



On being the wrong size, or the role of body mass in fish kills and hypoxia exposure

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Abstract Rising temperatures, drought, and oxygen depletion may be the greatest threats to aquatic animals in the twenty-first century. As a robust body of literature suggests, large-bodied fish are among the most vulnerable organisms in times of rapid climate change. While earlier studies showed an interspecific correlation between body size and sensitivity to hypoxia and thermal stress, comparisons within species remain debated. This review marshals a diverse body of literature on this topic, ranging from physiological studies to field reports and fish kill manuals, and evaluates the evidence for intraspecific size effects on hypoxia tolerance. While experimental studies and fisheries management literature sometimes contradict each other, we show that there is strong evidence for size effects on hypoxia tolerance within fish species. We argue that bringing fisheries management literature and physiological studies into a dialog with each other is of crucial importance in times of rapid climate change.

Keywords Hypoxia · Temperature · Fish kills · Climate change · Body size · Oxygen

Introduction

The relationship between body size and hypoxia in fishes is a point of debate since at least two decades (see, e.g., Nilsson and Östlund-Nilsson 2008; Rogers et al. 2016; 2021; Verberk et al. 2022). In a review of this issue, Nilsson and Östlund-Nilsson (2008) argued that large fish were more likely to survive when exposed to acute hypoxia or high temperatures. This seems counterintuitive from a fisheries management perspective, as it is commonly observed that larger individuals within a population are over-represented in hypoxia- and temperature-induced fish kill events. The over-representation of larger fish in hypoxia- and heat-induced die-off events is widely reported in field reports and informs most instructional manuals for fieldwork procedures after fish kills (see, e.g., Meyer and Barclay 1990; Helfrich and Smith 2009; Whitford 2009; Grant et al. 2014; Knowles et al. 2015, as well as the list of 20 manuals in Table 3).

Indeed, as these manuals often indicate, the size distributions of dead fish allow preliminary inferences on the causes of mass die-off event: while the observation of more small and juvenile fish being killed first are taken as an indication of either pesticidal pollution or toxic algal bloom, dead large fish are interpreted as a symptom oxygen depletion.

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In their instructional section on “*interpreting the scene*,” most manuals present a catalog of factors and causes of fish kills that also includes the timing of the observed mortality: as Meyer and Barclay (1990) and most other manuals listed in Table 1 indicate, “(l)arge fish killed first, eventually all sizes” is a typical symptom of exposure to hypoxia, while “(s)mall fish killed” points to toxic chemicals or algal blooms. Other manuals elaborate on the causes for size-related mortality in hypoxia-induced fish kills, e.g., “Small fish usually survive because they have a greater gill size ratio than do larger fish.” (Missouri Department of Conservation 1994); see also U.S. Environmental Protection Agency (1972).

This seeming discrepancy between laboratory studies and fieldwork experience raises the question about the reliability of such field manual instructions and the extent to which they are grounded in scientific consensus and, more widely, about the relationship between practice-based knowledge in fisheries management and experimental physiology. In this review, which is complemented by a small dataset on 3 drought-induced fish kills that occurred during the exceptionally dry summers of 2020 and 2022 in the Netherlands, we evaluate the evidence for intraspecific size-related mortality in hypoxia-induced fish kills. Resolving the apparent discrepancy between laboratory and field observations is urgently needed, as rapid climate change increases periods of drought and extreme heat worldwide. A better understanding of the tolerance of fishes in different size classes is of great importance because size- and age-structured mortality plays a key role in the reproductive future and the survival of the entire population. Bringing different types of literature into a dialog with each other allows for a harmonization of the existing knowledge in respiratory physiology, field ecology, and fisheries management literature. In addition to data on critical oxygen levels and mortality of fishes exposed to hypoxia, we also include literature on behavioral responses to oxygen deficiency, mainly aquatic surface breathing (hereafter ASR), as well as recovery from anaerobic metabolism and lactate concentrations in the body.

The question of body size in hypoxic environments is at the heart of the current debate about temperature impact on the metabolism and growth of fishes (Hoenig and Verberk 2015; Pauly 2019, 2021; Verberk et al. 2021, 2022). Temperature can induce hypoxia in

at least two ways: (i) by increasing oxygen demand in ectothermic animals and (ii) by reducing the amount of oxygen that is can be dissolved in warmer water, with the latter factor being far less importance than the former (Fig. 1). Both internal hypoxia and external hypoxia are thus very often a result of increased temperatures, especially during events leading to fish kills.

Atmospheric oxygen concentrations have been associated with the evolution of different body size in various classes of animals: insect gigantism occurred in geological periods when the oxygen concentrations were significantly higher than in the present—with records of up to 35% during the later Paleozoic (Harrison et al. 2010; Verberk and Bilton 2011; Ward 2006). Similarly, the fossil record provides evidence that the body sizes of fishes, both teleosts and elasmobranchs, declined in warmer periods and increased with more oxygen and lower temperatures (Troyer et al. 2022; Shimada et al. 2022).

In their review paper, titled “Does size matter for hypoxia tolerance in fish?”, Nilsson and Östlund-Nilsson (2008) presented a contrasting perspective. Citing data on 15 fish species from 8 studies, and adding their own findings on damselfish, they argued that “body size per se has little or no impact on the ability to take up oxygen during hypoxic conditions, primarily because the respiratory surface area matches metabolic rate over a wide size range.” However, they concluded that size should indeed matter because larger individuals have a higher capacity for anaerobic ATP production, which allow them to survive longer during severe hypoxia. Under this scenario, given the high levels of lactate that is released as a result of anaerobic metabolism, larger individuals would have an advantage over smaller ones because they would be more resistant to the effects of these waste products.

