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Minireview

Genetic improvement for disease resistance in oysters: A review

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ABSTRACT

Oyster species suffer from numerous disease outbreaks, often causing high mortality. Because the environment cannot be controlled, genetic improvement for disease resistance to pathogens is an attractive option to reduce their impact on oyster production. We review the literature on selective breeding programs for disease resistance in oyster species, and the impact of triploidy on such resistance. Significant response to selection to improve disease resistance was observed in all studies after two to four generations of selection for *Haplosporidium nelsoni* and *Roseovarius crassostrea* in *Crassostrea virginica*, OsHV-1 in *Crassostrea gigas*, and *Martelia sydneyi* in *Saccostrea glomerata*. Clearly, resistance in these cases was heritable, but most of the studies failed to provide estimates for heritability or genetic correlations with other traits, e.g., between resistance to one disease and another. Generally, it seems breeding for higher resistance to one disease does not confer higher resistance or susceptibility to another disease. For disease resistance in triploid oysters, several studies showed that triploidy confers neither advantage nor disadvantage in survival, e.g., OsHV-1 resistance in *C. gigas*. Other studies showed higher disease resistance of triploids over diploid as observed in *C. virginica* and *S. glomerata*. One indirect mechanism for triploids to avoid disease was to grow faster, thus limiting the span of time when oysters might be exposed to disease.

Contents

1. Introduction

Domestication is the adaptation of a population of plants or animals to rearing by humans through unconscious selection (Price, 1984). In contrast, genetic improvement is the intentional modification of plant or animal populations by humans to better adapt them to their needs (Gallais, 1990). The main goal of selection is then to exploit the genetic variation present for desirable qualities and to accumulate the best genes among individuals, which would be inherited in following generations (Gjedrem and Baranski, 2009).

In all species, plants or animals, selection is carried out on traits of high economic importance, mainly growth rate, yield, quality of

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the product, food conversion efficiency, and resistance to diseases (see Gjedrem, 1983 for review in aquaculture). Selection for disease resistance began very early in crop production whereas for livestock, selective breeding intensified only over the last few decades. Although some negative trade-offs between disease resistance and other economically important traits have been shown, selective breeding continues to be a useful tool to assist in disease control so long as one or more diseases exert a significant influence on livestock production (Stear et al., 2001).

World aquaculture production of fish and shellfish (molluscs and crustaceans) has doubled every decade since the 70s, reaching 67 million tons in 2012 (FAO, 2014). During this expansion, fish and shellfish movements have increased due to higher demand. Non-indigenous species have been introduced widely. Such transfers of live fish and shellfish between countries are known for spreading serious diseases with high economic losses in the industry (Hill, 2002). Striking examples include the appearance of viral hemorrhagic septicemia in European trout (Lorenzen and Olesen, 1997), gill disease in Portuguese oyster (Grizel and Héral, 1991), OsHV-1 oyster virus throughout Europe (EFSA, 2010), and the spread of white spot disease in shrimp farms in Asia (Flegel, 2012).

The threat of disease represents an important limiting factor for the development of aquaculture. By disease, we mean a pathological condition of a part, organ, or system of an organism resulting from various causes, such as infection, genetic defect, or environmental stress, and characterized by an identifiable group of signs or symptoms. Current methods to control or eradicate disease in fish aquaculture are mostly based on medication, vaccination, and disinfection of the facilities, as well as on genetic selection for disease resistance. The last approach offers economic, environmental and ethical advantages (Van Muiswinkel et al., 1999). In molluscs, especially oysters, the main sign of a disease is generally the observation of mortality. Due to their lack of immune memory and the open environment where they are farmed, it is impossible to vaccinate or disinfect. The only available tools to safeguard production are preventing the introduction of infected animals into disease-free environments or to limit pathogen spread, which relies on the surveillance of mollusc farms. But once introduced, the only ways to fight disease are changes in rearing practices or/and selection for resistant populations (Roch, 1999).

