Demonstration of herd immunity effects in DNA vaccinated rainbow trout

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Time-course study of the protection induced by an interferon-inducible DNA vaccine against viral haemorrhagic septicemia in rainbow trout
The highly effective DNA vaccines against diseases caused by fish rhabdoviruses in farmed fish consist of a DNA plasmid vector encoding the viral glycoprotein under the control of a constitutive cytomegalovirus promoter (CMV). Among others, attempts to improve efficacy and safety of these DNA vaccines have focused on regulatory elements of plasmid vectors, which play a major role in controlling expression levels of vaccine antigens. Depending on the context, use of a fish-derived promoter with minimal activity in mammalian cells could be preferable. Another aspect related to the CMV promoter is that constitutive expression of the vaccine antigen may lead to rapid elimination of antigen expressing cells in the fish and thereby potentially reduce the long-term effects of the vaccine. In this study, we compared DNA vaccines with the interferon-inducible Mx promoter from rainbow...
trout and the CMV promoter, respectively. Plasmid constructs encoding the enhanced green fluorescent protein (EGFP) were used for the in vitro analysis, whereas DNA vaccines encoding the glycoprotein (G) of the viral haemorrhagic septicaemia virus (VHSV) were applied for the in vivo examination. The in vitro analysis showed that while the DNA vaccine with the CMV promoter constitutively drove the expression of EGFP in both fish and human cell lines, the DNA vaccine with the Mx promoter inducibly enhanced the expression of EGFP in the fish cell line. To address the impact on protection, a time-course model was followed as suggested by Kurath et al. (2006), where vaccinated fish were challenged with VHSV at 2, 8 and 78 weeks post-vaccination (wpv). The DNA vaccine with the CMV promoter protected at all times, while vaccination with the DNA vaccine containing the Mx promoter only protected the fish at 8 wpv. However, following induction with Poly (I:C) one week before the challenge, high protection was also evident at 2 wpv. In conclusion, the results revealed a more fish host dependent activity of the trout Mx promoter compared to the traditionally used cross species-active CMV promoter, but improvements will be needed for its application in DNA vaccines to ensure long term protection.
Use of DNA vaccination for determination of onset of adaptive immunity in rainbow trout fry

Vaccine producers often recommend a minimum size of 5g for vaccination of rainbow trout, but implementation of prophylactic vaccination in smaller sized fish would be an advantage for several infectious diseases. To implement a cost efficient vaccination strategy, it is important to know the duration and nature of the protective immunity induced by the vaccines in the fish. The present work aimed at determination of the smallest size at which specific immunity could be induced in rainbow trout fry by DNA vaccination against viral haemorrhagic septicaemia (VHS). Earlier experiments revealed that intramuscular injection of the DNA vaccine encoding the viral glycoprotein G induced protective immunity to VHS in rainbow trout fry of 0.5g. However, the vaccine is known to induce both innate and adaptive protection. The present work therefore aimed at determination of which type of protection the DNA vaccine induced in such early life stages of rainbow trout. Vaccination trials were performed with fry at average sizes of 0.25 g and 0.5 g respectively and included both the homologous VHSV G-gene vaccine and a heterologous DNA vaccine encoding the G-protein of infectious haematopoietic necrosis virus (IHNV). The fish were challenged by immersion at different times post vaccination. Protective immunity was induced in both sizes of fish, but whereas clear-cut specific protection was evident in the fish vaccinated at 0.5g, the results suggested that the protection in the fish vaccinated at 0.25 g was mainly due to innate cross-reactive antiviral mechanisms of shorter duration. The critical size for induction of an adaptive immune response in rainbow trout to this type of vaccination thus appears to be between 0.25 and 0.5g. This work was supported by the “DAFINET” grant from the Danish Council for Strategic Research.
DNA vaccination of small rainbow trout fry against VHSV

Small rainbow trout fry were DNA vaccinated by intramuscular injection at 0.25g and other fish later at 0.5g. Vaccine groups included pcDNA3-vhsG, heterologous vaccine (pcDNA3-ihnG), empty vector (pcDNA3) and unhandled fish. Fry vaccinated at 0.25g were challenged with VHSV by immersion at 3wpv, 11wpv and 21wpv. The challenge at 3wpv was started 1wpv, however as no mortality was observed, the fish were re-challenged 3wpv using a modified setup. Fry vaccinated at 0.5g were challenged with VHSV by immersion at 1wpv. By early challenge (3wpv) of fish vaccinated at 0.25g both homologous and heterologous vaccines induced unspecific protection (10 % mortality for both). Challenge 11wpv showed waning unspecific protection (60 % mortality) but also a poor specific protection (30 % mortality). By challenge 21wpv, hardly no specific (75 % mortality) or unspecific (81 % mortality) protection was observed. In contrast, fish vaccinated at 0.5 g and challenged at 11wpv showed good specific protection.

