

Short communication

Detecting molecular adaptation at individual codons in the glycoprotein gene of the geographically diversified infectious hematopoietic necrosis virus, a fish rhabdovirus

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Abstract

Salmonid fishes, the principal hosts of the infectious hematopoietic necrosis virus (IHNV), are a candidate species for aquaculture in many countries. IHNV causes an acute disease resulting in severe economic loss in salmonid fish farming. Previous phylogenetic analyses revealed the existence of multiple genogroups of this virus throughout the geographical range of its host. Here, we report the importance of natural selection in shaping the evolution of certain codons at the surface glycoprotein (G-protein) gene of this virus. Maximum likelihood (ML)-based codon substitution analyses revealed that approximately 2.8% of the codons for the entire G-protein are shown to have higher nonsynonymous substitution per nonsynonymous site (d_n) than the synonymous substitutions per synonymous site (d_s) ($d_n/d_s = \omega > 4.335$). Thus, the data suggest that positive selection ($\omega > 1$) is the major driving force in the evolution of certain codons. However, majority of these positively selected sites cannot be mapped to the regions of antigenic determinants of IHNV. Based on the reports of previous studies, epitopes with positively selected sites are immunodominant and viruses can escape from immune responses by producing antigenic variation at positively selected sites, therefore, vaccines directed against these neutralizing epitopes of IHNV that consist of no positively selected sites will be more effective. Some of the positively selected sites showed radical change in amino acids with respect to their charge and polarity; however, it is unclear how these changes affect the fitness of the virus.

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Infectious hematopoietic necrosis virus (IHNV) of the genus *Novirhabdovirus*, and within the family *Rhabdoviridae* causes an acute disease in salmonid fish and a severe economic loss in the salmonid farming industry (Oshima et al., 1995; Nichol et al., 1995; Troyer and Kurath, 2003). This virus was first identified in western North America (Rucker et al., 1953; Watson et al., 1954; Guenther et al., 1959; Ross et al., 1960; Wolf, 1988), and now has spread to Japan (Kimura and Awakura, 1977; Sano et al., 1977; Yamazaki and Motonishi, 1992), Korea (Park et al., 1993), and many European countries (Baudin-Laurencin, 1987; Bovo et al., 1987; Enzmann et al., 1992; Fichtner et al., 2000; Enzmann et al., 2005; Vardić et al., 2007; Rudakova et

al., 2007). It is likely that IHNV may have been inadvertently spread throughout its host's geographical range in the USA by the historically common practice of salmon transplantations and the widespread use of raw, unpasteurized salmon viscera in feed for salmon fry in hatcheries (Wolf, 1988; Roppel, 1982; Burgner, 1991; Watson et al., 1954). The virus is believed to be spread by the movement of infected eggs and/or fry outside North America (Hill, 1992).

IHNV has a linear single-stranded, negative-sense RNA genome of approximately 11,000 base pairs, and contains six genes representing the nucleocapsid (N), phosphoprotein (P), matrix protein (M), glycoprotein (G), non-virion protein (NV) and RNA-dependent RNA polymerase protein (L) genes, respectively (Kurath et al., 1985; Gilmore and Leong, 1988; Morzunov et al., 1995; Hoffmann et al., 2005). The surface glycoprotein, which carries the neutralizing epitopes (Huang et al., 1994, 1996; Kim et al., 1994), showed relatively high genetic diversity compared to other genes, and therefore has been widely used to

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infer phylogenetic relationships among different IHNV isolates. Recent phylogenetic analyses revealed that multiple genogroups of this virus so far identified are restricted to different geographic regions (e.g., USA, Europe, and Asia) of its host (Kim et al., 2007; Nishizawa et al., 2006; Kurath et al., 2003; Enzmann et al., 2005; Garver et al., 2003; Troyer et al., 2000; Emmenegger et al., 2000; Nichol et al., 1995). Based on the analyses of the mid-G protein region of IHNV, Troyer and Kurath (2003) reported that the relatively high number of synonymous substitutions per synonymous site (ds) relative to the nonsynonymous substitutions per nonsynonymous site (dn) indicates that the vast majority of codons at the surface glycoprotein have experienced purifying selection ($dn/ds = \omega < 1$); however, certain codons within the mid-G protein might have experienced positive selection ($\omega > 1$). Analyzing the pattern of amino acid substitutions would provide insight into an understanding of protein adaptation by

identifying candidate codon sites on which positive Darwinian selection has been operating (e.g., Padhi et al., 2007). Here, we used Yang et al.'s (2000) maximum likelihood (ML)-based codon substitution approach and the single likelihood ancestral counting (SLAC) method (Kosakovsky Pond and Frost, 2005) implemented in the HyPhy web server to identify the putative amino acid sites under positive selection in the complete G-protein of IHNV and to infer whether positive selection has been operating at each amino acid site of the neutralization epitopes of the IHNV G-protein.

