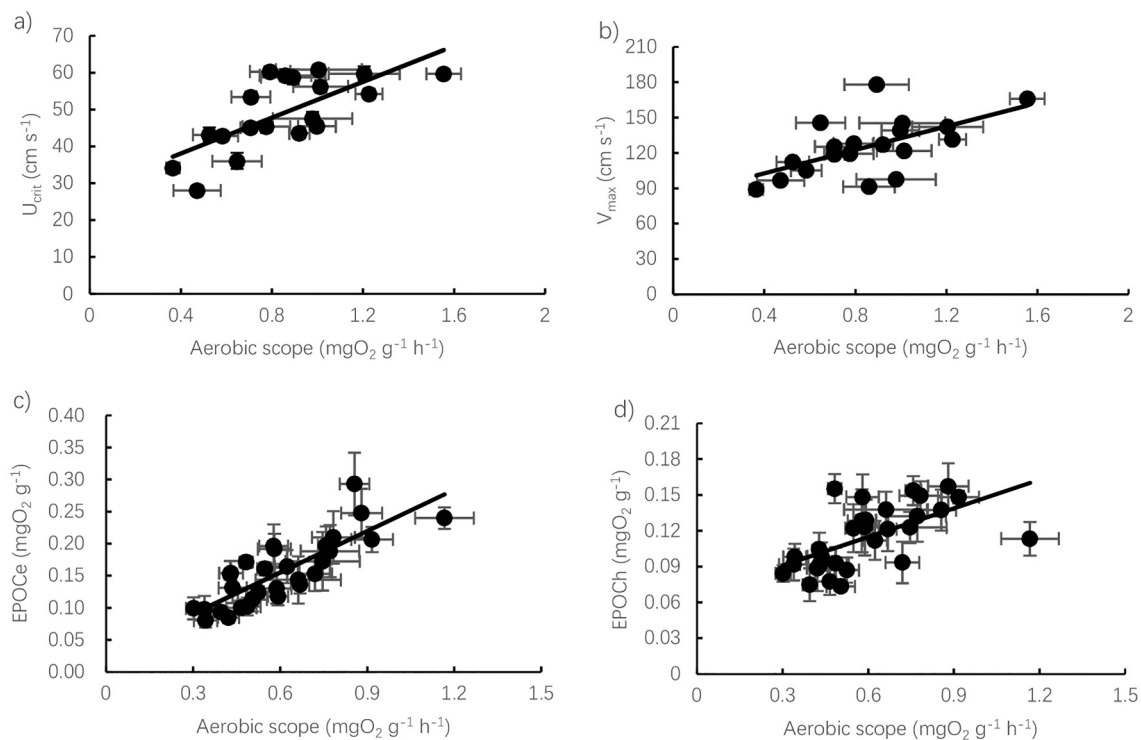


Fig. 3. Interspecies relationships between aerobic scope and critical swimming speed ($U_{crit} = 24.34AS + 28.36$, $R^2 = 0.503$, $P < 0.001$, $N = 19$)(a) and maximum anaerobic swimming speed ($V_{max} = 49.88AS + 82.61$, $R^2 = 0.357$, $P = 0.007$, $N = 19$) and excess post-exercise oxygen consumption ($EPOC_e = 0.215AS + 0.026$, $R^2 = 0.665$, $P < 0.001$, $N = 30$)(c) and excess post-hypoxia oxygen consumption ($EPOCH = 0.080AS + 0.067$, $R^2 = 0.362$, $P < 0.001$, $N = 30$) across freshwater fish species in China (data are presented as mean \pm S.E. which reanalyzed from Yan et al., 2013 and Pang et al., 2020).

and LOE (Fig. 4b, c). On the left side of the bell-shaped curve, the positive correlation suggested fish species with high anaerobic capacity might have poor hypoxia tolerance, possibly because anaerobic capacity stems from physiological functions other than hypoxia tolerance, such as higher swimming performance. Thus, species with the highest anaerobic capacity are those possess stronger swimming performance

but poor hypoxia tolerance. It is possible that hypoxia tolerance is more related to a species lifestyle and integrated physiological and behavioural phenotype, instead of specific physiological traits *per se*. Fish species in slow-flowing habitats evolved slow-lifestyles, low SMR and hence low P_{crit} for recruitment of anaerobic metabolism, low oxygen demand and anaerobic ATP requirement for maintaining essential

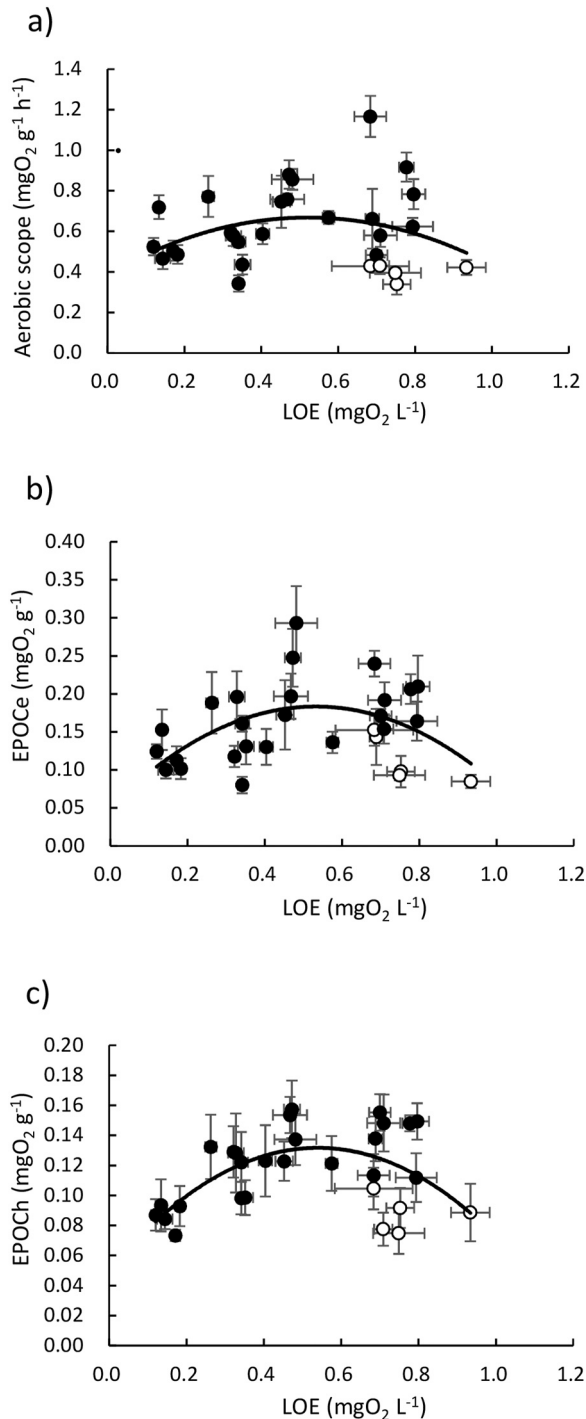


Fig. 4. Interspecies relationships between aerobic scope and LOE (a), EPOC and LOE ($EPOC_e = 0.046 + 0.503LOE - 0.469LOE^2$, $R^2 = 0.221$, $P = 0.039$, $N = 29$)(b) and EPOCH and LOE ($EPOCH = 0.047 + 0.307LOE - 0.280LOE^2$, $R^2 = 0.377$, $P = 0.002$, $N = 29$)(c) in 29 Chinese freshwater fish species (data are reanalyzed from Pang et al., 2020 but exclude the data of the air breathing species). The empty circle are data of fish species living in water body of slow-flowing but high dissolved oxygen level.

functions under P_{crit} (Ginneken and Thillart, 2009; Regan et al., 2013; Dhillon et al., 2018). Thus, for highly hypoxia-tolerant fish species with slow-lifestyle, anaerobic capacity is lower compared to fast-lifestyle fish living in fast-flowing habitats. However, for the fish species on the right side of the curve (Fig. 4b, c), the negative relationship between EPOCs and LOE values is similar to that between aerobic scope and LOE

(Fig. 4a). In other words, those fish species live in habitats with relaxed selection pressure on both hypoxia tolerance and swimming performance shaped species with lower anaerobic capacity for swimming and poor hypoxia tolerance capacity. Nevertheless, the changes in aerobic scope and EPOC are mainly related to energy expenditure associated with lifestyle (active fish with strong physiological performance have a large aerobic scope, and those with anaerobic capacity usually have low hypoxia tolerance). Thus, on one extreme are fish with a slow lifestyle, low aerobic scope but high hypoxia tolerance, whereas on the other extreme are fish with a fast lifestyle, high aerobic scope but low hypoxia tolerance. However, fish in slow-flow yet highly oxygenated habitats with relaxation of selection may have evolved distinct, different strategies such as a sluggish lifestyle but also low hypoxia tolerance.

In conclusion, a greater aerobic scope can favor both aerobic and anaerobic swimming performance. The relationships among anaerobic capacity, aerobic capacity and LOE are rather complicated and may be profoundly influenced by species lifestyle and selection pressure. Generally, fish with a slow lifestyle are more hypoxia tolerant, possibly due to the low maintenance metabolism and hence low oxygen tension to recruit anaerobic metabolism and are less O_2 deficient under hypoxic or anoxic conditions. Beyond this continuum, some species in low energy-demand habitats that seldom undergo hypoxia episodes may evolve special strategies for both low aerobic scope and anaerobic capacity and poor hypoxia tolerance due to relaxed selection pressure.

