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Alteration of host-pathogen interactions in the wake of climate change – Increasing risk for shellfish associated infections?

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ABSTRACT

The potential for climate-related spread of infectious diseases through marine systems has been highlighted in several reports. With this review we want to draw attention to less recognized mechanisms behind vector-borne transmission pathways to humans. We have focused on how the immune systems of edible marine shellfish, the blue mussels and Norway lobsters, are affected by climate related environmental stressors. Future ocean acidification (OA) and warming due to climate change constitute a gradually increasing persistent stress with negative trade-off for many organisms. In addition, the stress of recurrent hypoxia, inducing high levels of bioavailable manganese (Mn) is likely to increase in line with climate change. We summarized that OA, hypoxia and elevated levels of Mn did have an overall negative effect on immunity, in some cases also with synergistic effects. On the other hand, moderate increase in temperature seems to have a stimulating effect on antimicrobial activity and may in a future warming scenario counteract the negative effects. However, rising sea surface temperature and climate events causing high land run-off promote the abundance of naturally occurring pathogenic Vibrio and will in addition, bring enteric pathogens which are circulating in society into coastal waters. Moreover, the observed impairments of the immune defense enhance the persistence and occurrence of pathogens in shellfish. This may increase the risk for direct transmission of pathogens to consumers. It is thus essential that in the wake of climate change, sanitary control of coastal waters and seafood must recognize and adapt to the expected alteration of host-pathogen interactions.

1. Introduction

The ongoing global climate changes are predicted to proceed in the next hundred years (IPCC, 2014). The green-house effect, mainly caused by increasing anthropogenic emission of carbon dioxide (CO₂), will gradually increase the average temperature of the Earth's atmosphere by 1.8–4.0 °C by 2100 and also elevate sea surface temperature (SST). Moreover, absorption of CO_2 by the oceans is influencing seawater chemistry, with a subsequent decrease in pH values and the calcium carbonate (CaCO₃) saturation state (Orr et al., 2005; Doney et al., 2009). Ocean acidification (OA), has already caused a reduction in ocean pH values of about 0.1 units in comparison to pre-industrial levels. A further reduction of approximately 0.4 pH units is predicted for the end of this century (Caldeira and Wickett, 2003; Raven et al., 2005; IPCC, 2014).

Global warming is expected to occur heterogeneously, with high latitudes warming faster than mid-latitudes, and winters warming more than summers (IPCC, 2014). In the Northern hemisphere, changes in the hydrological cycle are assumed to increase precipitation, which will affect coastal salinity and inputs of terrestrial-derived pollutants and nutrients. The surplus of nutrients generates an overload of primary production, exacerbated by increasing water temperatures as a consequence of global warming (IPCC, 2014). This combined with overfishing that causes cascade effects between trophic levels (Frank et al., 2005; Casini et al., 2009; Carstensen et al., 2014) will, in turn, increase the biomass decomposed below the pycnocline. The degradation process creates periods of hypoxia, which is an expanding problem all over the Northern hemisphere (Diaz and Rosenberg, 2008), especially as climate change most likely will strengthen stratification of water masses (Rabalais et al., 2010). As the oxygen saturation of water decreases with increasing temperature, the lower saturation becomes an aggravating stressor for the organisms.

Moreover, during hypoxic periods manganese (Mn) which normally stays oxidized in the bottom sediments, becomes reduced and released into more bioavailable forms. Mn is one of the most abundant metals in soft bottoms of the oceans (Post, 1999) and predominantly bound to the

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sediment in a four-valent colloid state, MnO_2 . During hypoxic periods, lower than 20% of air saturation, the concentration of redox mobilized Mn can increase by a factor of 1000 and reach ~20 mg L⁻¹ (Trefry et al., 1984; Magnusson et al., 1996) in contrast to e.g. Cd, Cu, Pb and Zn, which get more strongly bound during hypoxia (Gerringa, 1991). In 1990, the first observation of Mn precipitation after hypoxic events was reported on gills of Norway lobsters (Baden et al., 1990). After that several investigations have verified bioavailability and accumulation of Mn in marine invertebrates during hypoxia (Baden et al., 1994; Nordahl-Hansen and Bjerregaard, 1995; Baden and Neil, 1998, 2003; Draxler et al., 2005; Magel et al., 2009).

Manganese plays essential roles in many metabolic functions, cellular protection, bone and skeleton mineralization processes and reproductive mechanisms (ATSDR, 2008; Santamaria, 2008). However, it has long been known that humans inhaling high concentrations of Mndust can get a central nervous disruption called manganism, with similarities to Parkinson's disease (Iregren, 1990; Verity, 1999). Marine invertebrates exposed to Mn-concentrations likely to be found in hypoxic bottom waters have manifested significant neurotoxic (Baden and Neil, 1998; Holmes et al., 1999; Sköld et al., 2015), behavioural (Krång and Rosenqvist, 2006) and immunotoxic effects (Hernroth et al., 2004, 2015; Oweson et al., 2006, 2008; Oweson and Hernroth, 2009) as well as disruption of embryonal morphogenesis (Pinsino et al., 2010, 2011).