This observation is indeed confirmed by an extensive body of literature, as large individuals often rely on anaerobic metabolism (Somero and Childress 1980 and the references in the section *Body size and anaerobic metabolism*), while smaller conspecifics usually do not possess this capacity. Indeed, the need for larger fish to resort to glycolysis (or other forms of anaerobic metabolism) in order to maintain their vital functions is well-documented. Goolish (1991), for example, noted that while smaller fish were able to perform energy-consuming sprints—up to their very

Table 1 Effects of size on sensitivity to hypoxia and/or high temperatures, with all but 5 entries suggesting that small fish survive hypoxia better than large fish or that hypoxia avoidance correlates with fish size

Species	Remark(s) and quote	Source
Largemouth bass, <i>Micropterus salmoides</i> (Lacepède, 1802)	Large individuals avoid hypoxia. “There was a significant ($P < 0.05$) correlation between fish mass and the level of dissolved aquatic oxygen that was selected. Small fish (23–500 g) utilized waters of lower oxygen levels than did the larger fish (1000–3000 g).”	Burleson et al. (2001)
Yellow perch, <i>Perca flavescens</i> (Mitchill, 1814)	Small is better and large individuals avoid hypoxia. “Significant variation in tolerance between small and large yellow perch was found, corroborating other studies that suggest that body size plays a role in this relationship.”	Robb & Abrahams (2003)
Fathead minnow, <i>Pimephales promelas</i> (Rafinesque, 1820)	Large individuals avoid hypoxia. “...a size effect in fathead minnow tolerance to extreme hypoxia was observed, where larger individuals had to be removed early due to loss of equilibrium.”	Robb & Abrahams (2003)
Red drum, <i>Sciaenops ocellatus</i> (Linnaeus, 1766)	“Hypoxia tolerance decreases with body size.”	Pan et al. (2016)
Nile perch <i>Lates niloticus</i> (Linnaeus, 1758)	“... over 70% of the dead fish were over 50 lb. in weight, many over 200 lb. and only about 1% were less than 10 lb. in weight. It seems likely that the larger fish were more closely dependent on optimum conditions of aeration than the smaller specimens.”	Fish (1956)
Nile perch, <i>Lates niloticus</i> (Linnaeus, 1758)	“Body size effects were present for <i>L. niloticus</i> suggesting a lower tolerance to hypoxia in larger-bodied individuals, thus limiting their ability to penetrate wetlands.”	Reid et al. (2013)
Cisco, <i>Coregonus artedii</i> (Lesueur, 1818)	“The upper ultimate lethal temperature of the young ciscoes was 26 °C (6 °C higher than the maximum sustained temperature tolerated by adult ciscoes in nature)...”	Edsall and Colby (1970)
Cisco, <i>Coregonus artedii</i> (Lesueur, 1818)	“Among the coregonids, and apparently among fishes in general, physiological plasticity and adaptability declines with age [...]. There is also some evidence that young coregonids are more tolerant of low oxygen levels than are larger and older fish.”	Frey (1955)
Cisco, <i>Coregonus artedii</i> (Lesueur, 1818)	“All fish in the die-off were adults, 20 to 30 cm long” and a “lack of young-of-the-year ciscoes in past die-offs in Halfmoon and surrounding lakes” was observed previously	Colby and Brooke (1969)
Cisco, <i>Coregonus artedii</i> (Lesueur, 1818)	“Most observed [dead] ciscoes were adults [...]. Many of these lakes may experience almost complete adult mortality in an extreme event.”	Jacobson et al. (2008)
Cisco, <i>Coregonus artedii</i> (Lesueur, 1818)	“Older fish are more sensitive to high temperatures and to unfavourable concentrations of dissolved gases.”	Fry (1937)
Vendace, <i>Coregonus albula</i> (Linnaeus, 1758)	“I assume that the disappearance of older cohorts is caused by the summer stagnation and the resulting decline in oxygen concentrations in the deeper layers.” (Translated from German)	Bauch (1949)

Table 1 (continued)

Species	Remark(s) and quote	Source
Vendace, <i>Coregonus albula</i> (Linnaeus, 1758)	<p>“If our assumption is correct that the oxygen requirements of fish increase with their age, then the lakes, which during hypoxic periods, still offer enough oxygen for the younger stages of vendace in their deeper zone, should not be suitable to the older age groups, and their young fish should survive while the older one should fade away.”</p> <p>“I tend to believe that the oxygen levels at deeper layers of Lake Narie [...] fall below the minimum requirements of vendace older than two summer, which will cause the majority to perish.” (Translated from German)</p>	Willer (1929)
Atlantic salmon, <i>Salmo salar</i> (Linnaeus, 1758)	“Large salmon died first and parr survived.”	Huntsman (1942)
Coho salmon, <i>Oncorhynchus kisutch</i> (Walbaum, 1792)	Large individuals are more vulnerable, despite anaerobic metabolism. “Post-exercise recovery of plasma testosterone was faster in jacks compared with full-size males, suggesting less impairment of the maturation trajectory of smaller fish. [...] It is noteworthy that the only fish that did not survive the thermal challenge in the present study was the largest male.”	Clark et al. (2012)
Chinook salmon, <i>Oncorhynchus tshawytscha</i> (Walbaum, 1792)	“We suggest that the critical thermal maximum for resting adult Chinook salmon is mass-dependent and lies around 25 °C for large fish (> 4 kg) and perhaps around 27 °C for smaller adult individuals.”	Clark et al. (2008)
Cutthroat trout, <i>Oncorhynchus clarkii</i> (Richardson, 1836)	“Interestingly, there was a size effect within treatments, wherein the T_{cmax} of larger fish was significantly lower than that of smaller fish acclimated to the same temperature.”	Underwood et al. (2012)
Common carp, <i>Cyprinus carpio</i> L	25,000 dead carp killed during a heatwave: “The dead carp were mainly large adults [...]”	Ouellet et al. 2010
Murray cod, <i>Maccullochella peelii</i> (Mitchell, 1838)	“[M]ainly large fish > 500 mm TL” reported in fish kills	Koehn (2004), see also King et al. (2012)
Eelpout, <i>Zoarces viviparus</i> (Linnaeus, 1758)	“The earlier loss in aerobic scopes of large individuals indicates that specimens do not grow beyond oxygen-dependent size limits set by temperature such that this size group displays low abundance all year round.”	Pörtner and Knust (2007)
<i>Erimyzon sucetta</i> (Lacepède, 1803)	“Survival among the less tolerant species was restricted to a small number of immature fish. It seems highly probable on the basis of this evidence that for these species, at least, the young have a greater heat tolerance than do the adults.”	Bailey (1955) ^{a)}
Delta smelt, <i>Hypomesus transpacificus</i> McAllister, 1963	“The thermal tolerance of Delta Smelt generally decreased among successive ontogenetic stages, and they had limited capacity to increase tolerance via thermal acclimation.”	Komoroske et al. (2014)

