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Introduction: Fishes in a warming and deoxygenating world

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Abstract This account serves as the introduction to a Special Issue of the journal *Environmental Biology of Fishes*. It includes 18 contributions, 12 of which deal predominantly with warming, four explicitly with deoxygenation, one providing the framework, and one addressing how warming and deoxygenation—which all contributions view, implicitly or explicitly, as leading to "oxythermic" stress—are used as a pretext to cover up overfishing. The "Mean Temperature of the Catch" (MTC) concept of Cheung et al. (2013, *Nature* 497:365–368) inspired five of the studies involving mainly temperature, including its first applications to fresh water and to the past, i.e., to the past 130, 7–8 thousand, and 2 million years. Four contributions, jointly representing 4200 + populations and 1100 + species, deal with the effect of temperature on the maximum and/or the asymptotic length of fish behaving as predicted by the Gill-Oxygen Limitation Theory (GOLT). This theory is also evoked in one of these studies to explain how cold denaturation causes fish to grow to a smaller size when temperatures decline below 4 °C. These contributions, which are here summarized and whose conceptual affinities are also presented in graphic form as a tree-like structure, provide a basis for understanding the changes in fish community composition and size structure resulting from marine or freshwater warming. Jointly, they explain some of the changes in fish behavior and position in the water column resulting from the deoxygenation of their habitats.

Dedicated to the memory of Jeffrey A. Hutchings.

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Introduction

The world of fish—71% of the Earth's surface—is becoming warmer and less well-oxygenated. As illustrated in Fig. 1, this squeezes marine and freshwater fish between essentially irresistible forces, one increasing their oxygen requirements, the other reducing the oxygen available to them, both because warmer water contains less dissolved oxygen and because of widespread deoxygenating events and/or processes.

The articles assembled in this Special Issue illustrate the responses of fish to these forces through case studies relying on data collected worldwide (Fig. 2), which, jointly, should facilitate a more comprehensive understanding of the effect of climate change on fish.

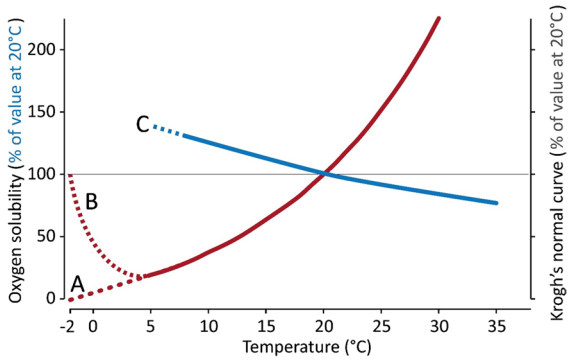

Fig. 1 Above 4–5 °C, the oxygen demand by fish and other water-breathing ectotherms tends to increase with temperature (line A; mainly due to protein denaturation), while the amount of oxygen that can be dissolved in water declines (line C, with the difference between sea and freshwater being too small to matter). This reduces the oxygen supply of fish and thus their ability to re-synthesize denatured proteins. Below 4 °C, cold denaturation of proteins increases with temperature decreasing (dotted line B). Based on Ege and Krogh (1914) and Pauly (1979, 2021); see also Lavin et al. 2022a, this issue)

These studies, arranged alphabetically by first author, can be summarized as follows:

Agiadi et al. (2022**, this issue)** explore the applicability of the mean temperature approach to fossil fish faunas by using otolith assemblage data from the eastern Mediterranean and the northern Adriatic coastal environments corresponding to the last 8000 years (Holocene) and the interval from 2.58 to 1.80 million years ago (Early Pleistocene). The case study showed that the mean temperatures inferred from otolith assemblages can successfully capture compositional shifts in marine fish faunas based on variations in their climatic affinity driven by regional climate differences.

Bakun (2022**, this issue)** follows up on the implications of the different effects of high levels of activity (i.e., leading to internal depletion of oxygen stores) in small and large fish. Notably, these different effects, which include longer recovery times for larger fish relative to small ones, imply that the large predators cannot exterminate the small fish that their superior swimming performance would otherwise allow. These and other insights that are non-obvious at first sight are evidence that our intuitions as air-breathing mammals need adjusting when thinking about the issues faced by fish and other animals that breathe water, i.e., a medium that contains little oxygen in the best of times.

Cheung et al. (2022**, this issue)** assess the risks of climate impacts to the population viability of 32 exploited demersal deep-sea species across the global ocean. They find that most exploited deep-sea fishes are likely to be at higher risk of local, or even global, extinction than previously assessed because of their high vulnerability to both climate change and fishing. Regional fisheries management organizations (RFMOs) have an obligation to incorporate climate change in their deliberations for overall risk reduction in the coming decades.

