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Natural environmental impacts on teleost immune function

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ABSTRACT

The environment in which teleosts exist can experience considerable change. Short-term changes can occur in relation to tidal movements or adverse weather events. Long-term changes can be caused by anthropogenic impacts such as climate change, which can result in changes to temperature, acidity, salinity and oxygen capacity of aquatic environments. These changes can have important impacts on the physiology of an animal, including its immune system. This can have consequences on the well-being of the animal and its ability to protect against pathogens. This review will look at recent investigations of these types of environmental change on the immune response in teleosts.

Contents

1. Introduction

The environment in which we live in can have profound impacts on our immune function. The study of these interactions is usually classified as either environmental physiology or ecophysiology. Many animals rely on behavioral strategies to overcome detrimental changes in their environment. They can move away from an immediate environmental stressor and find a less stressful environment. However, sessile organisms do not have that ability and instead have to 'tough it out'. To this end, sessile organisms will likely have a physiological adaptation that will allow them to limit the impacts of the environmental perturbation, at least in the short term. Although, aquacultured fish, such as salmon raised in sea cages are not sessile, they do not have the ability to relocate to avoid environmental stressors. Thus it is important to understand how such stressors can impact relevant organisms.

Long-term solutions to environmental change may occur through epigenetic changes or evolutionary adaptations. These adaptations can be defined by the acute or chronic nature of the

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environmental change [1]. Environmental impacts can be either abiotic (physical and chemical factors) or biotic (direct or indirect effects of other organisms) in nature. Some environments, such as the deep ocean, can be viewed as stable on timescales that are relevant to living organisms. Evolutionary or geological timescales can encompass changes such as sea level rises or the erosion/deposition of materials. More rapid changes can be defined on annual, lunar or daily cycles. Finally, changes can occur in seconds, minutes or hours such as the weather. Size of an organism can also impact its ability to respond to environmental change. Recent research is indicating that small adult animals are more resistant (tolerant) to a temperature change than larger animals, a finding that contradicts the variation in the volume/surface area ratio or isometric scaling [2]. Thus an organism does not have to resist a change in its environment, it can just be tolerant to those changes. Highly variable environments put a selective pressure on organisms that are physiologically versatile or tolerant rather than those which have precise adaptations.

When does an environmental change become a stressor and at what point does your stressor switch between being chronic or acute? This may be defined by the intensity, duration, predictability and controllability of the stressor, leading to an assessment of the severity. In addition, stressors, of many kinds and especially in natural environments, can occur in combination, which adds complexity to the understanding of the intensity [3]. Ultimately, if the stress becomes too severe or long-lasting the animal may no longer be capable of maintaining its homeostasis.

The physiological responses to environmental changes/stressors have been grouped into a simplistic primary, secondary and tertiary response model [4]. Primary responses involve the initial neuroendocrine responses, such as the release of catecholamines. Secondary responses involve changes to metabolism and respiration but also involve changes in immune function. Finally, tertiary responses affect the whole animal and include metabolic activity, and overall resistance to disease.

In a previous review we looked at the modulation of teleost immune function by their environment [5]. In the intervening time, researchers have continued to look at how the environment influences immune function. One area that has been increasingly spotlighted has been the impact of climate change and its various facets. Climate change has the potential to deliver a whole range of environmental impacts [6]. These could include temperature changes through perturbation of the climate, salinity changes through variations in fresh or salt-water input, perturbation of acidity due mainly to anthropomorphic pollution inputs and many of these can lead to variations in oxygen capacity or biological availability in water. Consequently, the factors that will be covered in this review include:

1. Temperature
2. Oxygen level
3. Acidity
4. Salinity
5. Particulates

Since the environment is rarely static, animals usually have some level of 'plasticity' in their response to environmental conditions. Genetic variability can differentiate this response within populations, among populations and between species [7]. This plasticity can be seen as acclimation. However, the conditions necessary to trigger an acclimation response will also vary between species. This complicates any attempt to generalize the response across a group of animals as diverse as fish.

New techniques are changing the way that we analyze the response to the environment. The development of transcriptome analysis, using techniques such as next generation sequencing and global gene expression analyses, has opened up the possibility to study the complete shift in genetic expression patterns due to controlled environmental challenges [8]. Another technique that can provide a similar level of detail is the use of microarrays to deliver partial gene expression profiles.

The scope of this review is intended to encompass those natural environmental parameters that can impact immune function, highlighting reports that have been published since our last review.

2. Temperature

Fish are usually considered poikilothermic, or more accurately ectothermic, in that they cannot maintain a constant body temperature against changes in the surrounding environmental temperature since they are reliant on external heat sources. Some species, such as tuna and other members of the suborder Scombroidei, use heat-exchange mechanisms to maintain elevated core temperature to improve swimming efficiency [9].

Short term acute changes in temperature can be compensated for, certainly at a cellular level, by processes such as the heat shock response [10]. However, more subtle chronic temperature changes are less likely to induce such responses and yet may impact the physiology of an organism [11–13]. Yet, there is little published data on the impacts of the rate of temperature change (ramp) directly. One paper investigated growth rates and stress responses under various regimes and found little variation in stress responses and reduced growth in some scenarios [13]. But these reports did not look at the impacts on the immune response.

One of the most common phenomena of the interaction between immune response and environmental temperature has been an increase in the antibody levels with increases in the water temperature. This has been reported in various fish species including; sea bass (*Dicentrarchus labrax*), blue tilapia (*Oreochromis aureus*), olive flounder (*Paralichthys olivaceus*), Atlantic halibut (*Hippoglossus hippoglossus*), ayu (*Pecoglossus altivelis*), Nile tilapia (*Oreochromis niloticus*), Atlantic cod (*Gadus morhua*), and turbot (*Scophthalmus maximus*) [5,14–21]. In the study on turbot, animals were initially acclimated to 16 °C. Then the temperature was raised, at a rate of 3 °C every 48 h, to a range of different temperatures between 16 °C and 28 °C. The authors reported temperature dependent expression changes in lysozyme, IgM, hepcidin and IL-1β [14]. Lysozyme is a common innate immune enzyme involved in the breakdown of the cell walls of gram-positive bacteria [22]. Immunoglobulin-M (IgM) form the predominant class of antibodies found in teleost species [23]. Hepcidins have been identified in more than 20 different teleost species and are associated with both anti-microbial function and iron metabolism [24]. Interleukin-1β is an important mediator of the inflammatory response [25].

A temperature trial on farm raised Atlantic cod involved raising the temperature from 10 °C to 19 °C [26]. They reported elevations in β_2-M, MHC class 1 and IgM-L mRNA when the temperature was raised up to 16 °C. These parameters then fall back to baseline at higher temperatures. Only the levels of IL-1β rose at 19 °C. The study on ayu raised the water temperature from 18 °C to 28 °C and observed increased agglutinating antibody titers against *Flavobacterium psychrophilium* and indicated that elevated water treatments could help induce protective immunity against this pathogen [21].

A recent study on turbot confirmed the importance of temperature as a driver of immunocompetence compared to, in this case, salinity, with increases in IgM levels in liver and kidney in animals exposed to elevated temperatures [27]. A study on *Catla catla* looked at expression of Toll-like and NOD-like receptors at elevated and lowered temperatures and found that expression of TLR2, TLR4