The results indicate that DNA vaccination of very small fry (0.25g) can induce an early innate response. However a late adaptive immune response is apparently not established. Vaccination of fry at 0.5g induces an adaptive response like in larger fish.

The experiment was repeated with same vaccination groups. Rainbow trout fry were vaccinated at 0.25g followed by challenge with homologous or heterologous virus at 13 dpv, 11 wpv and 21 wpv. At 13 dpv unspecific protection was induced with both homologous and heterologous challenge (5% mortality). At 11 wpv an unspecific protection with 30 % mortality was observed. At 21 wpv protection against VHSV had dropped further (50 % mortality). Protection against IHNV was better (10 % mortality) but equal for both homologous and heterologous vaccines confirming previous results, that vaccination of fry at 0.25g induces unspecific protection but no adaptive response.

Temperature influences the expression profiling of immune response genes in rainbow trout following DNA vaccination and VHS virus infection

A DNA vaccine encoding the glycoprotein (G) genes of the salmonid rhabdovirus viral haemorrhagic septicaemia virus (VHSV) has proven highly efficient against the disease caused by this virus in rainbow trout (Oncorhynchus mykiss). Several studies have demonstrated that this vaccine induces both an early unspecific antiviral response as well as a long-lasting specific protection. However, temperature appears to influence immune response with respect to the nature and duration of the protective mechanisms. In this study, groups of fish were temperature acclimated, vaccinated and challenged at three different temperatures (5, 10 and 15°C). Tissue and organ samples were collected at numerous time points post vaccination (pv) and post viral challenge (pch). Then, gene expression levels of a two immune genes (Vig-1 and Mx3) involved in unspecific antiviral response mechanisms were determined by Q-PCR. The expression profiles appeared similar for the two genes in terms of temperature dependency with a faster induction and shorter duration at the higher temperature. In order to analyze the temperature effect on the relative expression profiles across a larger set of immune genes time points displaying similar Mx3 expression levels post vaccination were identified: 4 days pv (15°C); 7 days pv (10°C); 23 days pv (5°C), respectively. A targeted trout immune gene array including probes for VHSV genes was used for analysis of vaccinated vs control fish per temperature (4-5 replicates). Temperature altered the transcriptome response to the viral challenge, and the number of responsive genes increased at higher temperature: 51 (5°C), 64 (10°C) and 72 (15°C), respectively, indicating that fish kept at higher temperature may have an enhanced immune response.

Additional correlation analysis allowed identification of genes that were significantly up- or down regulated synchronous with expression of the vaccine G gene. These findings encompass that for example in fish kept at 5°C , putative CD3, CD4, CD9, CD28, CD53, CD63, CD83, CD84 were up regulated, while CD59, CD83 were down regulated, potentially indicating balancing mechanism of the immune system. An experimental VHSV challenge was performed 7 weeks pv. Similar protection levels of approximately 10% mortality were found for the vaccinated fish, regardless of temperature during immunisation and challenge, whereas the course and level of mortality among the controls were temperature dependent. At day 5 post infection, the number of differentially regulated genes in the livers of vaccinated versus control fish was highest in fish kept at 10°C and lowest in fish at 5°C. This difference presumably reflects the temperature dependent progression of the disease in the controls. Further analysis of the obtained data with respect to gene regulation pathways as a result of DNA vaccination and/or viral infection will be presented.
The Protective Mechanisms Induced by a DNA Vaccine in Fish Depend on Temperature