Table 1 (continued)

Species	Remark(s) and quote	Source
Oscar, <i>Astronotus ocellatus</i> (Agassiz, 1831)	Large is better, but more ASR observed in larger individuals. "... larger oscars did perform ASR at approximately 50 mmHg, the tension at which the first significant drop in their $\dot{M}O_2$ was seen. Surprisingly, smaller Oscars postponed ASR to around 22 mmHg, well beyond the PO_2 at which they switched from oxyregulation to oxyconformation (70 mmHg)."	Sloman et al. (2006)
<i>Rhinichthys atratulus</i> (Hermann, 1804) and <i>Notropis cornutus</i> (Mitchill, 1817)	"There is [...] evidence of a trend for <i>Rhinichthys atratulus</i> , <i>Notropis cornutus</i> , and <i>Lepomis macrochirus</i> . In the first two of these species the largest fish tended to die first..."	Hart (1952)
<i>Lepomis macrochirus</i> (Rafinesque, 1819)	"... in [<i>R. atratulus</i> and <i>N. cornutus</i>] the largest fish tended to die first; in <i>Lepomis</i> , however, the opposite was true	Hart (1952)
Wolfish, <i>Hoplias malabaricus</i> (Bloch, 1794)	"[...] smaller size coincided with a higher PCO_2 , i.e., a more limited range for maintenance of O_2 uptake during hypoxia."	Kalinin et al. (1993)
Inanga, <i>Galaxias maculatus</i> (Jenyns, 1842)	Large is advantageous due to increased anaerobic metabolism. "... although bigger fish were forced to depress aerobic metabolism more rapidly than small fish when exposed to progressive hypoxia, they were better able to enact anaerobic metabolism, potentially extending their survival in hypoxia."	Urbina and Glover (2013)
Lost River sucker, <i>Deltistes luxatus</i> (Cope, 1879) and shortnose sucker, <i>Chasmistes brevirostris</i> (Cope, 1879)	"In each of the three kills, the majority of suckers were adult-sized; most shortnose suckers were > 330 mm FL and most Lost River suckers were > 400 mm FL."	Perkins et al. (2000)
Striped bass, <i>Morone saxatilis</i> (Cope, 1879)	"Most of the reported mortality was of medium sized to large adults (> 5 kg)."	Matthews (1985)
Cachama, <i>Colossoma macropomum</i> (Cuvier, 1816)	"For instance, juvenile of <i>C. macropomum</i> can survive during low water periods in shallow pools by efficiently using oxygen exudation of the roots of aquatic macrophytes and performing ASR. Medium and large-sized specimen will move out of the shrinking pools to the river or to other deep-water habitats before the pools become too shallow."	Soares et al. (2006)
Neon Goby, <i>Elacatinus oceanops</i> (Jordan, 1904)	"Temperature tolerance was negatively correlated with body size." "Smaller fishes may be more resilient during extreme heat events."	Di Santo and Lobel (2017) ^b
Nile tilapia, <i>Oreochromis niloticus</i> (Linnaeus 1758)	"When fish populations are faced with acute thermal stress, larger individuals may become constrained in their ability to perform aerobic activities at lower temperatures than smaller conspecifics."	Blasco et al. (2022)
Arctic grayling <i>Thymallus arcticus</i> (Pallas, 1776)	"Furthermore, our study demonstrated that adult Arctic Grayling have a higher tolerance to severe hypoxia than juveniles, supporting the theory that a large body size results in a greater tolerance to hypoxia in fish [...]."	Davis et al. (2019)

Table 1 (continued)

Species	Remark(s) and quote	Source
Leopard coral grouper, <i>Plectropomus leopardus</i> (Lacepède, 1802)	“ <i>CT</i> max declined from 38.3 to 37.5 °C with increasing body mass in adult fish (0.45–2.82 kg), indicating that larger individuals are more thermally sensitive than smaller conspecifics.”	Messmer et al. (2017)

^aThis study produced the same results for *Erimyzon sucetta* (Lacepède, 1803), *Notropis heterodon* (Cope, 1865), *Pimephales notatus* (Rafinesque, 1820), *Ameriurus nebulosus* (Lesueur, 1819), and *Noturus gyrinus* (Mitchill, 1817)

^bThe size effect demonstrated in this study was also found in the interspecific between *Elacatinus oceanops* and the smaller Caribbean neon goby, *Elacatinus lobelia*, Randall & Colin, 2009