Oysters are well suited to selective breeding because of their economic importance, the ease of controlling their biological cycle, their high fecundity, and their high genetic variability (Gosling, 2003). Significant heritability estimates have been found for a wide number of traits in oysters, but most have focused on growth rate. Disease resistance and/or survival represent less than 10% of these estimates (Dégremont, 2003). Disease resistance used to be considered a difficult trait to improve by genetic selection based on low heritability estimates for some fish species (Gjedrem, 1985). But lately, numerous studies have reported moderate to high heritability for disease resistance and/or survival in fish species due to improvements in challenge techniques (Gjerde et al., 2009; Henryon et al., 2005; Johnson et al., 2007; Lillehammer et al., 2013; Ødegård et al., 2007; Taylor et al., 2009), indicating that selective breeding to enhance disease resistance can be successful. In contrast, such estimates for disease resistance are absent for oyster species except for OsHV-1 µvar resistance in *Crassostrea gigas* (Dégremont et al., 2015a,b). Numerous observations of genetic variation for survival in oyster studies have been unaccompanied by disease screening, therefore survival cannot attributed to disease resistance *per se* (Dégremont et al., 2010a; 2007; Evans and Langdon, 2006; Usuki, 2002; Ward et al., 2005).

Oyster populations, wild and cultured, have been affected over the last century by catastrophic mass mortalities, some of these of 'unknown origin,' but numerous cases have been ascribed to epizootics caused by infections agents (Sindermann, 1975). In some cases, the epizootic has caused an oyster industry to collapse and come to a standstill, such as for bonamiosis and marteliosis in *Ostrea edulis* in France (Héral, 1989). In other examples, such as, haplosporidiosis and perkinsosis in *Crassostrea virginica* in the USA (Andrews and Wood, 1967), the industry is recovering after a period of low productivity. Response to epizootics have sometimes been met with the decision to introduce non-native species, as with the introduction of *C. gigas* in France during the 70s following massive mortality of *Crassostrea angulata* from gill disease (Grizel and Héral, 1991). An alternate way to sustain or recover oyster production, as has happened in the Chesapeake Bay, USA (Frank-Lawale et al., 2014), would be selective breeding programs to enhance survival and/or disease resistance, and judicious use of polyploids. In this paper, we review the state of the art on selection programs for disease resistance in oysters, as well as the impact of triploidy on resistance to disease.

2. Summer mortality and ostreid herpesvirus type 1 (OsHV-1) resistance in *C. gigas*

The Pacific oyster, *C. gigas,* is native to the northwest Pacific Ocean and has been introduced to numerous countries worldwide (Ruesink et al., 2005). Estimated production of *C. gigas* in 2012 was about 4.2 million tons (FAO, 2014), although a good part of that may be *C. angulata* in China (Wang et al., 2010). The Pacific oyster is therefore one of the most important species in aquaculture, and mortality regularly affects it.

Summer mortality could be considered one of the main disease threats. These mortalities were reported as early as 1915 in Japan (Takeuchi et al., 1960) and again in the late 1950s in USA (Glude, 1975) and during the early 1980s in France (Maurer et al., 1986). It affects both juveniles and adults, as well as both diploids and triploids (Cheney et al., 2000). Generally, these mortalities have not been explained by a single factor but rather by the combination of several parameters including the environment, rearing techniques, physiological condition, pathogens, and genetic predisposition (Dégremont et al., 2005). Pathogens have been associated with some cases of summer mortality (Elston et al., 1987a; Friedman et al., 1991; Lipovsky and Chew, 1972; Le Roux et al., 2002; Numachi et al., 1965), but in many other cases, no clear association was found (Cheney et al., 2000; Glude, 1975; Koganezawa, 1975; Samain et al., 2007).

The first studies on selective breeding to enhance survival during summer mortality were conducted on the west coast of the USA (Beattie et al., 1980). Their breeding program, realized for three generations, was initially based on challenging adult oysters to elevated temperature (21 °C) in the laboratory, which induced high mortality in adult *C. gigas* (Lipovsky and Chew, 1972). The survivors were then spawned by pair mating, and their offspring challenged with the same laboratory challenge of elevated temperatures. Most of the selected families showed higher survival than the control, indicating that selection was effective for improving resistance to thermal stress, one factor potentially involved with summer mortality. Families were next tested in several commercial grow-out beds with a history of summer mortality problems. Survival on commercial farms was then used as the selection criterion, rather than the laboratory-induced thermal stress. Most of the families of the first and second generations had higher survival than the control (Beattie et al., 1980; Perdue et al., 1981), while all selected families of the third generation showed a significant higher survival (81% on average) in comparison to the control (38%) (Table 1) (Hershberger et al., 1984). Genetic parameters were not estimated, but improvement was evident during summer mortality outbreaks on commercial beds. Additionally, even though the etiology of summer mortality was