6. Trade-off between digestion and locomotion

6.1. Specific dynamic action

The postprandial metabolic increase, i.e., specific dynamic action (SDA), is defined as increased heat production following a meal (Beamish, 1974; Jobling, 1981; Fu et al., 2005a, 2005b, 2005c; McCue, 2006; Secor, 2009; Stieglitz et al., 2018; Steell et al., 2019; Flikac et al., 2020). The physiological mechanisms, such as the components of SDA (Brown and Cameron, 1991), as well as the effects of experimental conditions, such as dietary composition (Fu et al., 2005c), meal size (Fu et al., 2006; Flikac et al., 2020) and temperature (Pang et al., 2011), have long been investigated in fish species, whereas the ecological relevance of SDA has received little attention (Willson and Hopkins, 2011; Norin and Clark, 2017; McLean et al., 2018). More than thirty years ago, it was noted that ‘there must be a continual conflict between the needs of locomotion and SDA’ and ‘this metabolic conflict lies at the root of the power budgeting problem that fish face all the time’ (Priede, 1985). Interestingly, previous studies in cod (*Gadus morhua*) found that the peak metabolic rate during digestion (PMR) might exceed the MMR during sustained aerobic swimming, and those species were defined as ‘visceral metabolism type’ (Soofiani and Hawkins, 1982; Soofiani and Priede, 1985). The most typical example of so-called ‘visceral metabolism type’ in the animal kingdom studied to date might be python (*Python molurus*), whose postprandial metabolic increase can reach 44-fold compared to its fasted status, and such an increase is far more profound than exercise-elicited metabolic increase in python (Secor and Diamond, 1998). However, there might not be many visceral metabolism-type fish species, and data for cod also remain questionable, as some studies of Atlantic cod report that MMR should be measured following a chase protocol rather than during sustained swimming at U_{crit} (Reidy et al., 1995). The most profound increases in postprandial metabolism of fish species might be those of some ambush catfish (e.g., southern catfish and Chinese catfish, *Silurus asotus*), which are 5- to 6-fold higher than SMR (Fu et al., 2005b, 2006). These are large predatory fish species at the top of the local food chain in the natural environment, usually with low predation pressure and a habit of lying or hiding during digestion (Fu et al., 2009a). Thus, digesting fish may allocate most of their aerobic scope to growth, leaving little aerobic scope for other metabolic activities (Hunt von Herbing and White, 2002; Cunha et al., 2007). For example, a recent study in an ambush predator, barramundi (*Lates*

calcarifer), found that SDA processes occupied up to 77% of the available aerobic scope (Norin and Clark, 2017). Nevertheless, SDA or feeding metabolism in fish species is potentially ecologically relevant because it can account for a large proportion of their aerobic scope (McLean et al., 2018; Steell et al., 2019).

Below, we examine two possible mechanisms underlying the trade-off between digestion and locomotion, i.e., (1) the relative magnitude of PMR and MMR (i.e., so-called metabolic type), and (2) the partitioning of aerobic scope between digestion and locomotion during postprandial swimming (i.e., so-called metabolic prioritization, Bennett and Hicks, 2001). In addition, we investigate connections among metabolic prioritization, lifestyle and habitat (fast lifestyle vs. slow lifestyle), and foraging mode (infrequent large predator vs. frequent forager).

6.2. Metabolic type

We searched all published data from Web of Science using the combination of subjects by keywords of 'fish', 'specific dynamic action or feeding metabolism' and 'swimming or locomotion'. From the resulting 1103 search results, we summarized available data for which both SDA and exercise were studied in the same studies listed in Table 1 (except for the data on Chinese catfish and pale chub, *Zacco platypus*, results for which are unpublished from S. Fu). We then examined whether there a continuum of digestive ("visceral") vs. locomotor types at the interspecific level, and whether visceral-type fish species have a higher postprandial metabolic peak than the maximum locomotion-elicited metabolic rate. We also sought to examine metabolic prioritization between swimming and digesting during locomotion after feeding.

First, PMR and MMR both vary profoundly, possibly due to the lifestyles of different species. The factorial scope of peak SDA (i.e., the ratio of PMR to SMR) varied from approximately 1.5 in some omnivorous, actively foraging species to 4 to 5 in some sit-and-wait predators (Fig. 5a). One species (lionfish, *Pterois spp.*), showed a higher PMR than the MMR elicited by exhaustive exercise (Steell et al., 2019). However, there might be more visceral-type species in nature, as the meal sizes in these studies were considerably lower than the satiation level (possibly because fish can regurgitate consumed food items during swimming if the meal size is too high in the respirometer chamber). For example, previous studies in Chinese fish found a 6-fold increase in PMR, which is similar to or slightly higher than the MMR elicited by exercise during chasing (Tang et al., 2010; Fu et al., 2006), whereas southern catfish also may show a PMR similar to MMR under a satiation feeding protocol or even higher than the MMR during the catch-up growth period after a long-term food shortage (Fu et al., 2018a). When looking at the feeding-elicited usage of available aerobic scope, the ratio of PMR varied greatly from approximately 10% to 180% of the aerobic scope (calculated by the difference between the MMR and SMR of fasting fish) (Fig. 5b). Thus, digestion-elicited metabolic increases can be higher (lionfish) or at least similar to MMR for sluggish carnivorous species after consumption of a large-size meal. In this manner, there appears to be a continuum of visceral to locomotor type species, according to the extent to which digestion can occupy space within their total aerobic scope. Notably, digesting MMR might be more appropriate to use for calculation of the aerobic scope in fish species for which MMR cannot solely be elicited by exercise (more detail in the next paragraph).

Second, among all 15 species for which both fasting MMR and digestion status were measured, six species showed higher digesting MMR than fasting MMR at their optimal temperature for maximizing MMR (i.e., 10 to 15 °C for salmon and trout but 25 °C for other species) (Fig. 6a). If acclimated close to their winter temperature, the results of all fish species available to date (four cyprinid fish species and one catfish species) show higher digesting MMR than fasting MMR. However, goldfish, Chinese bream (*Parabramis pekinensis*) and qingbo showed no difference between their fasting and digesting MMR at higher

temperatures (Fig. 6b). This finding suggests that exercise alone cannot occupy aerobic scope potential in a considerable number of species, and the number of species for which this is true will increase at low temperature due to the possible physiological and biochemical constraints on the locomotor tissues and hence the surplus oxygen supply from the cardiorespiratory organs (Pang et al., 2011).

In general, when measured at the optimal temperature for MMR, fish species in fast-flowing habitats usually achieve aerobic scope potential by exercise alone because they rely more on strong swimming performance to fulfill their routine activities (see Table 1 for the detail of habitats and lifestyle). However, fish species in slow-flowing habitats usually cannot achieve the aerobic scope by exercise alone which might be attributable to the combined effect of low swimming demand and/or high digestion capacity.

In addition to the absolute or relative postprandial increase related to SMR or aerobic scope, the duration of the elevation of metabolic rate post-feeding (i.e., time budget of feeding metabolism), also is vitally important for understanding tradeoffs within an animal's aerobic scope (McLean et al., 2018). Southern catfish, for example, can maintain postprandial metabolic rate at a level approximately 4-fold higher than SMR for more than 36 h after feeding, whereas goldfish can increase feeding metabolism by approximately 3- to 4-fold but maintain this level for only a very short duration (Fu et al., 2009a). The time budget is also very ecological relevant because the impaired capacity of locomotion during digestion might constrain their ability to defend themselves against potential predators or to engage in other behavioral activities (Fu et al., 2005b; McLean et al., 2018).

Another finding is that the effect of acclimation temperature on the occupation of aerobic scope by SDA varies with lifestyle. With increasing temperature, the PMR of so-called visceral-type species (i.e., high occupation rate of aerobic scope by SDA) increased more than the MMR and left less surplus scope for other aerobic physiological functions. For example, the occupation ratio of PMR to aerobic scope increased from 50% to 65% in southern catfish, 130% to 180% in lionfish, and 37% to 45% in goldfish, whereas it decreased from 26% to 11% in qingbo, a typical athletic-type species (Fig. 7). This suggested that, similar to a previous study of shorthorn sculpin, *Myoxocephalus scorpius*, visceral-type fish may exhibit decreased aerobic scope due to the increased SDA energy demand and leave little room for additional processes such as exercise (Sandblom et al., 2014). Thus, metabolic constraints on aerobic scope might be more severe under high temperature or warming situations for visceral metabolic-type fish species. However, it is noteworthy that the duration of SDA in southern catfish decreases with acclimated temperature (Pang et al., 2010), suggesting visceral-type fish species might benefit a fast digestion process, high food handling capacity and hence fast growth performance.