Clarke et al. (2022**, this issue)** focus on the organisms that inhabit Oxygen Minimum Zones (OMZ)

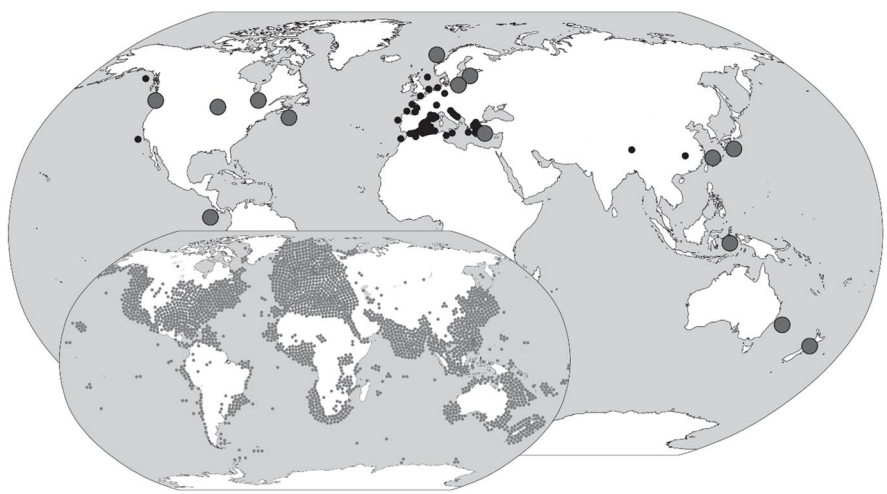

Fig. 2 Location on the globe of site-specific studies (large black dots on the larger map), with smaller black dots indicating where data were (also) collected. The smaller insert map marked with grey dots shows the approximate locations (from Froese and Pauly 2022; www.fishbase.org) where the data for the 4200 + growth parameter set analyzed in Palomares et al. (2022, this issue) were sampled

along the Pacific when examining the effect of ocean warming and hypoxia on their physiological performance and metabolic traits. There, the demersal species have specialized adaptations that allow them to survive within a very narrow range of environmental conditions, with even small environmental perturbations resulting in species distribution shifts that alter ecosystem trophodynamics. Their findings suggest that the effects of environmental temperature and oxygen levels on the structure of demersal communities within OMZs can be predicted when the oxygen demand of their component species is understood.

Dimarchopoulou and Tsikliras (2022**, this issue)** explore the geographic variability in the growth patterns of different populations of European pilchard/sardine (*Sardina pilchardus*) in the Atlantic and Mediterranean through the prism of sea temperature and dissolved oxygen, rather than that of trophic status, ecosystem productivity, or genetic distance as previously emphasized. They find that asymptotic length is negatively related to sea temperature and more strongly and positively related to oxygen levels, indicating that sardines grow to large body size in cooler waters that are well-oxygenated.

Dimarchopoulou et al. (2022**, this issue)** explore the fisheries catch responses to ocean warming along a latitudinal gradient in the western Pacific Ocean using the "Mean Temperature of the Catch" (MTC) index. They report a temperature-related increasing dominance of warm water species and an MTC increase in temperate Japan (0.33 °C per decade) and subtropical/temperate southeast Australia (0.24 °C per decade, 1.24 °C after 2002) from 1950 to 2016. On the other hand, the MTC in Indonesian tropical waters shows a gentle yet consistent decrease (0.05 °C per decade) that may be explained by the increase in deep-water species in Indonesian marine fisheries catches.

Froese et al. (2022**, this issue)** attempt to disentangle the impacts of warming and deoxygenation from the effects of mismanagement and overfishing of cod (*Gadus morhua*) and herring (*Clupea harengus*) in the western Baltic Sea. The study compares the depleted status of cod and herring with the satisfactory status and reproductive success of other local commercial species with similar life history traits. It concludes that sustained overfishing plus inappropriate size selectivity of the main fishing gears, and not climate change, has caused the drastic decline in spawning stock biomass of cod and herring.

Hillis et al. (2022**, this issue)** developed a method for estimating the "ancient Mean Temperature of the Catch" (aMTC) using Indigenous fisheries catch records from archaeological sites. They observe an increase in aMTC over a 7000-year period at two contemporaneously occupied archaeological sites in southwestern British Columbia, Canada, while documenting cooler catches from 5000 to 3000 cal yr BP (calibrated years before the present) and comparatively warmer catches from 1800 to 250 cal yr BP. These warmer temperatures are broadly consistent with palaeoceanographic sea surface temperature proxies from British Columbia and Alaska.