A total of 41 complete G-protein sequences, representing different hosts (salmonid fish) and covering wide geographic regions were retrieved from GenBank (Table 1). For selection analyses we reconstructed a ML tree using the appropriate nucleotide substitution model selected by the hierarchical likelihood ratio test (hLRT) implemented in Modeltest version 3.5

Table 1

GenBank accession number, geographic origin, host, year of collection, and sources of the IHNV G-protein sequences used in the present study

Accession number	Strain	Host	Country	Year of isolation	Source
AB250927	ChAb76	Chum salmon	Japan	–	Nishizawa et al. (2006)
AB250928	ChYu78	Chum salmon	Japan	–	Nishizawa et al. (2006)
AB250932	RtNag96	Rainbow trout	Japan	–	Nishizawa et al. (2006)
AB250934	RtTochi86	Rainbow trout	Japan	–	Nishizawa et al. (2006)
AB250935	RtToya80	Rainbow trout	Japan	–	Nishizawa et al. (2006)
AB288204	RtPy91	Rainbow trout	South Korea: Pyeongchang	1991	Kim et al. (2007)
AB288205	RtJe00	Rainbow trout	South Korea: Jecheon	2000	Kim et al. (2007)
AB288206	RtGu01	Rainbow trout	South Korea: Gumi	2001	Kim et al. (2007)
AB288207	RtUi02	Rainbow trout	South Korea: Uiseong	2002	Kim et al. (2007)
AF244128	G4	Rainbow trout	Japan: Gifu prefecture	1992	GenBank
AY331660	Fs8/99	–	Germany	–	GenBank
AY673684	IHNV-PRT	Rainbow trout	Korea	–	GenBank
DQ164099	Auke77	Sockeye salmon	USA	–	GenBank
L40871	193–110	Rainbow trout	USA, ID, Hagerman Valley	1984	Nichol et al. (1995)
L40872	Carson-89	Spring Chinook	USA, WA, Columbia River	1989	Nichol et al. (1995)
L40873	Col-80	Chinook salmon	USA, CA, Sacramento River	1980	Nichol et al. (1995)
L40874	Col-85	Steelhead trout	USA, CA, Sacramento River	1985	Nichol et al. (1995)
L40875	CST-82	Rainbow trout	USA, ID, Hagerman Valley	1982	Nichol et al. (1995)
L40876	HO-7	Steelhead × Rainbow	USA, ID, Hagerman Valley	1984	Nichol et al. (1995)
L40877	LR-73	Fall Chinook	USA, WA, Lewis River	1973	Nichol et al. (1995)
L40878	LR-80	Spring Chinook	USA, WA, Lewis River	1980	Nichol et al. (1995)
L40879	LWS-87	Fall Chinook	USA, WA, Columbia River	1987	Nichol et al. (1995)
L40880	RB-76	Steelhead	USA, OR, Deschutes River	1976	Nichol et al. (1995)
L40881	SRCV	Chinook	USA, CA, Sacramento River	1966	Nichol et al. (1995)
L40882	WRAC	Rainbow	USA, ID, Hagerman Valley	1982	Nichol et al. (1995)
NC_001652	WRACb	Chinook salmon	USA, ID	–	Morzunov et al. (1995)
U15170	RB-76	Rainbow trout	USA	–	Kim et al. (1994)
U50401	Round Butte 1	Rainbow trout	USA	–	GenBank
DQ164100	BLk94	Sockeye salmon	USA	–	GenBank
AB231686	HV7601	–	Japan	–	GenBank
AB250933	AyTochi86	Ayu	Japan	–	Nishizawa et al. (2006)
AY331657	332	–	Germany	–	GenBank
AY331658	Fs13	–	Germany	–	GenBank
AY331659	Fs28	–	Germany	–	GenBank
AY331661	Fs832/94	–	Germany	–	GenBank
AY331662	Fs30/95	–	Germany	–	GenBank
AY331665	FsK/88	–	Germany	–	GenBank
DQ164101	220–90	Rainbow trout	USA	–	GenBank
DQ164102	FR0031	Chinook salmon	USA	–	GenBank
DQ164103	FF030-91	Rainbow trout	USA	1987	GenBank
X73872	Strain K	–	France	–	Gilmore and Leong (1988)

Sequences without host names are all salmonid fishes, but the species names are not available.

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