In conclusion, maximal aerobic scope may be elicited by exercise alone or not, depending on the lifestyle which possibly due to the different selection forces on swimming and digestion. On some extreme examples, the aerobic scope potential in sedentary predators may have evolved to fulfill the metabolic requirements of SDA rather than to maintain the swimming capacity (whether digestion alone can elicit the aerobic scope potential needs further investigation, but there is a low probability based on the data of other sluggish predators, such as southern catfish, Fu et al., 2009a). An exercise protocol may therefore fail to elicit the potential of aerobic scope for some fish species, such as sluggish fish species and even good steady swimmers, when acclimated under lower temperature. In those cases, the definition and measurement protocol become questionable and might have to be reconsidered.

6.3. Metabolic prioritization

It has long been suggested that the 'the most important problem facing an animal trying to survive in the natural environment is simply to attain the power output necessary to live in its selected niche' (Priede, 1985). As previously discussed, whether aerobic swimming activity can

Table 1
Summary of standard metabolic rate (SMR), peak postprandial metabolic rate (PMR), maximum metabolic rate elicited by locomotion (either critical swimming or exhaustive chasing, MMR), occupation of SDA of aerobic scope (AS) and the change of critical swimming speed (U_{crit}) of fasting and digesting fish species.

Species	Body mass, g	Temp, °C	Feeding habit	Habitat	SMR, mgO ₂ kg ⁻¹ h ⁻¹	PMR*, mgO ₂ kg ⁻¹ h ⁻¹	MMR*, mgO ₂ kg ⁻¹ h ⁻¹	Digesting MMR**, mgO ₂ kg ⁻¹ h ⁻¹	Meal size, % body mass	Occupation of SDA on AE, %	Decrease in U_{crit}	References	Protocol
Zebrafish <i>Danio rerio</i>	0.4–0.5	24	Omnivorous, Frequent forager	Commercial	463	717 (1.97)	1066 (2.93)	/	5.0	50.3	/	Lucas and Priede, 1992	chasing
Pale chub <i>Zacco platypus</i>	4–10	25	Omnivorous, Frequent forager	Freshwater, Fast-flowing	203	581 (2.86)	1300 (6.40)	/	6.8	34.5	/	Fu et al., 2018b; Tang, 2019	U_{crit}
Chinese crucian carp <i>Carassius auratus</i>	7.72	25	Omnivorous, Frequent forager	Freshwater, Slow-flowing	220	470 (2.14)	680 (3.09)	900 +	3.0	54.4	No	Zhang et al., 2012	U_{crit}
Goldfish <i>Carassius auratus</i>	10.49	15	Omnivorous, Frequent forager	Freshwater, Slow-flowing	120	259 (2.15)	490 (4.07)	580 +	2.8	30.2	No	Pang et al., 2011	U_{crit}
Goldfish <i>Carassius auratus</i>	9.68	25	Omnivorous, Frequent forager	Freshwater, Slow-flowing	237	629 (2.65)	1100 (4.64)	1200 +	3.3	40.7	Yes	Pang et al., 2011	U_{crit}
Grass carp <i>Ctenopharyngodon idella</i>	7.42	25	Herbivorous, Frequent forager	Freshwater, Intermediate	191	296 (1.55)	1034 (5.40)	974 -	3.9	12.5	/	Fu et al., 2009b	Chasing
Rock carp <i>Procypris rabaudi</i>	19.52	25	Omnivorous, Frequent forager	Freshwater, Intermediate	115	201 (1.75)	780 (6.78)	795 -	2.0	12.9	/	Li et al., 2013	Chasing
∞ Chinese bream <i>Parabramis pekinensis</i>	8.27	15	Omnivorous, Frequent forager	Freshwater, Intermediate	86	133 (1.53)	547 (6.36)	696 +	3.0	9.9	No	Peng et al., 2014	U_{crit}
Chinese bream <i>Parabramis pekinensis</i>	4.62	25	Omnivorous, Frequent forager	Freshwater, Intermediate	290	500 (1.47)	1260 (4.56)	1240 +	2.1	13.3	Yes	Peng et al., 2014	U_{crit}
Common carp <i>Cyprinus carpio</i>	7.94	15	Omnivorous, Frequent forager	Freshwater, Intermediate	113	252 (2.24)	629 (5.59)	790 +	2.9	27.0	No	Pang et al., 2011	U_{crit}
Common carp <i>Cyprinus carpio</i>	7.56	25	Omnivorous, Frequent forager	Freshwater, Intermediate	256	464 (1.81)	1140 (4.45)	1300 +	3.1	23.5	No	Pang et al., 2011	U_{crit}
Black carp <i>Mylopharyngodon piceus</i>	4.62	25	Carnivorous, Frequent forager	Freshwater, Intermediate	220	350 (1.59)	1100 (5.00)	1120 -	1.7	14.8	Yes	Nie et al., 2017	U_{crit}
Qingbo <i>Spinibarbus sinensis</i>	7.72	15	Omnivorous, Frequent forager	Freshwater, Fast-flowing	103	209 (2.02)	510 (4.93)	640 +	2.7	26.0	No	Pang et al., 2011	U_{crit}
Qingbo <i>Spinibarbus sinensis</i>	7.71	25	Omnivorous, Frequent forager	Freshwater, Fast-flowing	160	283 (1.77)	1190 (7.44)	1150 -	2.9	11.9	No	Pang et al., 2011	U_{crit}
Southern catfish <i>Silurus meridonalsi</i>	22.45	15	Carnivorous, Infrequent forager	Freshwater, Slow-flowing	54	149 (2.75)	245 (4.53)	362 +	9.6	49.7	No	Pang et al., 2010	U_{crit}
Southern catfish <i>Silurus meridonalsi</i>	12.89	25	Carnivorous, Infrequent forager	Freshwater, Slow-flowing	114	510 (4.48)	761 (6.30)	902 +	16.0	65.7	Yes	Li et al., 2010a	U_{crit}
Chinese catfish <i>Silurus asotus</i>	c. 30	23	Carnivorous, Infrequent forager	Freshwater, Slow-flowing	98	222 (2.28)	351 (3.60)	433 +	8.7	49.2	/	Li et al., 2012	Chasing

(continued on next page)

Table 1 (continued)

Species	Body mass, g	Temp, °C	Feeding habit	Habitat	SMR, mgO ₂ kg ⁻¹ h ⁻¹	PMR*, mgO ₂ kg ⁻¹ h ⁻¹	MMR*, mgO ₂ kg ⁻¹ h ⁻¹	Digesting MMR**, mgO ₂ kg ⁻¹ h ⁻¹	Meal size, % body mass	Occupation of SDA on AE, %	Decrease in U _{crit}	References	Protocol
Darkbarbel catfish <i>Pelteobagrus vachelli</i>	6.65	25	Omnivorous, Frequent forager	Freshwater, Intermediate	235	341 (1.45)	1020 (4.34)	1300 +	6.9	13.5	No	Li et al., 2010b	U _{crit}
Chinook salmon <i>Oncorhynchus tshawytscha</i>	520	9	Carnivorous, Infrequent forager	Migratory fish, Fast-flowing	48	109 (2.28)	490 (10.20)	478 -	2.0	13.9	Yes	Thorarensen and Farrell, 2006	U _{crit}
Rainbow trout <i>Oncorhynchus mykiss</i>	4–8	15	Carnivorous, Frequent forager	Freshwater, Fast-flowing	189	591 (3.13)	787 (4.17)	803 -	Satiation	67.1	Yes	Alsop and Wood, 1997	U _{crit}
Seabass <i>Dicentrarchus labrax</i>	364	22.5	Carnivorous, Infrequent forager	Marine, Demersal	100	160 (1.60)	350 (3.50)	410+	2.0	24.0	No	Altimiras et al., 2008	U _{crit}
Snapper <i>Chrysophrys auratus</i>	105	17	Carnivorous, Infrequent forager	Marine, Reef associated	130	190 (1.46)	381 (2.93)	/	0.5–3.0	23.9	/	Flikac et al., 2020	U _{crit}
Snapper <i>Chrysophrys auratus</i>	107	21	Carnivorous, Infrequent forager	Marine, Reef associated	163	250 (1.53)	468 (2.87)	/	0.5–3.0	28.5	/	Flikac et al., 2020	U _{crit}
Yellow-eyed mullet <i>Aldrichetta forsteri</i>	30	17	Omnivorous, Frequent forager	Marine and freshwater, Benthic	104	195 (1.88)	686 (6.60)	/	0.5–3.0	15.6	/	Flikac et al., 2020	U _{crit} chasing
Yellow-eyed mullet <i>Aldrichetta forsteri</i>	29	21	Omnivorous, Frequent forager	Marine and freshwater, Benthic	124	210 (1.69)	799 (6.44)	/	0.5–3.0	12.7	/	Flikac et al., 2020	U _{crit} chasing
Mahi-mahi <i>Coryphaena hippurus</i>	706	26	Carnivorous, Pursue forager	Marine, Surface area	200	800 (4.00)	1364 (6.82)	1265 -	3.0–16.0	51.2	No	Stieglitz et al., 2018	U _{crit}
Lionfish <i>Pterois spp.</i>	135.5	26	Carnivorous, Infrequent forager	Marine, Demersal	90	443 (4.92)	352 (3.91)	/	13.0	134.7	/	Steell et al., 2019	Chasing
Lionfish <i>Pterois spp.</i>	135.5	32	Carnivorous, Infrequent forager	Marine, Demersal	166	491 (2.96)	346 (2.08)	/	13.0	180.6	/	Steell et al., 2019	Chasing

* Values in parentheses are factorial increases compared to SMR. *: '+' indicates that digesting MMRs are significantly higher than fasting MMRs, while '-' indicates no difference in MMR between digesting and fasting individuals.