Kang et al. (2022**, this issue)** report a sudden explosive rise in the abundance of the hypoxia-tolerant fish Bombay duck (*Harpadon nehereus*) in the East China Sea, linking this drastic increase in abundance to the growing ocean deoxygenation along the western edge of the north Pacific Ocean. They suggest that the very high water content of Bombay duck's muscle and other tissues (about 90% vs. 75–80% for other coastal fish) reduces its oxygen requirements and allows it to outcompete other fish in low-oxygen neritic and estuarine waters.

Kangur et al. (2022**, this issue)** apply the MTC index of Cheung et al. (2013) for the first time to data from a freshwater ecosystem, aiming to assess the responses to warming of a freshwater fish community. Their analysis covers 89 years of catch data from the temperate Lake Peipsi in Estonia/Russia, showing evidence of the MTC (temperature preference of fished species weighted by their annual catches) fluctuating initially, then increasing 0.85 °C per decade from 1987 to 2019.

Lavin et al. (2022a**, this issue)** analyze Norwegian trawl survey data from a latitude of ~ 55 to over 80°N, covering temperatures ranging from − 1 to ~ 9 °C. Of 10 fish species that were studied in detail, only three showed decreasing maximum length (L_{max}) with increasing temperature, five showed an increase of L_{max} with temperature, and two showed a humped relationship of L_{max} with temperature. These results do not correspond to the "temperature size rule" as conventionally understood (e.g., Atkinson 1994), but align with the Gill-Oxygen Limitation Theory (GOLT) as formulated originally (Pauly 1979; see also Fig. 1).

Lavin et al. (2022b**, this issue)** look into the relative influence of the climate-driven temperature and dissolved oxygen concentration changes on the maximum body length of six fish and invertebrate species caught by trawl survey in New Zealand waters. All six species display a temperature-size response; temperature is more important than dissolved oxygen concentration in determining maximum body length. Their results suggest that larger-bodied species experience the strongest temperature-size responses, and support expectations derived from the gill-oxygen limitation theory (GOLT).

Levangie et al. (2022**, this issue)** explore the influence of ocean warming on the size and hence natural mortality of marine fishes and find that a 10% decrease in the asymptotic length associated with a 1 °C ocean temperature increase is likely to exacerbate natural mortality (M) for most marine fishes. Chondrichthyans were less affected, while smaller-bodied fish species, for example, the Atlantic mackerel (*Scomber scombrus*), seem to experience greater absolute increases in M than larger-bodied species.

Ng and Cheung (2022**, this issue)** investigate the signature of climate-induced changes in seafood species served in restaurants by calculating the "Mean Temperature of Restaurant Seafood" (MTRS) and using historical and present-day restaurant menus from Vancouver, Canada, and cities south and north of it (Los Angeles and Anchorage). The observed temporal and spatial variations in MTRS, which increased by ~ 3 °C between 1888–1960 and 2019–2021 in Vancouver, and which was highest in Los Angeles and lowest in Anchorage, were closely related to observed patterns of mean sea surface temperatures. Note that these authors missed the opportunity to name their new index "Mean Temperature of the Catch of the Day," or MTCD.

Palomares et al. (2022**, this issue)** explore the interrelationship of temperature, growth parameters, and activity level in fishes. They find that temperature affects the asymptotic size of fish but increases their parameter K (the rate at which the asymptotic size is approached), and thus decreases traits associated with K (e.g., longevity). Also, their model suggests that A (the aspect ratio of the caudal fin) correlates with K values, implying that active fish have large gill areas supplying the oxygen required for both a high level of activity and rapid growth, both supported by a high feeding rate.

Pauly and Liang (2022**, this issue)** present a simple sine-wave model for predicting accelerated spring spawning caused by global warming in fish, where this reproductive acceleration is well-documented. The empirical equation they derived can be used to predict, in spring spawning fish, the number of days (Δd_{min}) that spawning is advanced due to a given increase in water temperature (Δ°C). Comparisons with field estimates confirmed that this simple model's robust predictions correspond to observed spawning shifts.

Rodrigues et al. (2022**, this issue)** suggest that climate-driven declines in oxythermal habitats in freshwater lakes can impose severe constraints on species that prefer cold, well-oxygenated habitats such as lake whitefish (*Coregonus clupeaformis*). Acoustic telemetry shows that activity patterns differ significantly across a gradient of oxythermal constraints. Changes in their movement patterns across the gradient of oxythermal habitat indicate that their behavioral responses to unfavorable conditions may lead to changes in foraging efficiency and exposure to physiological stress, which raise doubt about their populations' ability to maintain themselves.

