



Bacterial diseases in marine bivalves



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ABSTRACT

Bivalve aquaculture is seriously affected by many bacterial pathogens that cause high losses in hatcheries as well as in natural beds. A number of *Vibrio* species, but also members of the genera *Nocardia* and *Roseovarius*, are considered important pathogens in aquaculture. The present work provides an updated overview of main diseases and implicated bacterial species affecting bivalves. This review focuses on aetiological agents, their diversity and virulence factors, the diagnostic methods available as well as information on the dynamics of the host–parasite relationship.

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1. Introduction

Bacteria play important roles in the marine environment such as nutrient cycling, prey for other species, and influencing host health when in symbiotic relationships (Zilber-Rosenberg and Rosenberg, 2008). Parasitic or pathogenic relationships can govern population dynamics in both wild and farmed populations (Verschuere et al., 2000; Beaz-Hidalgo et al., 2010a; De Schryver and Vadstein, 2014). Bacterial pathogens have impacted marine molluscs for many years and a number of bacterial diseases have recently emerged or re-emerged. For example, *Vibrio coralliilyticus* (initially misidentified as *V. tubiashii*) re-emerged in northeast Pacific oyster hatcheries in 2005 where the bacterium caused catastrophic losses to Pacific oyster larvae (Elston et al., 2008). *Roseovarius crassostreae*, the causative agent of *Roseovarius* Oyster Disease (previously known as Juvenile Oyster Disease), became the first identified pathogen in the abundant marine *Roseobacter* clade (Boettcher et al., 2005). Some pathogens, such as *Nocardia crassostreae*, expanded their known geographic range (into Europe; (Engelsma et al., 2008)) or jumped to a new host (e.g. *N. crassostreae* infections in *Mytilus galloprovincialis* (Carella et al., 2013)).

Repeated episodes of mortality induced by pathogens constitute one of the main impediments to the culture of marine

molluscs. Infectious diseases impact production and can cause high economic losses. Some taxa have been shown to affect all life stages of their hosts, including some of the most prolific pathogens in the genus *Vibrio*. These bacteria infect larval, juvenile and adult molluscs including oysters, mussels, abalones, clams, and scallops (Paillard et al., 2004; Beaz-Hidalgo et al., 2010a). Other bacteria, such as the rickettsia that causes withering syndrome in abalone, are known to be pathogenic for specific hosts but are not associated with catastrophic losses (Friedman et al., 2002a; Friedman and Crosson, 2012; Crosson et al., 2014). The aim of this review is to provide an overview of bacterial taxa that infect marine bivalves, with a focus on groups that are considered most problematic. We provide a summary of aetiological agents, their diversity and virulence factors, diagnostic methods, host–parasite relationships, and future research needs.

In this review we define pathogenic organisms as those that can cause disease when they have successfully colonized a host. Bacterial taxa may contain species or strains within a species that vary from avirulent to virulent. Here we define virulence as a combination of infectivity (the ability to infect) and pathogenicity (the ability to cause disease and mortality in the host upon infection). Virulence results from the cooperation and sequential action of microbial components that can damage a susceptible host, and host responses, which together govern the host–microbe interaction (Casadevall and Pirofski, 2009). The dynamics of this interaction determine the outcome of the infection, including the

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severity of disease and level of mortality, which can be quantified to determine the level of virulence of a given taxon. It is important to recognize that virulence is not an independent microbial property and cannot be defined independently of a host (Casadevall and Pirofski, 2009).

2. Vibriosis

Bacteria within the genus *Vibrio* (Pacini, 1854) are highly abundant in marine waters and have free-living and symbiotic, including pathogenic, life strategies (Thompson et al., 2004). *Vibrio* spp. are rod-shaped, gamma-proteobacteria and include many species that are pathogenic to both terrestrial and marine vertebrates and invertebrates (Paillard et al., 2004; Thompson et al., 2004). A total of 118 species are recognized in this genus, wherein classification and accurate identification are still problematic (Gevers et al., 2005; Hoffmann et al., 2012; Richards et al., 2014a). Bacteria belonging to the *Splendidus* clade, *Harveyi* clade or to the species *V. aestuarianus*, *V. tubiashii*, *V. coralliilyticus*, and *V. tapetis* are commonly reported in association with hatchery or field bivalve mortality events. Unfortunately, these bacteria are often misidentified at the species and/or strain level, and thereby cause confusion regarding specific host–pathogen dynamics.

2.1. *Vibrio splendidus*-related

2.1.1. Etiological agent – initial description

Bacteria belonging to *Splendidus* clade have been repeatedly described in relation to mortality events (Nicolas et al., 1996; Sugumar et al., 1998; Lambert et al., 1999; Lacoste et al., 2001; Waechter et al., 2002; Gay et al., 2004b; Kesarcodi-Watson et al., 2009a; Beaz-Hidalgo et al., 2010b; Saulnier et al., 2010). Epidemiological studies of *Vibrio splendidus*-related strains associated with mollusc mortality outbreaks have demonstrated the importance of, and the high genetic diversity within, this poly-phyletic group (Le Roux et al., 2002, 2004). Such diversity has led to difficulties when classifying organisms within this particular clade (Fig. 1), and many authors have grouped closely related bivalve pathogens as either *V. splendidus* (Nicolas et al., 1996; Lacoste et al., 2001; Kesarcodi-Watson et al., 2009a), *V. splendidus* biovar II (Sugumar et al., 1998; Waechter et al., 2002;

Gomez-Leon et al., 2005) or *V. splendidus*-related (Lambert et al., 1999; Gay et al., 2003; Saulnier et al., 2010) strains. Whether or not these bacteria represent a single species or multiple taxa is difficult to confirm with currently available data.