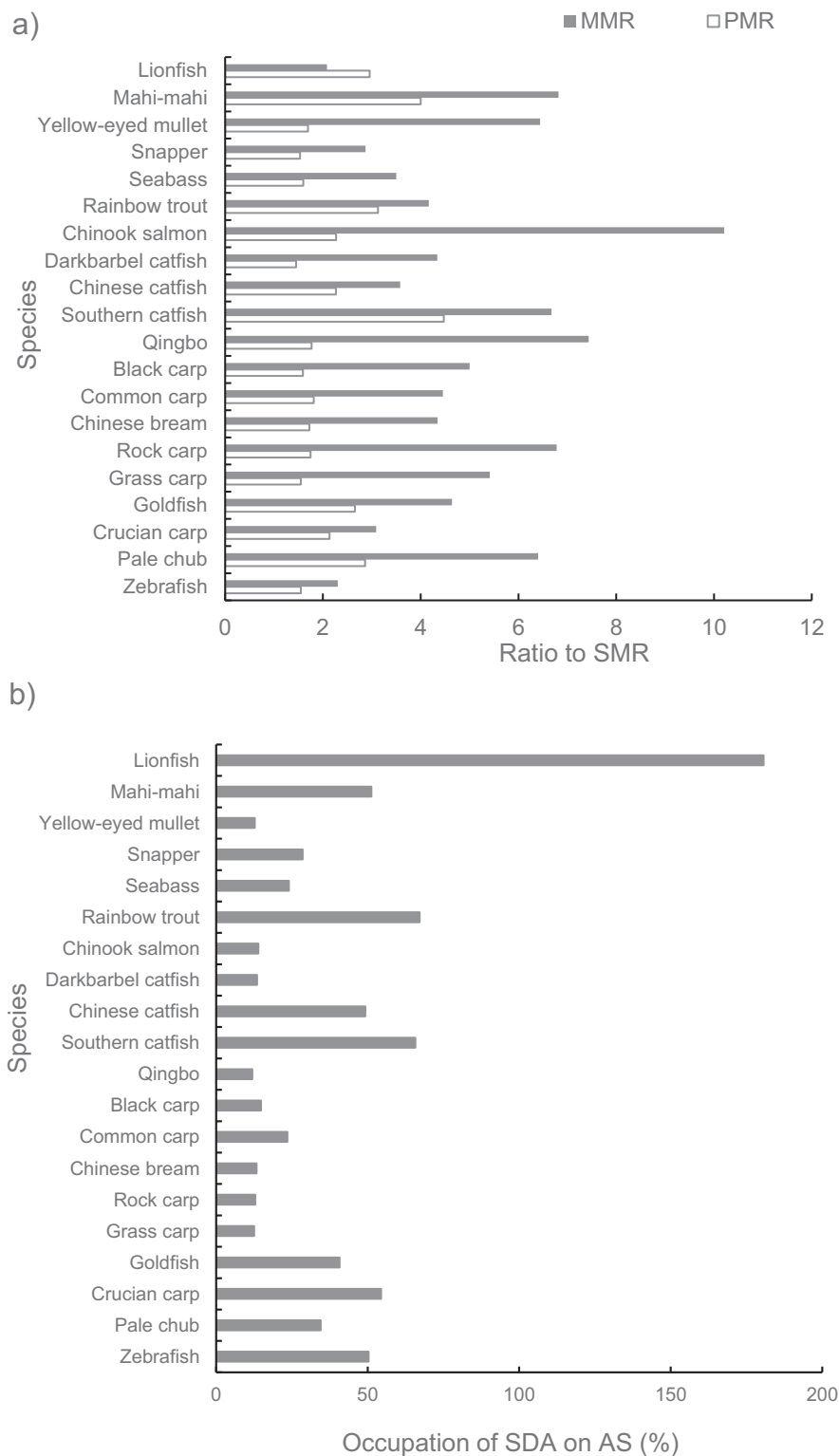


Fig. 5. Relative ratios of PMR (empty column) and MMR (filled column) to SMR (a) and occupation rates of SDA on aerobic scope (b) of fish species.

occupy the entire aerobic metabolic scope is species-specific (Table 1; Fig. 6). Thus, whether an organism can maintain its aerobic locomotion during digestion has attracted much research attention for the last several decades.

To date, at least 12 species have been studied to determine metabolic prioritization between digestion and locomotion, including different feeding habits (carnivores, omnivores and herbivores), foraging modes (sluggish infrequent and active foraging mode) and lifestyles or habitat

types (slow- and fast-flowing habitats). Among all species, six species showed unchanged U_{crit} while digesting as compared to during fasting (Table 1, Fig. 8). However, the underlying mechanisms involved in metabolic prioritization vary and can be roughly divided into two categories: (1) species with high flexibility, additive summation of MMR, in which MMR measured during swimming while digesting is higher than swimming after fasting), to support the aerobic scope requirements of simultaneous swimming and digestion (common carp, crucian carp,

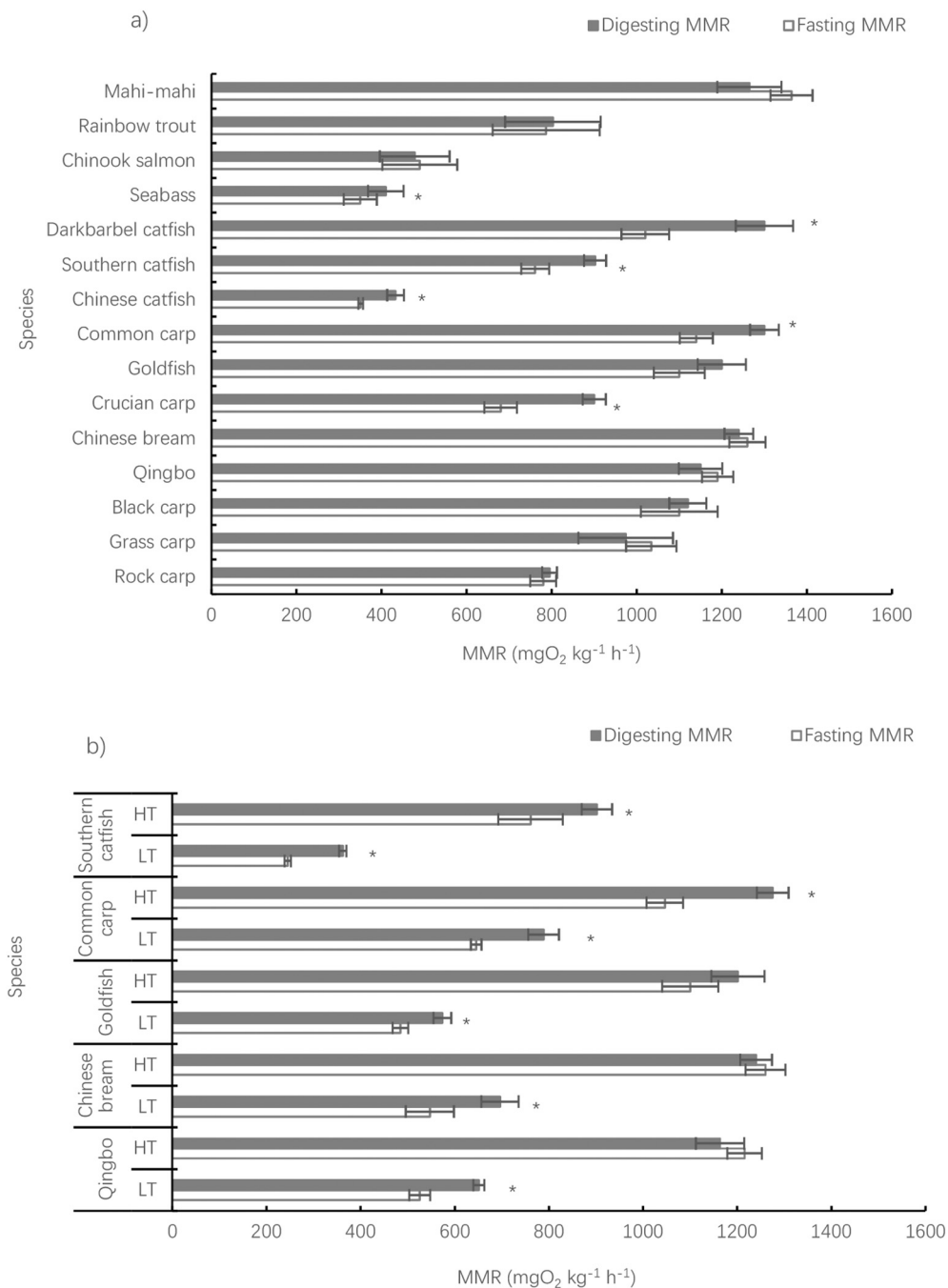


Fig. 6. Comparison of locomotion-elicited MMR between digesting (filled column) and fasting (empty column) fish species at the ecological optimum temperature (a) and between high (HT) and low temperature (LT) (b). Data are expressed as mean \pm S.E.