Strand et al. (2022**, this issue)** investigate how the decreased availability of dissolved oxygen caused by global climate change may disrupt predator–prey interactions in temperate lakes. They test the effects of hypoxia (dissolved oxygen ~ 1 ppm) on antipredator behavioral responses to conspecific alarm cues by fathead minnows (*Pimephales promelas*), and find that under oxygen stress, fathead minnows engage in aquatic surface respiration, i.e., "drinking" the surface film of oxygen-rich water, thereby exposing themselves to aerial predation.

A conceptual map

Another way of presenting the above studies is through a "conceptual map" that resembles an evolutionary tree but links its different elements based on their thematic focus. Figure 3 has two main "limbs." These limbs separate 12 studies that focus on "Mainly temperature" effects from four studies that focus on "Mainly oxygen" effects (or, more precisely, on hypoxia). This is despite the fact that temperature affects fish mainly through its influence on their oxygen requirements (Pauly 2021),

thereby generating the "oxythermal" habitat mentioned explicitly above or implicitly assumed by most authors (see also the center of Fig. 3).

On a smaller geographic scale, the MTC concept, which had been applied to marine waters in the near-present in various areas (e.g., in the eastern Mediterranean and Black seas (Tsikliras and Stergiou 2014; Keskin and Pauly 2018), China (Liang et al. 2018), and Uruguay (Gianelli et al. 2019)), was applied for the first time to a lake shared between Estonia and Russia (Kangur et al. 2022, this issue). In another first, the MTC was applied to the past in this Special Issue. Ng and Cheung (2022, this issue) reviewed Vancouver seafood menus ranging from the present to > 130 years ago. Hillis et al. (2022, this issue) analyzed fish