In veterinary vaccinology, DNA-vaccines encoding the viral glycoproteins of viral haemorrhagic septicaemia virus (VHSV) and infectious haematopoietic necrosis virus (IHNV) have proved highly efficient in fish under experimental conditions. In the early phase following vaccination, innate cross-protective mechanisms are dominating but the protection becomes highly specific within 3–4 weeks at 12–15°C. Temperature is known as an important external parameter affecting the immune response in fish and the present study aimed at characterizing temperature effects on the immune response to a VHS DNA vaccine. Rainbow trout fingerlings acclimated at 5, 10 or 15°C, were given an intramuscular injection of 1 μg purified plasmid DNA and challenged with virulent VHSV 9 or 36–40 days later. The vaccine protected the fish well at all three temperatures, however the non-specific mechanisms lasted for a longer period of time at lower temperatures, hereby apparently compensating for a delayed adaptive response. At 36 dpv fish kept at 5°C thus had no detectable response of neutralising antibodies while 67% of the fish kept at 15°C had seroconverted. Immunohistochemical time-course studies of the injection site of vaccinated fish also showed a clear effect of temperature: in fish maintained at 15°C the vhsG-protein occurred earlier on the surface of transfected myocytes than in fish kept at the lower temperatures and the inflammatory response clearing away these myocytes similarly arose earlier at high temperature. Long persistence of transfected myocytes expressing the vaccine antigen might explain the prolonged stimulation of innate protective mechanisms at low temperature. Quantitative gene expression profiles suggested interferon related mechanisms as the explanation for the early protection and also supported their temperature dependent kinetics.
Experimental vaccination of small turbot against bacterial and viral pathogens

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Expression Profiling of Immune Response Genes in Rainbow Trout Following DNA Vaccination and VHS Virus Infection

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N-Linked Glycans on the Viral Glycoprotein are not Required for Induction of Protective Immunity to VHSV when Delivered as a DNA Vaccine

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Protection Against Viral Haemorrhagic Septicemia Virus (VHSV) in Rainbow Trout Using a DNA Vaccine with MX1 Promotor Controlled Expression of the Viral G Protein

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Temperature effects on vaccine induced immunity to viruses in fish

Abstract In poikilothermic vertebrates such as teleost fishes, temperature affects all physiological processes including host-pathogen interactions like immune response and propagation of infection. Whether an infection with a pathogenic virus in fish results in development of clinical disease often depends on the balance between virus multiplication and anti viral immune reactions in the host. Water temperature is one of the most important factors influencing the balance between the fish and its environment. Usually, an optimal immune response of a particular fish species is obtained at its normal summer temperature whereas low temperatures may be immunosuppressive. Although innate and adaptive immune response mechanisms should be considered as integrated parts of the immunodefence, low temperatures appears to affect (inhibit) adaptive mechanisms more than innate mechanisms. This might represent a problem in terms of inducing a protective immune response by vaccination in aquaculture, since it is often desirable to vaccinate fish during autumn, winter, or spring. In experimental vaccination trials with rainbow trout (Oncorhynchus mykiss) using a DNA-vaccine encoding the viral glycoprotein of viral haemorrhagic septicaemia virus (VHSV), non-specific as well as specific immune mechanisms seemed to be delayed at low temperature. At five weeks post vaccination fish kept at 5°C had no detectable response of neutralising antibodies while two thirds of the fish kept at 15°C had sero-converted. While protective immunity was still established at both temperatures, specificity analysis suggested that protection at the lower temperature was mainly due to non-specific innate antiviral mechanisms, which appeared to last longer at low temperature. This was presumably related to a prolonged persistence of the vaccine. In DNA vaccination trials with spring viremia of carp (SVC) in common carp (Cyprinus carpio), protection at low temperature (10°C) appeared to require considerable longer time to develop compared to at 19°C, stressing that determination of optimal vaccination strategies in terms of temperature related effects need to be based on experimental evidence with the actual host and pathogen species rather on general principles.

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Functional demonstration of adaptive immunity in zebrafish using DNA vaccination.

Due to the well characterized genome, overall highly synteny with the human genome and its suitability for functional genomics studies, the zebrafish is considered to be an ideal animal model for basic studies of mechanisms of diseases and immunity in vertebrates including humans. While several studies have documented existence of a classical innate immune response, there is mainly indirect evidence of functional adaptive immunity. To address this aspect, groups of zebrafish were vaccinated with DNA-vaccines against the rhabdoviruses VHSV, IHNV and SVCV. Seven weeks later, the fish were challenged with SVCV by immersion. Despite some variability between replicate aquaria, there was a protective effect of the homologous vaccine and no effect of the heterologous vaccines. The results therefore confirm the existence of not only a well developed but also a fully functional adaptive immune system in zebrafish.