* indicate significant differences between fasting and digesting MMR ($P < 0.05$).

darkbarbel catfish and seabass (*Dicentrarchus labrax*, Fig. 8); and (2) species with conservative MMR (digesting MMRs are not different from fasting MMRs) but in which digestion is sacrificed in favor of swimming post-feeding [i.e., locomotor prioritization mode, Mahi-mahi (*Coryphaena hippurus*) and qingbo]. For the locomotor-prioritization, maintaining locomotion capacity might be important, while halting digestion for a short time might not be an ecological cost for most fish species. For fish species that adopt the additive model, darkbarbel catfish are frequent, active foragers with relatively small meal sizes and low PMR increases (i.e., little increase in MMR compared to fasting status). The additive metabolic priority mode of crucian carp and common carp might be the byproduct of the surplus oxygen uptake capacity evolved

for hypoxia tolerance rather than for a great aerobic scope to handle different aerobic physiological activities.

The remaining six species showed decreased U_{crit} while digesting, suggesting impaired swimming performance while maintaining digestion activity, i.e., digestive prioritization. Again, however, the underlying mechanisms can be roughly categorized into two groups: (1) fish with a conservative MMR (digesting MMRs are not different from fasting MMRs) and for which U_{crit} is decreased even with a small increase in SDA (such as rainbow trout, goldfish, Chinook salmon, black carp and Chinese bream, Fig. 8); and (2) fish species for which MMR is further increased during a postprandial swimming (digesting MMRs are higher than fasting MMRs) but they still cannot fulfill the two functions

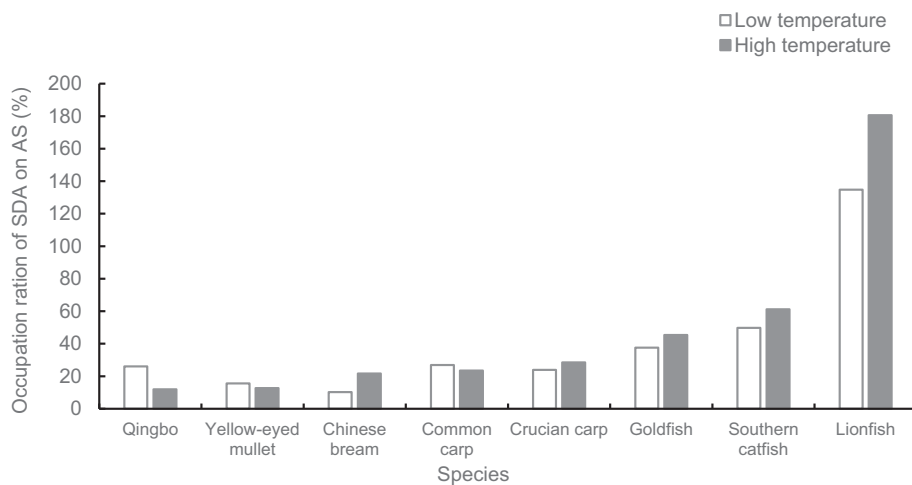


Fig. 7. Effect of acclimation temperature on the occupation ratio of SDA (specific dynamic action) on the aerobic scope of fish species with different metabolic types (locomotion type vs visceral type according to the relative magnitude of occupation ratio). Note that all fish species showing relatively high SDA occupation ratio (i.e., more visceral type) increase their occupation ratio under a warmer situation (on the right side), whereas the opposite is true (on the left side) for the locomotion type, with one exception in Chinese bream.

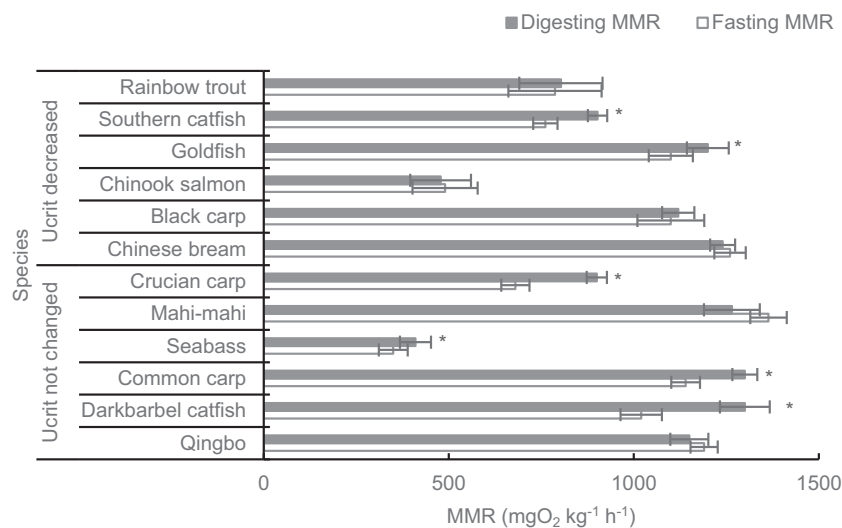


Fig. 8. Change of U_{crit} (Critical swimming speed) during digestion in relation to the postprandial MMR change.

* indicate significant differences between fasting and digesting MMR ($P < 0.05$).

simultaneously due to an exceedingly large PMR (southern catfish). The ecological implications for the digestive-prioritization are not clear because maintaining locomotion potential might be more important than digestion in the wild, as the impaired capacity of locomotion during digestion might constrain their ability to defend themselves against potential predators or to engage in other behavioral activities. This finding might be observed because SDA reflects metabolic processes in muscle tissues (for example, protein synthesis and growth), which cannot be quickly regulated. For example, it has been found in seabass that SDA was maintained despite decreased blood flow to the gastrointestinal tract under digesting swimming conditions (Altimiras et al., 2008).

Notably, when acclimated to low temperature (15 °C), all measured fish species (including southern catfish and goldfish which showed decreased U_{crit} during digestion acclimated at high temperature) (Table 1) showed unchanged swimming speed while digesting. This is possibly due to the constrained physiological performance of locomotion and digestion under low temperature, thus, MMR can accommodate both physiological activities simultaneously (Pang et al., 2011).

In conclusion, the partitioning of metabolic scope between locomotion and digestion is related to (1) the relative magnitude of aerobic scope compared to the sum of aerobic locomotion and digestion; and (2) which physiological functions are being sacrificed while swimming and

digesting. The former may be more shaped by energy-demanding situations (it might not be easy to adopt an additive mode in a fast-flowing habitat), whereas the latter may be shaped by the lifestyle related to the foraging mode (place in the food chain and predation pressure). The former situation can be tested by manipulating environmental conditions (e.g., temperature, hypoxia, hypercapnia). As mentioned before, both the locomotor (qingbo) and digestive prioritization (e.g., goldfish and southern catfish) become additive due to reduced competition for aerobic scope allocation when acclimated at low temperature (Pang et al., 2010, 2011). However, the effect of oxygen tension on the metabolic priority mode is rather complicated. For example, the metabolic prioritization of Chinese crucian carp changed from additive to digestion prioritization as aerobic scope decreased at very low oxygen tensions (Zhang et al., 2012). However, common carp, a species exhibiting additive prioritization in normoxia, still exhibits this pattern under 12.5% oxygen saturation as digestion, locomotion and digesting MMR all decrease in parallel with hypoxia (Zhang et al., 2012). A similar situation has been demonstrated in sea bass under 50% oxygen saturation (Dupont-Prinet et al., 2009). Thus, metabolic prioritization across species and the relationships with lifestyle and environmental conditions require further exploration.

7. Conclusions

In summary, by re-analyzing existing data from the literature, we have uncovered several interesting trends with regard to potential trade-offs within the aerobic scope of teleost fishes, including:

- (1) For freshwater species in China, both aerobic scope and anaerobic capacity may have been evolved for swimming performance and lifestyle and thus are usually negatively correlated with hypoxia tolerance. This is because fish with a slow lifestyle and hence low maintenance energy expenditure have low critical oxygen tension and small anaerobic requirements at P_{crit} . However, some species that dwell in particular habitats (e.g., slow-flowing habitats with high levels of dissolved oxygen) evolved a slow lifestyle but also poor hypoxia tolerance, resulting in a bell-shaped curve between hypoxia tolerance and aerobic or anaerobic capacity.
- (2) The relationship between swimming performance and hypoxia tolerance at the intraspecific level might shift via aerobic scope across habitats: a trade-off between aerobic scope and hypoxia tolerance is observed only in fast-flowing habitats, possibly due to the energy-demanding situations these habitats create.
- (3) Many species in slow-flowing water cannot elicit their metabolic ceiling by exercise alone; however, in fast-flowing habitats, exercise usually can elicit the MMR at the upper range of their ecologically relevant temperature but not at their lower ecologically relevant temperature, due to the physiological and biochemical constraints on peripheral tissues.
- (4) Fish exhibit a continuum of metabolic types, i.e., visceral metabolic type to locomotion metabolic type, with some sedentary predators that possess a higher postprandial metabolic rate than exercise-induced MMR.
- (5) Fish in fast-flowing habitats and of the locomotion type can maintain swimming capacity either by sacrificed digestion in favor of exercise in a postprandial swimming situation (locomotor prioritization) or via their high oxygen uptake and distribution capacity (additive summation of aerobic scope). In contrast, fish of visceral metabolic type usually show decreased swimming performance while digesting, as their MMR cannot further elevate or the increased MMR cannot meet all digestion requirements during digestion in a postprandial situation.