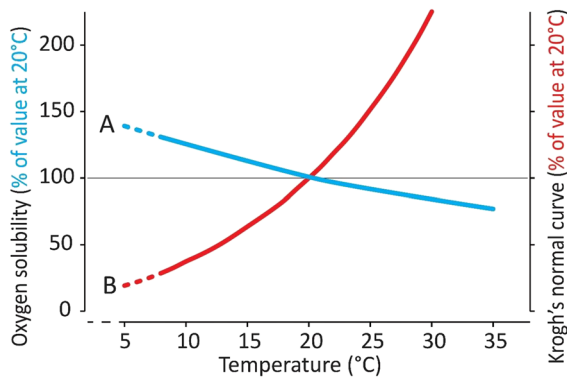


Fig. 1 Above 4–5 °C, the oxygen demand by fish and other water-breathing ectotherms tends to increase with temperature (mainly because of the increasing rate of spontaneous denaturation of proteins), as represented by Krogh’s normal curve (Ege and Krogh 1914). Oxygen solubility only decreases with temperature. Jointly, these two processes, above 4–5 °C, cause fish to suffocate at temperatures higher than those to which they are adapted

physical limits—without using anaerobic resources, larger fish could not perform even moderate physical exercise without glycolysis. Their capacity of oxygen uptake was limited compared to smaller individuals and they depended on an alternative supply to maintain their active metabolism. Nilsson and Östlund-Nilsson (2008), however, turned this observation on its head and concluded that larger fish were therefore not oxygen-limited.

A strong negative correlation between body mass and hypoxia tolerance was found in a recent review by Verberk et al. (2022) which, however, mainly focused on differences between species and on physiological literature. The interspecific size differences of the species in their dataset spanned several orders of magnitude, which made it difficult to tease out

differences in ontogeny within species. While this interspecific comparison has invaluable macroecological implications, and may also explain larger biogeographical patterns, intraspecific effects of body size on hypoxia tolerance and thermal sensitivity remain unclear and require a more comprehensive evaluation. In this contribution, we revisit such effects within species by comparing different bodies of literature, from physiological studies based on laboratory data to fieldwork manuals and fish kill reports. We then discuss a number of caveats that should be considered when interpreting available data relating hypoxia to fish size.

Materials and methods

We conducted a literature search in Google Scholar, Science Direct, and the Biodiversity Heritage Library and collected data on three described phenomena: (1) sensitivity to hypoxia and high temperatures, (2) aquatic surface breathing, and (3) size-related scaling of anaerobic metabolism. The latter is relevant, since Nilsson and Östlund-Nilsson (2008) build their argument around the increased anaerobic capacity of large fish. For (1), we only included publications that explicitly mentioned size-related differences in hypoxia tolerances within a given species (both positive and negative effects of size). We excluded studies on air-breathing fishes, as well as on larvae and young hatchlings, and limited our focus to data on juveniles and adults of various sizes. As Doudoroff and Shumway (1970) have argued, data on the hypoxia tolerance of fishes during the first days after hatching are notoriously contradictory and highly vulnerable to disruptive factors that may not directly correlate with high temperatures and hypoxia but result from poor conditions to which young larvae are more prone

in general. We also excluded publications that did not directly specify the species being killed but only mentioned a prevalence of killed adults compared to juveniles (e.g., Martin 1989; Mallin et al. 2002), although they also supported the argument that will be made below. In addition, we reviewed 20 fish kill manuals with fieldwork instructions and extracted their statements about size-related mortality during mass die-offs.

In addition to the literature review, we present data on three fish kills that occurred in the hot summers 2020 and 2022 in Brabant, the south of the Netherlands. The summers from 2018 to 2022 were extremely dry, and both groundwater and surface water levels fell to record lows, especially in the southeastern part of the country (Brakkee et al. 2022). During all three die-off events, the water levels of various freshwater bodies fell quickly, in two cases to puddles > 30 cm (see Table 4), and the management intervention was to save surviving fish and to release them in nearby water bodies in accordance with Dutch regulations. Given that the drought had reduced some water bodies to shallow puddles, it was possible to catch most surviving fish and exclude the possibility of large individuals being overlooked.

Only numbers and sizes of survivors were recorded. As Labay and Buzan (1999) have argued, the numbers of smaller dead fish are often underestimated in fish kill investigations, and larger fish are typically overrepresented in the resulting reports (see also Koehn 2004 and King et al. 2012). Despite the limited scope of our observations, their relevance lies in the fact that they do not suffer from this shortcoming because we focused on the survivors and not on the dead fish and could exclude large undiscovered surviving individuals. This approach allowed for a more realistic perspective on the role of size in hypoxia-induced mass die-offs, and we suggest to follow this approach in future surveys (if drought-induced low water levels allow for comprehensive estimates of the fish that actually survived).

Results

Body size and sensitivity to hypoxia and thermal stress

The reviewed literature as well as the new data present robust evidence for a positive correlation between body size and sensitivity to hypoxia and heat stress. In

30 of the 35 species listed in Table 1, body size was a factor that reduced the tolerance of hypoxia and higher temperature. The species for which a higher degree of hypoxia tolerance at greater body sizes was indicated are likely to possess more anaerobic capacity at larger size. Oscar, *Astronotus ocellatus* (Agassiz, 1831), for example, a cichlid known for its hardiness in hypoxic environments and tolerance of heat stress and oxygen depletion, increases with size because larger fish are more resistant to the resulting waste products of anaerobic metabolism (Almeida-Val et al. 2000). However, larger individuals were still more likely to show aquatic surface breathing, which indicates that they are more oxygen-limited despite their increased capacity to produce ATP anaerobically.