Interference of an ERM-vaccine with a VHS-DNA vaccine in rainbow trout

Simultaneous vaccination of fish against several diseases is often desirable in order to minimise cost and handling of the fish. Intramuscular DNA-vaccination of rainbow trout against viral haemorrhagic septicaemia virus (VHSV) has proved to provide very good protection. However, preliminary results showed that intraperitoneal injection of a commercial vaccine against Enteric Redmouth Disease (ERM) based on formalin-killed bacteria in oil adjuvant immediately followed by intramuscular injection of an experimental DNA-vaccine against VHSV, decreased the protective effect of the DNA-vaccine against challenge with VHSV 11 weeks post vaccination (pv). This experiment was performed with rainbow trout of 30 g injected with 0.5 g VHS-DNA vaccine. The experiment was later repeated with smaller fish (2.5 g) and using two different doses of DNA-vaccine, 1 g and 0.05 g. Both doses provided good protection in the control groups not given the ERM vaccine. But among fish given both vaccines, those vaccinated with the lower DNA dose had significantly higher mortality when challenged with VHSV 9 weeks pv. When challenged with VHSV 8 days pv, not even the 1 µg DNA dose protected such fish. A plasmid dose of 0.05 g VHSV DNA vaccine would normally induce good protection in small fish (2-3 g). To ensure complete protection in larger fish, higher doses are needed. This could explain the negative effect of ERM vaccination observed in the 30 g fish described above. It thus appears, that if the fish are vaccinated with a VHS-DNA vaccine dose according to their size, a simultaneous intraperitoneal vaccination against ERM can compromise the protective effect of the DNA-vaccine. The negative effect appears to be strongest in the early phase following vaccination. The immune mechanisms behind this interference will be discussed.

The protective mechanisms induced by a fish rhabdovirus DNA vaccine depend on temperature

DNA vaccines encoding the viral glycoproteins of viral haemorrhagic septicaemia virus (VHSV) and infectious haematopoietic necrosis Virus (IHNV) have proved highly efficient in rainbow trout (Oncorhynchus mykiss) under experimental conditions. Non-specific as well as specific immune mechanisms seem to be activated. Temperature is an important external parameter affecting the immune response in fish. The present study aimed at determining the
effectiveness of a DNA vaccine against VHS at different temperatures. Rainbow trout fingerlings acclimated at 5 degrees C, 10 degrees C or 15 degrees C, were given an intramuscular injection of 1 microgram purified plasmid DNA and challenged with virulent VHSV 8 or 36-40 days later. The vaccine protected the fish well at all three temperatures, but the involvement of innate and adaptive mechanisms differed: at low temperature, non-specific protection lasted longer and at 36 dpv fish kept at 5 degrees C had no detectable response of neutralizing antibodies while 67% of the fish kept at 15 degrees C had seroconverted. Induction of Mx as measured in liver samples was delayed at 5 degrees C with no detectable response 7 dpv whereas fish maintained at 10 C had significantly elevated levels of Mx3-transcripts at that time point. Immunohistochemical studies of the injection site of vaccinated fish also showed a clear effect of temperature: in fish maintained at 15 degrees C the vhsG-protein appeared earlier on the surface of transfected myocytes and the inflammatory response clearing away these myocytes arose earlier. Compared to fish kept at the lower temperatures of 5 and 10 degrees C.

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THE PROTECTIVE MECHANISMS INDUCED BY A FISH RHABDOVIRUS DNA-VACCINE DEPENDS ON TEMPERATURE
DNA-vaccines encoding the viral glycoproteins of viral haemorrhagic septicaemia virus (VHSV) and infectious haematopoietic necrosis virus (IHNV) have proved highly efficient in rainbow trout (Oncorhynchus mykiss) under experimental conditions. In the early phase following vaccination, innate cross-protective mechanisms are dominating but the protection becomes highly specific within 3-4 weeks at 12-15°C. Temperature is known as an important external parameter affecting the immune response in fish and the present study aimed at characterizing temperature effects on the immune response to a VHS DNA vaccine. Rainbow trout fingerlings acclimated at 5°C, 10°C or 15°C, were given an intramuscular injection of 1g purified plasmid DNA and challenged with virulent VHSV 9 or 36-40 days later. The vaccine protected the fish well at all three temperatures, however the non-specific mechanisms lasted for a longer period of time at lower temperatures, hereby apparently compensating for a delayed adaptive response. At 36 dpv fish kept at 5C thus had no detectable response of neutralising antibodies while 67% of the fish kept at 15C had seroconverted. Immunohistochemical time-course studies of the injection site of vaccinated fish also showed a clear effect of temperature: in fish maintained at 15°C the vhsG-protein occurred earlier on the surface of transfected myocytes than in fish kept at the lower temperatures and the inflammatory response clearing away these myocytes similarly arose earlier at high temperature. Long persistence of transfected myocytes expressing the vaccine antigen might explain the prolonged stimulation of innate protective mechanisms at low temperature. From a practical point of view the results suggest that DNA vaccination against rhabdoviruses might be applied as a prophylactic measure within a broad temperature range.

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**Improved vaccination strategies in marine aquaculture**

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