Overall, species in fast-flowing habitats have generally evolved a fast lifestyle with high aerobic scope for locomotive function, poor hypoxia tolerance and locomotive metabolic type, whereas slow-flowing habitats have more room for species evolving to their specific ecotype, although these species are usually more visceral-type with lower swimming performance and higher hypoxia tolerance (Table 2). These results suggest that the ecological relevance of aerobic scope is closely related to habitat condition and the particular lifestyle of a given species due to the difference of routine energy expenditure, hypoxia challenge and demanding of swimming ability on routine activities, which all have important effects on aerobic scope.

Based on these findings, there are a number of research questions that require further study going forward in our attempts to understand the ecological relevance of aerobic scope:

- (1) Is the exercise protocol appropriate to elicit the aerobic scope for fish species? Based on the available evidence, it seems quite common across species that exercise alone cannot elicit the true metabolic ceiling for the calculation of aerobic scope, especially for species with additive or digestive metabolic prioritization, and fish living in fast-flowing habitats that are acclimated to low temperature.
- (2) Is the critical oxygen tension for aerobic swimming and other physiological functions lower, i.e., less oxygen-dependent, during additive metabolic prioritization in species such as darkbarbel

Table 2

Summary of habitat conditions, lifestyles and physiological functions related to aerobic scope in the present paper.

Habitat	Fast-flowing	Slow-flowing
Environmental condition	High energy-demanding	Low energy-demanding
Lifestyle	Fast lifestyle	Slow lifestyle
Natural selection	Swimming performance	Hypoxia tolerance
Swimming performance	Strong with less variation	Usually less strong with high variation
Maintenance metabolism	High	Relatively low but with high variation
Hypoxia tolerance	Poor	Usually strong
Aerobic scope	High	Relatively low but with high variation
Relationship between locomotion and aerobic scope	Positive	Positive
Relationship between hypoxia tolerance and aerobic scope and swimming performance	Negative	No
Postprandial metabolic increase	Low with less variation	Relatively high with large variation
Temperature effect on SDA	Less profound	More profound
Metabolic type	Locomotion type	Visceral type
Change of U_{crit} during digestion	No or very little	Decreased or no change
Metabolic priority type	Locomotion priority or digestion priority	Additive mode or digestion priority mode
Mechanism underlying metabolic priority mode	Low meal size and SDA magnitude, high swimming performance	Large meal size and SDA magnitude, high cardiorespiratory capacity and O_2 uptake capacity as a byproduct of hypoxia tolerance
Can exercise elicit the metabolic ceiling?	Yes, but at optimal temperature	Usually not

catfish and common carp? How do some species still exhibit additive metabolic prioritization in hypoxia?

- (3) Is the ratio of different physiological functions varied or consistent in a given species across environmental temperature conditions, and does the pattern vary among species with different lifestyles? For example, if the ratio of SDA to aerobic scope increases more profoundly with acclimation temperature in visceral-type fish species, this suggests that warming may have a more profound effect on visceral-type fish species.
- (4) Is there a common rule underlying which metabolic priority mode, metabolic type, hypoxia tolerance and other physiological features coevolved across habitats and lifestyles?
- (5) What role does acclimation play when evaluating the effects of environmental conditions, and the species habitat and lifestyle on aerobic scope?

Declaration of Competing Interest

This study was supported by the National Natural Science Foundation of China (31172096; 31670418). There is no conflict of interest.

References

- Alsop, D.H., Wood, C.M., 1997. The interactive effects of feeding and exercise on oxygen consumption, swimming performance and protein usage in juvenile rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* 200, 2337–2346.
- Altamiras, J., Claireaux, G., Sandblom, E., Farrell, A.P., McKenzie, D.J., Axelsson, M., 2008. Gastrointestinal blood flow and postprandial metabolism in swimming sea bass *Dicentrarchus labrax*. *Physiol. Biochem. Zool.* 81, 663–672.
- Beamish, F.W.H., 1974. Apparent specific dynamic action of largemouth bass, *Micropterus salmoides*. *J. Fish. Res. Board Can.* 31, 1763–1769.
- Beamish, F.W.H., 1978. Swimming capacity. In: Hoar, S., Randall, D.J. (Eds.), *Fish Physiology*, vol. VII. Academic Press, Inc, New York, pp. 101–138.