2.1.2. Etiological agent – diversity

As mentioned above, classification within the *Splendidus* clade is constantly changing and species discrimination may be difficult among the 16 described member species: *V. artaborum* (Dieguez et al., 2011), *V. atlanticus* (Dieguez et al., 2011), *V. celticus* (Beaz-Hidalgo et al., 2010b), *V. chagasii* (Thompson et al., 2003c), *V. crassostreae* (Fauray et al., 2004), *V. cyclitrophicus*, *V. fortis* (Thompson et al., 2003b), *V. gallaecicus* (Beaz-Hidalgo et al., 2009), *V. gigantis* (Le Roux et al., 2005), *V. hemicentroti* (Kim et al., 2013), *V. kanaloae* (Thompson et al., 2003c), *V. lentus* (Macian et al., 2001), *V. pelagius* (Macián et al., 2000), *V. pomeroyi* (Thompson et al., 2003c), *V. splendidus* (Reichalt et al., 1976), *V. toranzoniae* (Lasa et al., 2013), *V. tasmaniensis* (Thompson et al., 2003d). Groups of strains, belonging to the following species can be pathogenic to molluscs: *V. celticus*, *V. crassostreae*, *V. cyclitrophicus*, *V. tasmaniensis* and *V. splendidus* (Guisande et al., 2004; Prado et al., 2005; Saulnier et al., 2010; Vanhove et al., 2014). However, non-virulent strains of these species can also be found.

Given the difficulty of identifying bacteria within the *Splendidus* clade, another and, possibly better, way to describe groups of strains implicated in mortality events may focus on a description of ecological populations, or communities (based on *hsp60* sequences or concatenated sequences of 16S rRNA, *gyrB* and *pyrH*, but also on shared properties such as season of isolation, ecological habitat, and virulence (Hunt et al., 2008; Wendling et al., 2014)). Recent work on a field-based disease study confirmed that a cluster of microdiverse *Vibrio* genotypes belonging to an ecologically cohesive population may drive oyster mortalities (Lemire et al., 2014). High-throughput experimental infection with a large collection of *Vibrio* collected after a field outbreak revealed that the majority of virulent strains (75%) clustered into a subclass of an ecological population containing the *V. crassostreae* type strain (Lemire et al., 2014). *Vibrio crassostreae* was first isolated from diseased *C. gigas* (Fauray et al., 2004), and the type strain LGP7T, as well as many other strains isolated from oysters, were

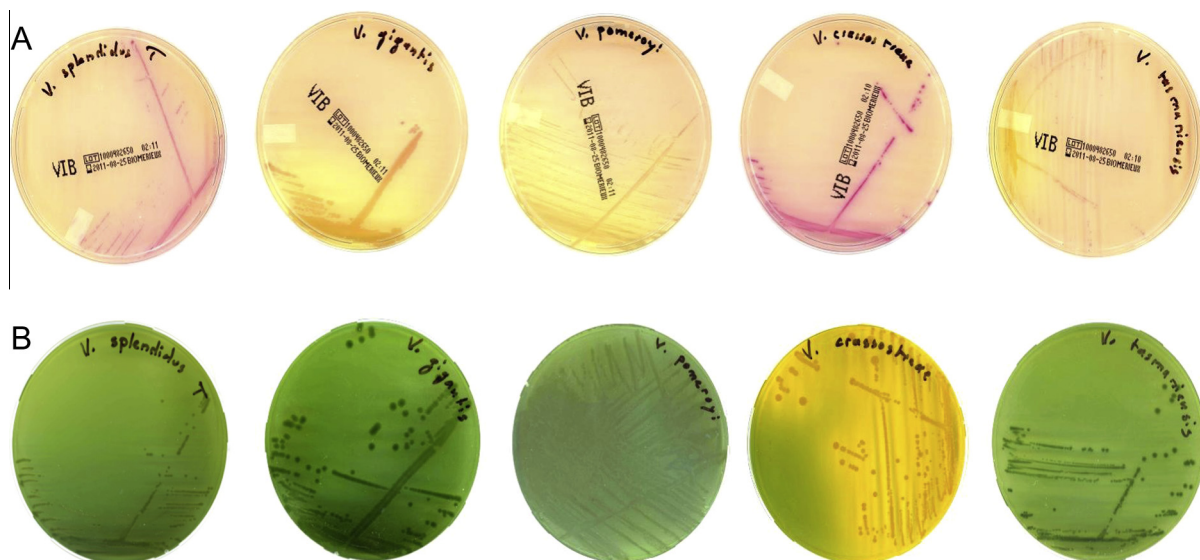


Fig. 1. Phenotypic diversity on (A) ChromAgar and (B) TCBS, of strains belonging to the large *Splendidus* clade and particularly to *V. splendidus*, *V. gigantis*, *V. pomeroyi*, *V. crassostreae*, *V. tasmaniensis* species (P. Haffner).

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