Our results are largely in line with the results of an earlier review by Davis (1975), as far as interspecific size differences are evaluated there (Table 4). We did not use these results, however, because his compilation of data on different fish sizes are from different studies, and the indication of size and temperatures was not always precise enough to allow for direct inferences of the role of size.

Aquatic surface breathing (ASR)

The authors of most studies on ASR reported an increase in surface breathing behavior with increasing body size (Table 2). The exception was Schofield and Chapman (2000) who did not observe a correlation in *Lates niloticus* (L.), in contrast to Reid et al. (2013). Sukhum et al. (2016) found a positive correlation between aquatic surface breathing and brain size in different species of Osteoglossomorph species, but did not evaluate body mass.

Body size and anaerobic metabolism

The studies by Goolish (1989ab; 1991; 1995), Kieffer (1995; 2000; 2010), Kieffer et al. (1996), Kieffer and Tufts (1998), Ferguson et al. (1993), Gingerich and Suski (2012), Somero and Childress (1980); Zhang et al. (2014), Urbina and Glover (2013), McDonald et al. (1998), Moyes and West (1995), and Clark et al. (2012) on anaerobic metabolism all reported a positive correlation with body size. Urbina and Glover's (2013) statement on Inanga, *Galaxias maculatus* (Jenyns, 1842), may apply to more species and perhaps to fish in general: "Owing to their size and higher lactate production rates,

Table 2 Effects of size on aquatic surfacing respiration (ASR)

Species	Effect of size on ASR behavior	Source
Oscar, <i>Astronotus ocellatus</i> (Agassiz, 1831)	More ASR in larger individuals	Sloman et al. (2006)
Shortfin molly, <i>Poecilia mexicana</i> (Steindachner, 1863)	More ASR in larger individuals, especially females (which grow to larger sizes)	Plath et al. (2011)
Guppy, <i>Poecilia reticulata</i> (Peters, 1859)	More ASR in larger females, less in larger males (which are smaller than females)	Kramer and Mehegan (1981)
Nile perch, <i>Lates niloticus</i> (Linnaeus, 1758)	More ASR in larger individuals	Reid et al. (2013)
Nile perch, <i>Lates niloticus</i> (Linnaeus, 1758)	No correlation observed	Schofield and Chapman (2000)
Tidepool sculpin, <i>Oligocottus maculosus</i> (Girard, 1856)	More ASR in larger individuals	Sloman et al. (2008)
Great barracuda, <i>Sphyraena barracuda</i> (Edwards, 1771)	ASR only in larger individuals within a juvenile size range	Kramer (1983)
Zebrafish, <i>Danio rerio</i> (Hamilton, 1822)	ASR increases with size	Abdallah et al. (2015)
African Osteoglossomorph species: <i>Gnathonemus petersii</i> (Günther, 1862), <i>Brevimyrus niger</i> (Günther, 1866), <i>B. brachyistius</i> (Gill, 1862), <i>Campylomormyrus</i> spp., and <i>Pollimyrus adspersus</i> (Günther, 1866)	More ASR in species and lineages with greater brain size	Sukhum et al. (2016)
Gulf killifish, <i>Fundulus grandis</i> (Baird & Girard, 1853)	More ASR in larger individuals	Rees and Matute (2018)

larger inanga can accumulate up to 16.6 times more lactate than small fish. Therefore, these data suggest that the capacity for anaerobic metabolism is size dependent and scales with fish size.”

Fish kill manuals

Nineteen out of 20 reviewed fish kill manuals that specify hypoxia-induced die-offs indicate a greater sensitivity to hypoxia in adults compared to juveniles (Table 3). One manual (Dallas and Day 2004) indicates the opposite and a greater vulnerability in juveniles. However, this greater vulnerability appears to apply to the longer-term “secondary” effect of fish kills rather than the short-term deaths caused by hypoxia.

Survival of juvenile fishes in three fish kills in the Netherlands

The three fish kills documented in Table 4 confirm the inference that can be drawn from the literature presented in Table 1: hypoxia and heat stress affect larger fish far more drastically than

smaller individuals. Since these data focused on survivors, the counting bias described by Labay and Buzan (1999) and suggested by Koehn (2004) and King et al. (2012) did not affect our results. In all cases, juvenile cyprinids had the greatest probability of survival, while older and larger size classes were often wiped out entirely. In places where sticklebacks occurred naturally, they made up the main portion of survivors—perhaps due to their tolerance of high salinity levels, which are typical at extreme drought events. Pike, perch, and tench only survived as juveniles (all smaller than 10–15 cm). In the case of Omleidingkanaal Groote Beerze, perch were the first to die, and dead large perch were first reported on August 26, 2022, after a short heatwave had driven up local (air) temperatures up to 33.5 °C. The other fish died in the following days when the air temperatures were already lower but the water level had sunk quickly. While drought-induced fish kills may result in a higher vulnerability for larger individuals to avian predators, because they can be easier located in shallow water, this seems unlikely at locations 1 and 2 (Strijpsche Beek), where the fish had access to culverts or where a culvert was the only spot that still held water.