- Behrens, J.W., Svendsen, J.C., Neuenfeldt, S., Andersen, N.G., van Deurs, M., 2018. Individual variation in aerobic scope affects modeled vertical foraging migration in Atlantic cod *Gadus morhua*, but only in moderate hypoxia. *Mar. Ecol. Prog. Ser.* 599, 201–208.
- Bennett, A.F., Hicks, J.W., 2001. Postprandial exercise: prioritization or additivity of the metabolic responses? *J. Exp. Biol.* 204, 2127–2132.
- Brauner, C.J., Matey, V., Zhang, W., Richards, J.G., Dhillon, R., Cao, Z.D., Wang, Y., Fu, S.J., 2011. Gill remodeling in crucian carp during sustained exercise and the effect on subsequent swimming performance. *Physiol. Biochem. Zool.* 84, 535–542.
- Brett, J.R., 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish Res. Bd. Can.* 21, 1183–1226.
- Brown, J.R., Cameron, J.N., 1991. The relation between specific dynamic action and protein synthesis rates in channel catfish. *Physiol. Zool.* 64, 298–309.
- Bushnell, P.G., Steffensen, J.F., Schurmann, H., Jones, D.R., 1994. Exercise metabolism in two species of cod in Arctic waters. *Polar Biol.* 14, 43–48.
- Chabot, D., Steffensen, J.F., Farrell, A.P., 2016. The determination of standard metabolic rate in fishes. *J. Fish Biol.* 88, 81–121.
- Chen, B.J., Fu, S.J., Cao, Z.D., Wang, Y.X., 2019. Effect of temperature on critical oxygen tension (P_{crit}) and gill morphology in six cyprinids in the Yangtze River, China. *Aquaculture* 508, 137–146.
- Claireaux, G., Chabot, D., 2016. Responses by fishes to environmental hypoxia: integration through Fry's concept of aerobic metabolic scope. *J. Fish Biol.* 88, 232–251.
- Claireaux, G., Lefrançois, C., 2007. Linking environmental variability and fish performance: integration through the concept of scope for activity. *Philos. Trans. R. Soc. B* 362, 2031–2041.
- Claireaux, G., Webber, D.M., Lagardère, J.P., Kerr, S.R., 2000. Influence of water temperature and oxygenation on the aerobic metabolic scope of Atlantic cod (*Gadus morhua*). *J. Sea Res.* 44, 257–265.
- Clark, T.D., Sandblom, E., Jutfelt, F., 2013. Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. *J. Exp. Biol.* 216, 2771–2782.
- Cunha, I., Conceição, L.E.C., Planas, M., 2007. Energy allocation and metabolic scope in early turbid, *Scophthalmus maximus*, larvae. *Mar. Biol.* 151, 1397–1405.
- DeWitt, T.J., Troendle, N.J., Mateos, M., Mauricio, R., 2022. Population genetics and independently replicated evolution of predator-associated burst speed ecophenotypy in mosquitofish. *Heredity* 128, 45–55.
- Dhillon, R.S., Yao, L., Matey, V., Chen, B.J., Zhang, A.J., Cao, Z.D., Fu, S.J., Brauner, C.J., Wang, Y.S., Richards, J.G., 2013. Interspecific differences in hypoxia-induced gill remodeling in carp. *Physiol. Biochem. Zool.* 86, 727–739.
- Dhillon, R.S., Mandic, M., Yao, L., Cao, Z.D., Fu, S.J., Brauner, C.J., Wang, Y.S., 2018. Ethanol metabolism varies with hypoxia tolerance in ten cyprinid species. *J. Comp. Physiol. B* 188, 283–293.
- Domenici, P., Kapoor, B.G., 2010. Fish locomotion: an eco-ethological Perspective. Science Publishers, Enfield.
- 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* 154, 233–240.
- Ejbye-Ernst, R., Michaelsen, T.Y., Tirsgaard, B., Wilson, J.M., Jensen, L.F., Steffensen, J.F., Pertoldi, C., Aarestrup, K., Svendsen, J.C., 2016. Partitioning the metabolic scope: the importance of anaerobic metabolism and implications for the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis. *Conserv. Physiol.* 4, cow019.
- Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., Gale, M.K., Patterson, D.A., Hinch, S.G., Farrell, A.P., 2011. Differences in thermal tolerance among sockeye salmon populations. *Science* 332, 109–112.
- Ern, R., 2019. A mechanistic oxygen- and temperature-limited metabolic niche framework. *Philos. Trans. R. Soc. B* 374, 20180540.
- Flikac, T., Cook, D.G., Davison, W., 2020. The effect of temperature and meal size on the aerobic scope and specific dynamic action of two temperate New Zealand finfish *Chrysophrys auratus* and *Aldrichetta forsteri*. *J. Comp. Physiol. B* 190, 169–183.
- Fry, F.E.J., 1947. Effects of the environment on animal activity. Publications of the Ontario Fisheries Research Laboratory 68, 1–62.
- Fry, F., Hart, J.S., 1948. Cruising speed of goldfish in relation to water temperature. *J. Fish. Res. Board Can.* 7, 169–175.
- Fu, S.J., Xie, X.J., Cao, Z.D., 2005a. Effect of fasting on resting metabolic rate and postprandial metabolic response in southern catfish (*Silurus meridionalis* Chen). *J. Fish Biol.* 67, 279–285.
- Fu, S.J., Xie, X.J., Cao, Z.D., 2005b. Effect of meal size on postprandial metabolic response in southern catfish (*Silurus meridionalis*). *Comp. Biochem. Physiol. A* 140, 445–451.
- Fu, S.J., Xie, X.J., Cao, Z.D., 2005c. Effect of dietary composition on specific dynamic action in southern catfish, *Silurus meridionalis*. *Aquac. Res.* 36, 1384–1390.
- Fu, S.J., Cao, Z.D., Peng, J.L., 2006. Effect of meal size on postprandial metabolic response in Chinese catfish (*Silurus asotus* Linnaeus). *J. Comp. Physiol. B* 176, 489–495.
- Fu, S.J., Cao, Z.D., Peng, J.L., Wang, Y.X., 2008. Is peak postprandial oxygen consumption positively related to growth rate and resting oxygen consumption in a sedentary catfish *Silurus meridionalis*? *J. Fish Biol.* 73, 692–701.
- Fu, S.J., Zeng, L.Q., Li, X.M., Pang, X., Cao, Z.D., Peng, J.L., Wang, Y.X., 2009a. The behavioral, digestive and metabolic characteristics of fishes with different foraging strategies. *J. Exp. Biol.* 212, 2296–2302.
- Fu, S.J., Zeng, L.Q., Li, X.M., Pang, X., Cao, Z.D., Peng, J.P., Wang, Y.X., 2009b. Effect of meal size on excess post-exercise oxygen consumption in fishes with different locomotive and digestive performance. *J. Comp. Physiol. B* 179, 509–517.
- Fu, S., Cao, Z., Yan, G., Fu, C., Pang, X., 2013. Integrating environmental variation, predation pressure, phenotypic plasticity and locomotor performance. *Oecologia* 173, 343–354.
- Fu, S.J., Fu, C., Yan, G.J., Cao, Z.D., Zhang, A.J., Pang, X., 2014. Interspecific variation in hypoxia tolerance, swimming performance and plasticity in cyprinids that prefer different habitats. *J. Exp. Biol.* 217, 590–597.
- Fu, S.J., Peng, J., Killen, S.S., 2018a. Digestive and locomotor capacity show opposing responses to changing food availability in an ambush predatory fish. *J. Exp. Biol.* 221, jeb173187.
- Fu, C., Peng, J.L., Fu, S.J., 2018b. Effects of acclimation temperature on locomotion performance and behavior of pale chub. *Chinese J. Ecol.* 37, 1889–1896.
- Genz, J., Jyde, M.B., Svendsen, J.C., Steffensen, J.F., Ramløv, H., 2013. Excess post-hypoxic oxygen consumption is independent from lactate accumulation in two cyprinid fishes. *Comp. Biochem. Physiol. A* 165, 54–60.
- GINNEK, V.V., THILLART, G.V.D., 2009. Metabolic depression in fish measured by direct calorimetry: A review. *Thermochim. Acta* 483, 1–7.
- Halsey, L.G., Killen, S.S., Clark, T.D., Norin, T., 2018. Exploring key issues of aerobic scope interpretation in ectotherms: absolute versus factorial. *Rev. Fish Biol. Fish.* 28 (2), 405–415.
- Hedrick, M.S., Hancock, T.V., Hillman, 2015. Metabolism at the max: How vertebrate organisms respond to physical activity. *Comp. Physiol.* 5, 1677–1703.
- Hunt von Herbing, I., White, L., 2002. The effects of body mass and feeding on the metabolic rate in small juvenile Atlantic cod. *J. Fish Biol.* 61, 945–958.
- Hvas, M., Oppedal, F., 2019. Influence of experimental set-up and methodology for measurements of metabolic rates and critical swimming speed in Atlantic salmon *Salmo salar*. *J. Fish Biol.* 95, 893–902.
- Jobling, M., 1981. The influences of feeding on the metabolic rate of fishes: a short review. *J. Fish Biol.* 18, 385–400.
- Jung, E.H., Brix, K.V., Brauner, C.J., 2019. The effect of temperature acclimation on thermal tolerance, hypoxia tolerance and aerobic scope in two species of sheephead minnow; *Cyprinodon variegatus variegatus* and *Cyprinodon variegatus hubbsi*. *Comp. Biochem. Physiol. A* 232, 28–33.
- Kieffer, J.D., 2010. Perspective—exercise in fish: 50? years and going strong. *Comp. Biochem. Physiol. A* 156, 163–168.
- Kulesza, A., Leonard, E.M., McClelland, G.B., 2020. Influence of 96h sub-lethal copper exposure on aerobic scope and recovery from exhaustive exercise in killifish (*Fundulus heteroclitus*). *Aquat. Toxicol.* 218, 105373.
- Lahti, D.C., Johnson, N.A., Ajie, B.C., Otto, S.P., Hendry, A.P., Blumstein, D.T., Coss, R.G., Donohue, K., Foster, S.A., 2009. Relaxed selection in the wild. *Trends Ecol. Evol.* 24, 487–496.
- Langerhans, R.B., 2009. Predictability of phenotypic differentiation across flow regimes in fishes. *Integr. Comp. Biol.* 48, 750–768.
- Lee, G.C., Farrell, A.P., Lotto, A., Hinch, S.G., Healey, M.C., 2003. Excess post-exercise oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon following critical speed swimming. *J. Exp. Biol.* 206, 3253–3260.
- Li, X.-M., Cao, Z.-D., Fu, S.-J., 2010a. The effect of exercise training on the metabolic interaction between feeding and locomotion in the juvenile southern catfish (*Silurus meridionalis* Chen). *J. Exp. Zool.* 313A, 557–563.
- Li, X.M., Cao, Z.D., Peng, J.L., Fu, S.J., 2010b. The effect of exercise training on the metabolic interaction between digestion and locomotion in juvenile darkbarbel catfish (*Pelteobagrus vachelli*). *Comp. Biochem. Physiol. A* 156, 67–73.
- Li, K.G., Cao, Z.D., Fu, S.J., 2012. Effect of feeding on excess post-exercise oxygen consumption in juvenile Chinese catfish (*Silurus asotus*). *Acta Hydrobiol. Sinica* 36, 1035–1040.
- Li, X.M., Yu, L.J., Cao, Z.D., Fu, S.J., Zhang, Y.G., 2013. The effects of exhaustive chasing training on the growth performance and postprandial metabolic response in *Spinibarbus sinensis* and *Procypris rabaudi*. *Freshwater Fish.* 43, 63–68.
- Lowe, C.J., Davison, W., 2006. Thermal sensitivity of scope for activity in *Pagothenia borchgrevinkii*, a cryopelagic Antarctic nototheniid fish. *Polar Biol.* 29, 971–977.
- Lucas, M.C., Priede, I.G., 1992. Utilization of metabolic scope in relation to feeding and activity by individual and grouped zebrafish, *Brachydanio rerio* (Hamilton-Buchanan). *J. Fish Biol.* 41, 175–190.
- Marcek, B.J., Brill, R.W., Fabrizio, M.C., 2019. Metabolic scope and hypoxia tolerance of Atlantic croaker (*Micropogonias undulatus* Linnaeus, 1766) and spot (*Leiostomus xanthurus* Lacepède, 1802), with insights into the effects of acute temperature change. *J. Exp. Mar. Biol. Ecol.* 516, 150–158.
- Marras, S., McKenzie, D.J., Claireaux, G., 2010. Individual variation in swimming performance of European sea bass, *Dicentrarchus labrax*. *J. Exp. Biol.* 213, 26–32.
- McCue, M., 2006. Specific dynamic action: a century of investigation. *Comp. Biochem. Physiol. A* 144, 381–394.
- McLean, S., Persson, A., Norin, T., Killen, S.S., 2018. Metabolic costs of feeding predictively alter the spatial distribution of individuals in fish schools. *Curr. Biol.* 28, 1144–1149.
- Milinkovitch, T., Marras, S., Antognarelli, F., Lefrançois, C., Floch, S.L., Domenici, P., 2020. The effects of hypoxia on aerobic metabolism in oil-contaminated sea bass (*Dicentrarchus labrax*). *Chemosphere* 253, 126678.
- Milligan, C.L., 1996. Metabolic recovery from exhaustive exercise in rainbow trout. *Comp. Biochem. Physiol. A* 113, 51–60.
- Murray, L., Rennie, M.D., Svendsen, J.C., Enders, E.C., 2017. Respirometry increases cortisol levels in rainbow trout *Oncorhynchus mykiss*: implications for measurements of metabolic rate. *J. Fish Biol.* 90, 2206–2213.
- Nespolo, R.F., Solano-Iguaran, J.J., Bozinovic, F., 2017. Phylogenetic analysis supports the aerobic-capacity model for the evolution of endothermy. *Am. Nat.* 189, 13–27.
- Nie, L., Fu, S., 2017. Metabolic, behavioral, and locomotive effects of feeding in five cyprinids with different habitat preferences. *Fish Physiol. Biochem.* 43, 1531–1542.