The future scenario of stressors, directly caused by climate change (increasing SST, decreasing pH; hypercapnia, reduced saturation of carbonate minerals) has shown to be of great importance for the wellbeing of marine organisms and ecosystems (Kroeker et al., 2010, 2013). Meta-analysis of impact of OA and warming revealed decreased survival, calcification, growth, development and abundance, in response to acidification and with enhanced tendency at higher temperatures, but with great differences between taxa (Kroeker et al., 2013). Several additional stress factors will be more common in coastal waters due to indirect effects of climate change such as increased precipitation causing more land run-off (Trenberth, 2011), leading to lower salinity, increased load of colored dissolved organic matter and changes in phytoplankton composition (Harvey et al., 2015). Obviously, the stressors one by one or in combination could impact biota differently depending e.g. on intensity and timing of each stressor, the structure of habitats and adaptation or the life stage of the organisms (Byrne and Przeslawski, 2013; Gunderson et al., 2016), making interpretation of climate impact on ecosystems in future scenarios complex.

For a very large part of the human population the oceans provide the resources needed to have an income and getting the protein needed to stay healthy. As humans are "fishing down the food web" (Pauly et al., 1998; Jackson et al., 2001) the consumption of invertebrates is globally increasing. Impaired immunity of the invertebrates could decrease their fitness and biomass and as well prolong the residence time of pathogens with enhanced risk for transmission to consumers. However, vulnerability and response of marine organisms to climate change are highly variable and there is a considerable lack of knowledge about the impacts on host-pathogen relationships (Burge et al., 2014). During the last decade our research group has gathered data on how different environmental stressors related to climate change (temperature, OA, hypoxia, excess of Mn) affect the immunity of marine bivalves and crustaceans (as illustrated in Fig. 1). In addition, we have conducted both field and laboratory studies of environmental impact (focusing particularly on land run-off and temperature) on prevalence and survival of human pathogens in marine environment. However, subsequent consequences of these climate related stressors on alteration of host-pathogen interactions, and ultimately the risk for transmission of pathogens to human consumers have so far not been compiled. Being aware of all limitations, the present review, based on our own and literature data, will focus on how these direct and indirect stressors caused by climate change, may exacerbate the incidence of human infectious diseases.

2. Impact of environmental stressors on marine invertebrate immunity

2.1. Model organisms

This review has focused on the potential impact of climate change on immunological functions of crustaceans and bivalve mollusks, used for human consumption. The crustacean is here represented by Norway lobster, Nephrops norvegicus (L.), which is distributed all along the eastern coastline of the Atlantic, from Iceland to, and including the Mediterranean Sea. It is a stationary inhabitant of soft bottom sediments where it occupies borrows at depths below the pycnocline. Natural variations in pH of seawater occur with temperature and season but is in borrows even more variable. However, N. norvegicus is known to be relatively pH tolerant and can counteract low pH through stirring activities increasing water circulation (Zhu et al., 2006). The studies on bivalve mollusks have mainly focused on the blue mussel, Mytilus edulis (L.). It is common on hard and sandy bottoms at a broad range of depths (1-10 m) in Northern Atlantic, in the Pacific around Japan but also in the estuarine Baltic Sea. Bivalves are sessile filter feeders and can utilize microorganisms as food resource. Therefore, they constitute a particular risk for transmission of pathogens to human consumers (Wilson and Moore, 1996; Lees, 2000; Potasman et al., 2002; Rehnstam-Holm and Hernroth, 2005).

2.1.1. Invertebrate immunity

With the current discoveries of the wide variety of genes, which are essential in immunity and non-self-recognition (as reviewed by Ghosh et al. (2011)), there is no doubt that invertebrates, although lacking adaptive immunity, are well prepared to face invading pathogens. They are particularly dependent on the immune response (briefly summarized in Table 1) of immunocytes, which in crustaceans and bivalves are called hemocytes. These are developed from proliferating stem cells in the hematopoietic tissue (Hpt), localized as described in Table 1. The Hpt progenitors are further differentiated to different categories of circulating hemocytes. Granulae of lobster hemocytes contain the so called pro-phenol oxidase activating system (ProPO-AS) that through degranulation can be released to act extracellularly. Activation of this zymogen package induces a cascade of reactions including the bactericidal enzyme phenoloxidase, which further catalases the production of toxic quinone intermediates. The end product is melanin which encapsulates the invaders to prevent spreading of the infection (Söderhäll and Cerenius, 1998; Johansson et al., 2000; Cerenius and Söderhäll, 2004; Cerenius et al., 2010). In contrast to the crustaceans the immune defense of bivalve mollusks is not very dependent on ProPO-AS but mainly based on the high capacity of phagocytosis and encapsulation, including central bactericidal mechanisms such as reactive oxygen radicals and lysosomal enzymes (Cheng, 1983; Leippe and Renwrantz, 1988; Pipe, 1990, 1992; Song et al., 2010).

An increasing number of constitutive and inducible antimicrobial peptides (AMPs) have been demonstrated important for immune defense in all phyla (reviewed by e.g. Zasloff, 2002; Yeaman and Yount, 2003). The most prominent groups of crustacean AMPs are the crustins and penaeidins (reviewed by Smith et al. (2008) and Cuthbertson et al. (2002), respectively). However, according to Cerenius et al. (2010) the upregulation of these in response to microbial challenge is limited. In contrast, AMPs seem to play a particular role in the defense of *M. edulis* (Wotton et al., 2003). *M. edulis* has shown to express three different kinds of AMPs; mytilin, mytimicin and defensins (reviewed by Tincu and Taylor (2004)). Recently, mytcin A that previously has been reported from the closely related mussel, *M. galloprovincialis* (Mitta et al., 1999) was found upregulated in gill epithelium of *M. edulis* in response to LPS (Hernroth et al., 2016; Hörnaeus et al., 2016).

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