Table 3 Size effects reported in fish kill manuals suggesting that it is mostly large fish that are killed by hypoxic events, with the last entry suggesting, however, that larger fish are less impacted (when they survive) by the secondary effect of such events

Size effects and quotes	Reference
“[...] if the fish kill event is characterized by large fish specimens and fish observed to still be alive are gulping air at the surface of the water body, it is likely that the mechanism of death that resulted in the fish kill event is related to low dissolved oxygen concentrations as large fish have a higher metabolic requirement than smaller fish.”	Grant et al. (2014)
Oxygen depletion: “Large fish killed first, eventually may all sizes and species”	Meyer and Barclay (1990)
Toxic algal bloom and pesticide toxicity: “Small fish killed first, eventually may all sizes and species.”	
Oxygen depletion: “Large fish die first.”	Whitford (2009)
Toxic substances: “Small fish die first.”	
“Juvenile life stages of many aquatic organisms are more sensitive than adults to physiological stress arising from oxygen depletion, and in particular to secondary effects such as increased vulnerability to predation and disease.”	Dallas and Day (2004)
“Larger fish and species with high oxygen requirements are affected first.”	Knowles et al. (2015)
“Larger fish and species with high oxygen requirements are affected first.” (citing Knowles 2015)	Danks et al. (2017)
“Symptoms of oxygen depletion may include an abnormal distribution of fish gulping at the water surface or at the pond inlet or edges. Large fish may die first, but all sizes of fish are usually affected.”	Helfrich and Smith (2009)
“A finding that only the smaller fish died or that large fish died but small fish survived is important in distinguishing between oxygen depletion and toxic causes. The key difference is gill surface ratio to total body mass. Small fish, being relatively more rapid in absorbing water solutes, withstand marginal oxygen depletion but succumb first to toxic materials.”	U.S. Environmental Protection Agency (1972)
“Fish will be at the surface gasping for air and the larger fish die first.”	Mississippi Department of Wildlife, Fisheries, and Parks (2012)
“(L)arger fish die earlier than smaller fish of the same species [...]”	Ramachandra et al. (2016)
“Low DO levels kill aquatic life; large fish die before small fish and species requiring higher concentrations of DO die first.”	American University of Beirut (2013)
“If it is a DO-related fish kill, large fish tend to be affected first and more severely than other fish.”	Francis-Floyd et al. (2004)
“Usually larger fish are affected by low DO before smaller fish are.”	Francis-Floyd (1997)
“Larger and more active fish species, such as Murray cod, tend to become stressed and/or die first due to their greater oxygen requirements.”	New South Wales Department of Primary Industries (2022)
“Larger fish die earlier than smaller fish of the same species.”	Lutz and Grodner (1992)
“Small fish usually survive because they have a greater gill size ratio than do larger fish. This enables them to extract enough oxygen from low dissolved oxygen water to survive.”	Missouri Department of Conservation (1994)
“So the result may be that larger fish, such as bass, die, leaving the smaller, immature fish in the pond.”	Krauch (1982)

Table 3 (continued)

Size effects and quotes	Reference
“The size of the affected fish is also an important observation. Typically, a fish kill caused by depressed oxygen levels will not include smaller fish unless critically low concentrations are reached. [...] The reason for his phenomenon is that younger, smaller-bodied fish require relatively less oxygen than larger fish.”	Poukish and Driscoll (1999)
“Large fish die first”	Texas Parks and Wildlife Department (1970)
“The large fish die first, because they require more oxygen, and will suffocate first.”	Wickman (1980)

Table 4 Surviving fish in 3 fish kills that occurred in the summer of 2020 and 2022 in the Netherlands

Species present	Size of survivors ^{a)}	Numbers of survivors
Strijpsche Beek (south), 51° 35' 19.6" N and 5° 51' 55.7" E; August 14, 2020		
European pike (<i>Esox lucius</i> L.)	N.A	0
Tench (<i>Tinca tinca</i> L.)	< 10	< 10
Roach (<i>Rutilus rutilus</i> L.)	< 10	< 30
Strijpsche Beek (north), 51° 35' 48.9" N and 5° 52' 48.4" E; August 16, 2022		
European pike (<i>Esox lucius</i> L.)	< 15	< 10
Tench (<i>Tinca tinca</i> L.)	< 15	< 50
Roach (<i>Rutilus rutilus</i> L.)	< 10	< 100
Stone loach (<i>Barbatula barbatula</i> (L.))	< 5	< 20
Spined loach (<i>Cobitis taenia</i> L.)	< 5	< 20
Three-spined stickleback (<i>Gasterosteus aculeatus</i> L.)	< 5	> 5000
Omleidingkanaal Groote Beerze, 51° 29' 29.1" N and 5° 15' 59.1" E; August 30, 2022		
European pike (<i>Esox lucius</i> L.)	< 15	< 10
Tench (<i>Tinca tinca</i> L.)	< 15	< 50
Roach (<i>Rutilus rutilus</i> L.)	< 10	< 100
European perch (<i>Perca fluviatilis</i> L.)	< 15	< 50
Rudd (<i>Scardinius erythrophthalmus</i> (L.))	< 10	< 100

^{a)}Sizes are in centimeter total length

Discussion

The existing literature on hypoxia sensitivity, aquatic surface breathing, and anaerobic metabolism, as well as the data on the survival of juveniles in fish kills, allows for drawing three conclusions:

- 1) Adult fish, especially larger individuals, are more sensitive to hypoxia and heat stress.
- 2) Adult fish, especially larger individuals, show more and earlier surface breathing when exposed to hypoxia.

- 3) Larger fish are more capable of (and dependent on) anaerobic metabolism, which can allow them to resist hypoxia for short periods.

Nineteen out of 20 of the fish kill manuals reviewed here confirmed these findings. If the role of size was mentioned, they indicated a correlation between size/age and the risk of being killed by thermal stress and/or oxygen depletion. However, this does not imply that these manuals necessarily provide correct explanations for this phenomenon. Indeed, field personnel sometimes overestimate the metabolic

and oxygen demand of larger fish. As Grant et al. (2014) argue “[...] larger fish are more susceptible to dissolved oxygen depletion due to their higher metabolic requirements relative to smaller individuals, but are often found in higher abundances in the lower reaches of a watercourse.” This explanation is not entirely accurate because oxygen consumption does not scale proportionally to body weight; rather, it shows a negative allometry, which implies a reduction of mass-specific oxygen consumption in larger fish (see, e.g., Schmidt-Nielsen 1984).