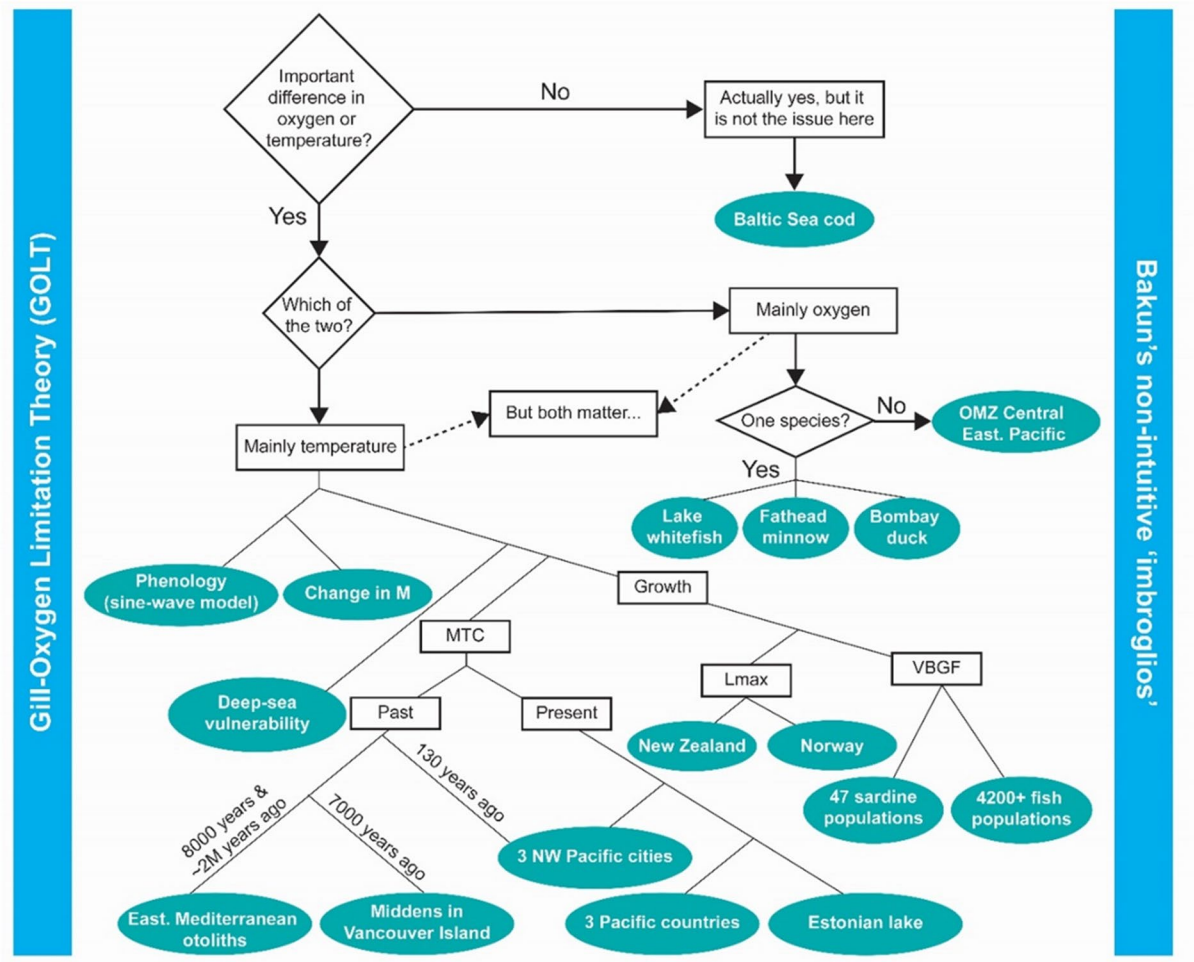

Fig. 3 A conceptual view of the relationship between 17 of the articles (green ellipses) in this Special Issue. From top to bottom, and from left to right, these are Baltic Sea cod (Froese et al. 2022, this issue); OMZ Central East. Pacific (Clarke et al. 2022, this issue); Lake whitefish (Rodrigues et al. 2022, this issue); Fathead minnow (Strand et al. 2022, this issue); Bombay duck (Kang et al. 2022, this issue); Phenology (Pauly and Liang 2022, this issue); Change in M (Levangie et al. 2022, this issue); Deep-sea vulnerability (Cheung et al. 2022, this issue); New Zealand L_{max} (Lavin et al. 2022b, this issue); Norway L_{max} (Lavin et al. 2022a, this issue); 47 sardine populations (Dimarchopoulou and Tsikliras 2022, this issue); 4200 + fish populations (Palomares et al. 2022, this issue); 3 NW Pacific cities (Ng and Cheung 2022, this issue); East. Mediterranean otoliths (Agiadi et al. 2022, this issue); Middens in Vancouver Island (Hillis et al. 2022, this issue); 3 Pacific countries (Dimarchopoulou et al. 2022, this issue); and Estonian lake (Kangur et al. 2022, this issue), with considerations of the 18th article in this Special Issue (Bakun 2022, this issue) and the Gill-Oxygen Limitation Theory (Pauly 2019, 2021) providing the framework

bones from the middens in two First Nation villages on Vancouver Island ranging from a few hundreds to 7000 years ago, and the eastern Mediterranean otoliths studied by Agiadi et al. (2022, this issue) originated from 8000 years to 2 million years ago.

The other "branch" of the "Mainly temperature" limb includes articles on the impact of ambient temperatures on the growth parameters of fish (i.e., one species with numerous populations; Dimarchopoulou and Tsikliras 2022, this issue) and over 4200 growth parameter sets in 1155 species (Palomares et al. 2022, this issue), as well as on the maximum size of fish (Lavin et al. 2022b, this issue). The latter also unexpectedly confirmed an aspect of the GOLT that had remained untested since its initial proposal (Pauly 1979), and which is illustrated by the low-temperature upward twist of the oxygen demand curve (see Fig. 1, line A and dotted line B). This branch of Fig. 3 also carries studies, harder to classify, on the effects of temperature on natural mortality (Levangie et al. 2022, this issue) and other vulnerabilities of fish (Cheung et al. 2022, this issue).

The other limb of Fig. 3, labeled "Mainly oxygen," includes studies that emphasize deoxygenation effects, which are rather spectacular in the case of Bombay duck off China (Kang et al. 2022, this issue), and more subtle in the central eastern Pacific (Clarke et al. 2022, this issue), in lake whitefish (Rodrigues et al. 2022, this issue), and fathead minnows (Strand et al. 2022, this issue) in North American lakes.

Framing and concluding

Two cross-cutting ideas frame the conceptual map in Fig. 3. On the right is the contribution of Bakun 2022, this issue), whose vision of the marine realm contradicts our terrestrial, air-breathing mammalian biases (see also Bakun 2011). Bakun (2022, this issue) proposes, through a series of (resolved) conundrums, that we must develop new intuitions to apprehend processes and constraints impacting fish and other water breathers. On the left is another item, not explicitly represented by any articles in this Special Issue, but cited by several of them, the Gill-Oxygen Limitation Theory (GOLT; Pauly 2019, 2021). Like the contribution by Bakun (2022, this issue), the GOLT requires that one fully appreciates the difficulties and implications of breathing water through gills if any understanding is to be achieved of how fish will fare in a warming and deoxygenating world.

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