

Seasonal variation and the immune response: A fish perspective

Tim J. Bowden ^{a,*}, Kim D. Thompson ^b, Alison L. Morgan ^b,
Remi M.L. Gratacap ^b, Sami Nikoskelainen ^c

^a *Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, Scotland, UK*

^b *Institute of Aquaculture, University of Stirling, Stirling FK9 4LA, Scotland, UK*

^c *Department of Biochemistry and Food Chemistry, University of Turku, Vatselankatu 2, Turku 20014, Finland*

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Abstract

The environment in which an animal lives affects the physiology and psychology of that animal. The greater the distance from the equator the more profound this influence becomes, as the environment becomes more variable over the years. Temperature, photoperiod, precipitation and other environmental conditions, which are directly or indirectly controlled by the season, can affect an animal. It is becoming apparent that these conditions may impact on the immune system, and this can affect animal health. This review looks at the known mechanisms for transducing environmental cues and how these can affect immune parameters and function. The main focus is fish, especially in relation to aquaculture and the associated disease risks. Work on other animal classes is included for comparison.

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1. Introduction

Short-term environmental impacts on our well being are usually reasonably obvious. Most people prefer the long sunny days of summer to the dark cold days of winter (a Scottish or Finnish summer is usually preferable to a Scottish or Finnish winter). This is especially true if you live at higher latitudes where the annual variation is more pronounced. We talk about seasonal affective disorder (SAD) with a certain degree of humour, yet it is clear that seasonal variations can have a very real impact on our bodies and our psychology [1]. One report discusses the causes of seasonal variation in the number of violent suicides, not very happy reading, but indicative nonetheless [2]. Much of the study in this area has been centred on the effect of photoperiod and temperature on animals in general and it is clear that these factors play a principle role in setting a daily and seasonal cycle by which animals can function. One of the main areas of study is reproduction [3,4]. Understanding the environmental triggers of reproduction in domesticated plant and animal species has allowed us to manipulate those factors so that we may control their reproductive cycle, allowing out-of-season reproduction.

* Corresponding author. Tel.: +44 1224 31 5656.

E-mail address: t.bowden@abdn.ac.uk (T.J. Bowden).

The daily cycles are called circadian rhythms. These are, approximately, 24-h cycles in the physiological processes of living beings including, animals, plants, fungi, and cyanobacteria. The name comes from the Latin ‘circa’ meaning roughly and ‘dies’ meaning day. Strictly speaking circadian rhythms are endogenously generated. However, light and temperature can both modulate this response.

The behaviour and physiology of fish are strongly influenced by light (both seasonal and manipulated) conditions. For example, in winter, post-smolts of Atlantic salmon (*Salmo salar*), exposed to continuous light in 14 m deep-sea cages, maintain a constant swimming speed [5]. However, fish kept under natural photoperiod cease swimming at dusk and are more dispersed during the dark-phase. The reproductive cycle of rainbow trout is controlled by the yearly pattern of photoperiod. Rainbow trout are highly responsive to abrupt changes in day length with combinations of long and short-day signals producing advances and delays in spawning [6].

There are now strong indications that these circadian and seasonal cycles can affect the health of an animal. From a personal viewpoint, we are interested in how such factors affect the immune system of fish and whether we can intervene and control these effects to improve the health of fish at particular times of year. Fish appear to exhibit seasonal fluctuations in their susceptibility to different infectious diseases [7–9]. Whether this is due to increased prevalence of the pathogen, or due to increased susceptibility in the host, is important. For example gilthead sea bream (*Sparus aurata*) cultured in the Mediterranean Sea can be affected by “winter syndrome”. This causes chronic mortalities during the winter months becoming acute as the temperature begins to rise [10]. Cold-water vibriosis as the name suggests is a bacterial disease that is most frequently observed in winter in a variety of cultured species including the salmonids [11]. Fungal pathogens of fish also demonstrate a seasonal pattern of infection [12]. Epizootic ulcerative syndrome (EUS) outbreaks across Asia-Pacific usually occur during the colder seasons of the year when the temperature is below 25 °C. Proliferative Kidney Disease (PKD) is a temperature-dependent parasitic disease of freshwater salmonid fish. Studies have shown that naturally infected fish subsequently held under laboratory conditions developed clinical PKD at 12–18 °C but not at 9 °C [13]. Consequently, water temperature regimes have been used to prevent the occurrence of PKD.

This review looks at environmental factors with a seasonal periodicity that can impact on the immune system, and consequently on health. The review will focus on issues relating to aquaculture species, as this is of particular interest. However, wider issues such as an understanding of how environment, and specifically seasonality, affects psychology, as seen in human subjects, allow us the possibility to extrapolate into species that we can only investigate from an objective standpoint.

2. Seasonality

Many organisms respond to seasonal change physiologically, behaviourally or both. Fish display a strong association to season, especially with regard to their breeding strategies, with young fish often being produced when environmental conditions are most favourable. Thus, seasonality dominates the life cycle of fish. It co-ordinates their reproductive activity, affects body weight and condition, influences food intake and locomotor activity and is also believed to co-ordinate their immune response [14]. All these events are synchronised with seasonal changes in climate (mainly temperature), day length and food supplies [14]. The complex mechanism that allows eurythermal fish to synchronise these events to seasonal change requires the animal to sense physical changes in the environment (e.g. temperature, photoperiod) with a corresponding transduction into molecular signals. This mechanism is not yet completely understood, although it is known that eurythermal fish rely on cues from the external environment to achieve this synchronisation [15]. These cues are often described as “proximate” whilst those that give an animal the greatest chance of survival are described as “ultimate” cues [14]. Although a number of environmental cues have been suggested as possible proximate cues, day length, or photoperiod, has received the most attention. It has been found to be the principle determinant in the sexual maturation of salmonids, bass, the breams, mullet, flatfish, the sciaenids and serriolids [14], which collectively comprise the major intensively farmed species.

Thus, seasonality is a complex event made up of many potential cues, with the principle cues being changes in temperature and day length. The responses of some animals to seasonality are controlled through one of the principle cues or a combination of them both. The secondary cues can be directly related to the principle cues (e.g. water quality, food supply and quality, pollution). Species living in arid or semi-arid habitats, for example, are likely to adapt their life cycle through the cessation of reproduction during periods of water shortage [16]. The magnitude of information

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