However, this imperfect understanding of metabolic scaling is still more in line with empirical observations than the interpretation of data on oxygen demand and supply by Nilsson and Östlund-Nilsson (2008). What both perspectives fail to consider is that while oxygen consumption is indeed reduced with increasing body size, so is the ratio between gill surface area and body mass. In fact, the latter is the cause of the former, i.e., the relative decrease in respiratory surface explains both why larger fish switch to anaerobic metabolism and why they are still more vulnerable to severe hypoxia. While larger organisms may indeed have a short-term advantage due to their anaerobic capacity, this resource is not endless, and after a while, they have to switch back to aerobic metabolism. This explains why large fish may seem more hypoxia-tolerant in short-term laboratory settings and can show enhanced swimming capacity in hypoxic water (Oldham et al. 2019) but are in fact more vulnerable to oxygen depletion than smaller individuals.

Our findings further support the conclusions of Leiva et al. (2019) and Verberk et al. (2022), who inferred correlations between hypoxia tolerance and body size from a wide variety of experimental data but focused on comparisons between species. Given the urgency of increasing drought events and heatwaves in a warming climate, these results require a more general explanation. A mechanism that is a priori excluded by Nilsson and Östlund-Nilsson (2008) is the scaling relationship between respiratory surfaces and the body mass they have to provide with oxygen at different body sizes. As they argue, “oxygen consumption and gill surface area show virtually identical scaling exponents, suggesting that gill surface area is matched with the requirement for oxygen uptake over a large body size range, and that the ability to take up oxygen during hypoxia is independent of

size”. While it is obviously correct that oxygen consumption rate and gill surface area scale with similar exponents, the idea that “the ability to take up oxygen during hypoxia is independent of size” needs revision, as suggested by the observation that both anaerobic metabolism and the recovery period increase with body mass. If oxygen uptake capacity was indeed independent of size, larger fish would not have to rely on anaerobic metabolism for even moderate physical activities (see the studies cited above in the section *Body size and anaerobic metabolism*).

Similar assumptions also underly the arguments in Scheuffele et al. (2021) and Seibel and Deutsch (2020) who contend that the similar (or identical) scaling exponents of oxygen consumption and gill surface area rule out the possibility of oxygen limitation because “as whole-animal metabolic rate increases with size, the oxygen supply capacity increases to match it” (Seibel and Deutsch 2020). This statement overlooks the fact that large adults invest less energy in growth because almost all is needed for maintenance metabolism. If the growth of adults were to continue at the same rate as in juveniles, it is clear that no gills could exist (within the constraints of fish anatomy) with a surface area that could support their growing body with sufficient oxygen. The assumption that the similar scaling exponents of gill surface area and oxygen uptake suggest size-independence of aerobic capacity is only valid if growth expenditure can be excluded from the metabolic rate that is measured. However, this is rarely the case. As Rosenfeld et al. (2015) demonstrate, measured standard metabolic rate (SMR) is “strongly affected by growth rate, that is, elevated metabolism associated with tissue synthesis will affect whole-body metabolism even when organisms are at rest [...]”. Even after sufficient fasting periods, overhead costs of growth can still play a significant role during respirometry. The authors therefore recommend maintenance rations weeks in advance of the experiments. In the data that are cited in the current literature, this is not the case, which points at a problem that may be specific to fish physiology: “Because of the strong influence of growth on SMR, physiologists studying maintenance metabolism in birds and mammals generally work on adults; in contrast, fish physiologists commonly measure SMR on actively growing juveniles in laboratory experiments [...]” (Rosenfeld et al. 2015).

Despite the helpful and now widely adopted suggestions by Chabot et al. (2016), who define a number of guidelines on how to measure standard metabolic rate in fish, the data that are available and cited in the literature so far, do not typically conform to these standards. Following Rosenfeld et al. (2015), Chabot et al. (2016) recommend that “standard metabolic rate” should be defined as metabolic rate excluding growth expenditure (for an overview of debates on definitions of relevant parameters, see also Claireaux and Chabot 2016). However, most of the studies cited in Scheuffele et al. (2021), Seibel and Deutsch (2020), or Lefevre et al. (2017) do not even indicate that they measure standard metabolic rate but often refer to resting metabolic rate (RMR). Studies that indicate the exact protocol according to which fasting periods and maintenance rations were determined are still rare (but see, e.g., Tirsgaard et al. 2015). The interspecific exponents of either SMR and RMR that are reported in the existing literature vary between 0.79 and 0.94 (see, e.g., Clarke and Johnston 1999; Killen et al. 2007; Lefevre et al. 2017; Jerde et al. 2019; Ye et al. 2021; Harter et al. 2022).

The observation that smaller and younger fish have a larger aerobic scope (which allows them to grow but also to compensate for a temperature-induced increase in energetic costs) is consistent with, and can be coherently explained by, the Gill-Oxygen Limitation Theory (GOLT) as developed by Pauly (1979, 2019, 2021). According to the GOLT, gill surface area is a limiting factor for fish growth because gills, as two-dimensional surfaces, have to support three-dimensional bodies, even if they grow with positive allometry. While fish growth slows down once the respiratory surfaces supply the body with relatively less oxygen, a drastic increase in temperature and critical levels of hypoxia are more difficult to cope with for individuals that are already near the limit of their capacity to supply the body with oxygen (Fig. 2).

