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Review

Virulence, genomic features, and plasticity of *Aeromonas* salmonicida subsp. salmonicida, the causative agent of fish furunculosis



Stéphanie Dallaire-Dufresne ^{a,b}, Katherine H. Tanaka ^{a,b}, Mélanie V. Trudel ^{a,b}, Andrée Lafaille ^c, Steve J. Charette ^{a,b,d,*}

- ^a Institut de biologie intégrative et des systèmes, Pavillon Charles-Eugène-Marchand, Université Laval, 1030 avenue de la Médecine, Ouebec City, OC, Canada G1V 0A6
- ^b Centre de recherche de l'Institut universitaire de cardiologie et de pneumologie de Québec (Hôpital Laval), 2725 Chemin Sainte-Foy, Quebec City, QC, Canada G1V 4G5
- ^c Faculté de Médecine Vétérinaire, Université de Montréal, 3200 rue Sicotte, St-Hyacinthe, QC, Canada J2S 7C6
- ^d Département de biochimie, de microbiologie et de bio-informatique, Faculté des sciences et de génie, Université Laval, 1045 avenue de la Médecine, Quebec City, QC, Canada G1V 0A6

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ABSTRACT

The bacterium *Aeromonas salmonicida* subsp. *salmonicida* is the causative agent of furunculosis, a systemic disease of fish in the salmonid family. Furunculosis is a ubiquitous disease that affects aquaculture operations worldwide and is characterized by high mortality and morbidity. A better understanding of the bacterium is required to find a cure. Thereby, this review centers on *A. salmonicida* subsp. *salmonicida*, its major virulence factors, and its genome. The classification and characteristics of *A. salmonicida* subsp. *salmonicida*, the virulence factors, such as the A-layer, extracellular molecules, and type three secretion system as well as the characteristics and plasticity of its genome are described.

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^{*} Corresponding author at: Institut de biologie intégrative et des systèmes (IBIS), Pavillon Charles-Eugène-Marchand, 1030 avenue de la Médecine, Université Laval, Quebec City, QC, Canada G1V 0A6. Tel.: +1 418 656 2131x6914; fax: +1 418 656 7176.

E-mail address: steve.charette@bcm.ulaval.ca (S.J. Charette).

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1. Furunculosis

Aquaculture-raised fish are subjected to greater stresses than fish in the wild. The high organic content of the environment, low level in dissolved oxygen, and close proximity of the individuals contribute to increasing the susceptibility of fish to infections (Barton and Iwama, 1991). It is possible for opportunistic pathogens to cause significant economic disruptions under these conditions. The bacterium *Aeromonas salmonicida* subsp. *salmonicida* is the causative agent of furunculosis, a systemic disease of salmonids (salmon, trout, *etc.*) characterized by high mortality and morbidity (landa and Abbott, 2010).

Furunculosis is a complex disease that takes different forms depending on the health, age, and species of fish as well as the environmental conditions, especially temperature (Bernoth, 1997). Furunculosis derives its name from the furuncles or boils that develop on the skin and musculature of fish affected by the sub-acute or chronic form of the disease (Fig. 1) (Austin and Austin, 2007). This form, which usually occurs in older fish, is characterized by darkened skin, melanomas, loss of appetite, lethargy, and bleeding at the base of the fins. The sub-acute or chronic form of the disease has also a slow onset of symptoms and

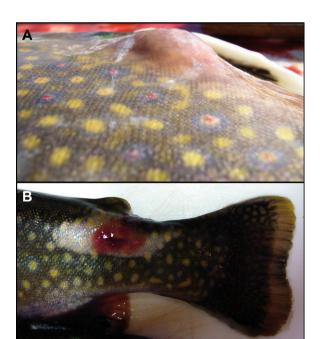


Fig. 1. Clinical manifestations of *A. salmonicida* subsp. *salmonicida* infections. (A) Large furuncle on the surface of an infected fish. (B) The swollen skin lesion or furuncle under the skin is filled with pink fluid containing blood and necrotic tissue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

low mortality. In the acute form, more commonly seen in juvenile salmonids, the disease rapidly leads to septicemia resulting from the formation of necrotic lesions in the skin and bleeding in internal organs. The acute form causes sudden mass death with no evident clinical signs except for darkened skin pigmentation, lethargy, and loss of appetite. These infections are often fatal in two to three days (Boyd et al., 2003; Burr et al., 2005). There is also a latent form, in which the fish are subclinical carriers of the causative agent (Plumb and Hanson, 2011).

The disease occurs in wild and farmed Atlantic salmon and other salmonid species. The infection has a significant impact on wild fish, but the consequences are especially severe in farmed fish in the absence of vaccination (Bergh, 2008). However, efficient vaccines against furunculosis are very expensive and may also cause different side effects (Midtlyng, 1997). In fact, while vaccines are constantly being improved, they still have some limitations and/or complications, depending on the type of vaccine. Immune protection may decrease at low temperatures or over time, the injections may cause health problems and lower fish production and, lastly, there is no guarantee that the disease will not be transmitted after the prophylactic treatment (Cipriano and Austin, 2011).

Furunculosis is a ubiquitous disease that is very common worldwide (Bernoth, 1997). It spreads through contact with infected fish or simply by exposure to water contaminated with *A. salmonicida* subsp. *salmonicida*. Care must thus be taken when adding new individuals to a cohort and when exporting aquaculture products in order to avoid infecting healthy populations.

2. The bacteria

Bacteria of the order *Aeromonadales* are members of the *Gammaproteobacteria* class and make up a single family, the *Aeromonadaceae*, with the genus *Aeromonas* as a model. The 26 species (*Aravena-Roman* et al., 2012) contained in the *Aeromonas* genus are Gram-negative, facultative anaerobic bacilli that include non-motile, motile, mesophilic, and psychrophilic species. While this genus is found in both fresh and saltwater environments, and has been regularly isolated from aquatic animal species, some strains of *Aeromonas* are primary or opportunistic pathogens of humans and other warm-blooded animals as well as poikilotherms (Boone et al., 2001).

A. salmonicida is a non-motile psychrophilic species made up of five subspecies (salmonicida, achromogenes, masoucida, pectinolytica, and smithia) (Boone et al., 2001). A. salmonicida isolates belonging to the salmonicida subspecies (A. salmonicida subsp. salmonicida) are generally considered to be typical strains of A. salmonicida and are associated with systemic infections in salmonids (Burr and Frey, 2007). The four other subspecies, and isolates that cannot be classified in any of the five subspecies,

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