- Nie, L.J., Cao, Z.D., Fu, S.J., 2017. Digesting or swimming? Integration of the postprandial metabolism, behavior and locomotion in a frequently foraging fish. *Comp. Biochem. Physiol. Part A* 204, 205–210.
- Nilsson, G.E., Östlund-Nilsson, S., 2004. Hypoxia in paradise: widespread hypoxia tolerance in coral reef fishes. *Proc. R. Soc. Lond. B* 271, S30–S33.
- Nilsson, G.E., Renshaw, G.M., 2004. Hypoxic survival strategies in two fishes: extreme anoxia tolerance in the North European Crucian carp and natural hypoxic preconditioning in a coral-reef shark. *J. Exp. Biol.* 207, 3131–3139.
- Norin, T., Clark, T.D., 2016. Measurement and relevance of maximum metabolic rate in fishes. *J. Fish Biol.* 2016 (88), 122–151.
- Norin, T., Clark, T.D., 2017. Fish face a trade-off between 'eating big' for growth efficiency and 'eating small' to retain aerobic capacity. *Biol. Lett.* 13, 20170298.
- Oufifiro, C.E., Walsh, M.R., Reznick, D.N., Garland Jr., T., 2011. Swimming performance trade-offs across a gradient in community composition in Trinidadian killifish (*Rivulus hartii*). *Ecology* 92, 170–179.
- Pang, X., Cao, Z.D., Peng, J.L., Fu, S.J., 2010. The effects of feeding on the swimming performance and metabolic response of juvenile southern catfish, *Silurus meridionalis*, acclimated at different temperatures. *Comp. Biochem. Physiol. A* 155, 253–258.
- Pang, X., Cao, Z.D., Fu, S.J., 2011. The effects of temperature on metabolic interaction between digestion and locomotion in juveniles of three cyprinid fish (*Carassius auratus*, *Cyprinus carpio* and *Spinibarbus sinensis*). *Comp. Biochem. Physiol. A* 159, 253–260.
- Pang, X., Shao, F., Ding, S.H., Fu, S.J., Zhang, Y.G., 2020. Interspecific differences and ecological correlations of energy metabolism traits in freshwater fishes. *Funct. Ecol.* 34, 616–630.
- Pang, X., Pu, D.Y., Xia, D.Y., Liu, X.H., Ding, S.H., Li, Y., Fu, S.J., 2021. Individual variation in metabolic rate, locomotion capacity and hypoxia tolerance and their relationships in juveniles of three freshwater fish species. *J. Comp. Physiol. B* 191, 755–764.
- Peng, J., Cao, Z.D., Fu, S.J., 2014. Effects of temperature and digestion on the swimming performance of juvenile Chinese bream. *Aquat. Biol.* 21, 183–189.
- Penghan, L.Y., Cao, Z.D., Fu, S.J., 2014. Effect of temperature and dissolved oxygen on swimming performance in crucian carp. *Aquat. Biol.* 21 (57–65), 2014.
- Plambech, M., Van Deurs, M., Steffensen, J.F., Tirsgaard, B., Behrens, J.W., 2013. Excess post-hypoxic oxygen consumption in Atlantic cod *Gadus morhua*. *J. Fish Biol.* 83, 396–403.
- Pörtner, H., Grieshaber, M., 1993. Critical PO₂ (s) in oxyconforming and oxyregulating animals: gas exchange, metabolic rate and the mode of energy production. In: *The Vertebrate Gas Transport Cascade: Adaptations to Environment and Mode of Life*, pp. 330–357.
- Pörtner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315, 95–97.
- Priede, I.G., 1985. Metabolic scope in fishes. In: Tytler, P., Calow, P. (Eds.), *Fish Energetics*, Ed 1. Croom Helm Ltd, Beckenham, pp. 33–64.
- Regan, M.D., Gosline, J.M., Richards, J.G., 2013. A simple and affordable calorimeter for assessing the metabolic rates of fishes. *J. Exp. Biol.* 216, 4507–4513.
- Reidy, S.P., Nelson, J.A., Tang, Y., Kerr, S.R., 1995. Post-exercise metabolic rate in Atlantic cod and its dependence upon the method of exhaustion. *J. Fish Biol.* 47, 377–386.
- Sandblom, E., Gräns, A., Axelsson, M., Seth, H., 2014. Temperature acclimation rate of aerobic scope and feeding metabolism in fishes: implications in a thermally extreme future. *Proc. R. Soc. B* 281, 20141490.
- Schurmann, H., Steffensen, J.F., 1997. Effects of temperature, hypoxia and activity on the metabolism of juvenile Atlantic cod. *J. Fish Biol.* 50, 1166–1180.
- Secor, S.M., 2009. Specific dynamic action: a review of the postprandial metabolic response. *J. Comp. Physiol. B* 179, 1–56.
- Secor, S.M., Diamond, J., 1998. A vertebrate model of extreme physiological regulation. *Nature* 395, 659–662.
- Slesinger, E., Andres, A., Young, R., Seibel, B., Saba, V., Phelan, B., et al., 2019. The effect of ocean warming on black sea bass (*Centropristis striata*) aerobic scope and hypoxia tolerance. *PLoS One* 14, e0218390.
- Sollid, J., De Angelis, P., Gundersen, K., Nilsson, G.E., 2003. Hypoxia induces adaptive and reversible gross morphological changes in crucian carp gills. *J. Exp. Biol.* 206, 3667–3673.
- Soofiani, N.M., Hawkins, A.D., 1982. Energetic costs at different levels of feeding in juvenile cod, *Gadus morhua* L. *J. Fish Biol.* 21, 577–592.
- Sørensen, C., Munday, P.L., Nilsson, G.E., 2014. Aerobic vs. anaerobic scope: sibling species of fish indicate that temperature dependence of hypoxia tolerance can predict future survival. *Glob. Chang. Biol.* 20, 724–729.
- Steell, S.C., Van Leeuwen, T.E., Brownscombe, J.W., Cooke, S.J., Eliason, E.J., 2019. An appetite for invasion: digestive physiology, thermal performance and food intake in lionfish (*Pterois spp.*). *J. Exp. Biol.* 222, jeb209437.
- Stieglitz, J.D., Benetti, D.D., Grosell, M., 2018. Nutritional physiology of mahi-mahi (*Coryphaena hippurus*): Postprandial metabolic response to different diets and metabolic impacts on swim performance. *Comp. Biochem. Physiol. A* 215, 28–34.
- Svendsen, J.C., Steffensen, J.F., Aarestrup, K., Frisk, M., Etzrodt, A.P., Jyde, M., 2012. Excess posthypoxic oxygen consumption in rainbow trout (*Oncorhynchus mykiss*): Recovery in normoxia and hypoxia. *Can. J. Zool.* 90, 1–11.
- Tang, J.Y., 2019. Why do fish species have different personalities: energy expenditure and ecological consequences. Master Thesis, Chongqing.
- Tang, H.F., Cao, Z.D., Fu, S.J., 2010. The relationship among resting metabolic rate, body composition and excess post-excess oxygen consumption during fasting in *Silurus asotus*. *Acta Hydrobiol. Sinica* 34, 190–195.
- Thorarensen, H., Farrell, A.P., 2006. Postprandial intestinal blood flow, metabolic rates, and exercise in chinook salmon (*Oncorhynchus tshawytscha*). *Physiol. Biochem. Zool.* 79, 688–694.
- Wegner, N.C., Drawbridge, M.A., Hyde, J.R., 2018. Reduced swimming and metabolic fitness of aquaculture-reared California Yellowtail (*Seriola dorsalis*) in comparison to wild-caught conspecifics. *Aquaculture* 486, 51–56.
- Willson, J.D., Hopkins, W.A., 2011. Prey morphology constrains the feeding ecology of an aquatic generalist predator. *Ecology* 92, 744–754.
- Yan, G.J., He, X.K., Cao, Z.D., Fu, S.J., 2013. An interspecific comparison between morphology and swimming performance in cyprinids. *J. Evol. Biol.* 26, 1802–1815.
- Yan, G.J., He, X.K., Cao, Z.D., Fu, S.J., 2015. Effects of fasting and feeding on the fast-start swimming performance of southern catfish *Silurus meridionalis*. *J. Fish Biol.* 86, 605–614.
- Zhang, W., Cao, Z.D., Peng, J.L., Chen, B.J., Fu, S.J., 2010. The effects of dissolved oxygen level on the metabolic interaction between digestion and locomotion in juvenile southern catfish (*Silurus meridionalis* Chen). *Comp. Biochem. Physiol. A* 157, 212–219.
- Zhang, W., Cao, Z.D., Fu, S.J., 2012. The effects of dissolved oxygen levels on the metabolic interaction between digestion and locomotion in Cyprinid fishes with different locomotive and digestive performances. *J. Comp. Physiol. B* 182, 641–650.
- Zhou, L.Y., Fu, S.J., Fu, C., Ling, H., Li, X.M., 2019. Effects of acclimation temperature on the thermal tolerance, hypoxia tolerance and swimming performance of two endangered fish species in China. *J. Comp. Physiol. B* 189, 237–247.