This is especially the case in fishes that have grown to larger sizes in cooler environments. At higher temperatures, fish do typically not reach the maximum sizes that would be possible for their species (see, e.g., Dimarchopoulou and Tsikliras 2022). The GOLT explains this difference in growth as a result of the difference between anabolism and catabolism, i.e.,

$$dw/dt = HW^d - kW,$$

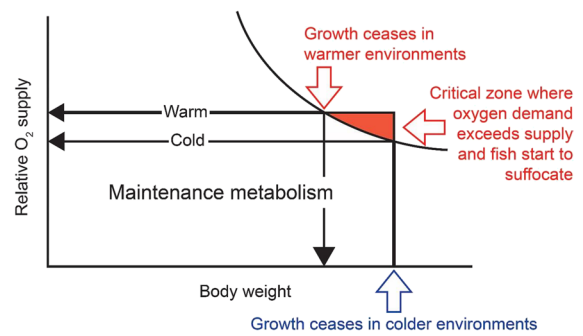


Fig. 2 Oxygen supply and demand relative to body weight under different temperatures and resulting metabolic rates (see text)

where dw/dt is the growth rate, HW^d is the rate of protein synthesis, which requires oxygen, and kW is the rate at which proteins spontaneously denature, a process that does not require oxygen itself but that implies the need to re-synthesize and replace the denatured proteins (see Pauly 2019, 2021; Pauly and Lam 2023). The parameter d , which in fish, ranges from 0.6 to 0.9, is the exponent in the relationship linking the surface area (S) of the gills to body weight (W), such that $S \propto W^d$. As shown by Scheuffele et al. (2021), d tends to be equal or very close to the scaling exponent of measured oxygen uptake (which is often not the same as “standard metabolic rate” in juvenile and growing fish, if we follow the definition of Chabot et al. 2016). Since kW increases with W , it will gradually approach HW^d , which will cause growth to slow down and stop (when $HW^d = kW$). Thus, if temperature increases protein denaturation and thus kW (which it does, see Fig. 2), $HW^d = kW$ is reached at smaller sizes.

This phenomenon, which is often described as the “temperature-size rule,” can then be explained as a physiological mechanism that occurs in individual ontogenies. In environments where heat stress occurs, this mechanism may also have an adaptive advantage: if fish remain small, they may be better able to survive in hot and hypoxic environments. Reduced final sizes at higher temperatures can then be regarded as “[b]enefits of being small in a changing world” (Clark et al. 2012)—benefits that do not come without a cost, for example, fewer and smaller eggs (Hislop 1988). For the thermal and hypoxia tolerance of individuals, however, the advantage of smallness in hypoxic and hyperthermic conditions can be explained as a result

of the relationship between respiratory surfaces and body volume, even when the scaling exponents of gill surface area and oxygen uptake are similar or equal. As Blasco et al. (2022) argue, even if “AS [aerobic scope] scales isometrically with body mass across multiple species,” this only applies within a limited thermal range. With increasing temperatures, larger animals are more oxygen-limited because “gill functional respiratory surface area declines with mass in fishes.” It should be noted that many fish species can alter their gill surface area as a response to higher demand, for example, during hypoxia or hyperthermia. However, the capacity to increase their respiratory surfaces is only very limited (or even absent) in marine species, and its efficiency in freshwater fish is impeded by the resulting ion loss that would be a result of larger gills (Bowden et al. 2014; Wood and Eom 2021). According to Bowden et al. (2014), it is therefore unclear if such forms of gill plasticity (or gill remodeling) will allow for sufficient adaptation, especially under current climate predictions. In the case of hypoxic events or heatwaves, gill remodeling is also unlikely to be effective as it requires time and such events often occur quickly.

A possible hypothesis that could be further examined in future studies would be that the size effects discussed above may depend on the combined effect of hypoxia and thermal stress. This would also explain why studies on winter fish kills do not report strong size effects or even show an advantage of larger adults over smaller individuals or juveniles (see, e.g., Davis et al. 2019). According to our model, it is possible that temperature may have a stronger impact on size-related oxygen limitation than hypoxia, since hypoxia does not increase maintenance metabolism. In summer fish kills, the effects of the two factors are difficult to tease apart because both thermal and hypoxic stress contribute to internal hypoxia in fish.

Literature on aquatic invertebrates suggests that our observations allow for generalizations that extend oxygen limitation in fishes only and that they can be applied to other phyla. Data on molluscs, and especially clams, report the same pattern: larger animals rely more heavily on anaerobic metabolism, but are nonetheless the first to die in hypoxic environments and under heat stress (Clark et al. 2013; Cueto-Vega et al. 2022; Aguirre-Velarde et al. 2019; Garlo et al. 1979). Clark et al. (2013) generalize this as follows: “... older animals have a proportionally smaller gill

surface for oxygen extraction. Older animals have a lower metabolic rate, but tissue scaling probably contributes towards the age-related stress effects seen in older animals.” This mechanism may eventually apply to all water-breathing organisms but more research is needed here (for a comparison between different phyla, see Table 2 in Pauly et al. 2022).

As J.B.S. Haldane (1926) elegantly put it in his seminal essay *On Being the Right Size*, “Comparative anatomy is largely the story of the struggle to increase surface in proportion to volume.” The struggle for surface in relation to volume also underlies the survival of water-breathing animals in times of rapid climate change, and it is their adaptability to new thermal environments that will decide their fate in a warming world.

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Data availability All data generated or analyzed during this study are included in this published article. More documentation can be provided at request.

Declarations

Ethical approval Not applicable. The animals from which the data for case 5 were used were captured (and released) as part of a drought rescue intervention in accordance with the Dutch *Uitvoeringsregeling visserij, hoofdstuk 1, § 60a*, and for which Sportvisserij Zuidwest Nederland was commissioned.

Conflict of interest The authors declare no competing interests.

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