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EXPERT OPINION

The importance of long-term data collection to understand the historical and evolutionary ecology of marine diseases: the eastern oyster disease system in the USA, as a case study

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The epizootics in eastern oysters, *Crassostrea virginica*, of haplosporidiosis or "MSX" disease caused by *Haplosporidium nelsoni,* and perkinsosis or "dermo" disease caused by *Perkinsus marinus,* were two of the most significant marine disease events of the last century. *Haplosporidium nelsoni*, a protozoan parasite native to Asian populations of the Pacific oyster *Crassostrea gigas*, emerged in Delaware Bay in 1957 and Chesapeake Bay in 1959 (Andrews, 1962; Haskin et al., 1966), and in the decades that followed caused major mortality events from the Mid-Atlantic region of the USA to Atlantic Canada. *Perkinsus marinus* is a native pathogen, also a protozoan, that had always been present in southern US (and Mexican) Atlantic and Gulf waters as far north as the Chesapeake Bay region; it dramatically intensified in its activity and impacts in the mid-1980s, however, causing reduction and loss of oyster populations from the Chesapeake Bay region north to the New England region of the USA as it expanded its range rapidly northward (Burreson and Andrews, 1988; Ford, 1996). The ecological and economic damage caused

by the depletion of oyster resources, disease compounding the effects of more than a century of over-harvesting, produced substantial despair with regard to the future prospects for improvement in *C. virginica* resources. C. Ronald Franks, the Secretary of Natural Resources of the Chesapeake Bay region state of Maryland, USA, included the following words in a statement to the Sub-Committee on Fisheries Conservation, Wildlife and Oceans, of the Committee on Resources, US House of Representatives (October 14, 2003, Annapolis, Maryland, USA; serial no. 108-67):

The oyster diseases Dermo and MSX are a dominant influence, and unless they are substantially controlled--and no evidence suggests that they can be--the trend and the outlook for the native oyster [i.e., C. virginica] is bleak. There is little reason for optimism and even less evidence that we are making any progress in defeating these oyster diseases.

As early as the 1980s, serious consideration was given to introducing *C. gigas* to the Chesa-

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peake Bay, and the states of Maryland and Virginia with the US Army Corps of Engineers came very close to introducing Asian oyster species *Crassostrea ariakensis* to the Chesapeake Bay in the early 2000s (National Research Council, 2004). Around the same time introduction of *C. ariakensis* was being explored, "terraforming" of Chesapeake Bay with disease-resistant, hatchery produced, domesticated lines of native *C. virginica* to "genetically rehabilitate" flawed natural populations was also proposed (Allen et al., 2003). That these potential interventions were appealing to proponents reflected a deep lack of optimism that *C. virginica* populations would ever begin to recover naturally, and this lack of optimism was, at least on the surface, not unfounded: after a half-century of exposure to *H. nelsoni*, and perhaps centuries, if not millennia, of exposure to *P. marinus*, oyster resources were in a worse state than ever. On what basis should there be any hope for improvement by natural processes?

The recent revelation that the 1980s intensification of *P. marinus* was due to the emergence and rapid dispersal of a hypervirulent *P. marinus* phenotype, which hypothetically arose due to alteration of the adaptive landscape for *P. marinus* through the earlier anthropogenic introduction of *H. nelsoni* (Carnegie et al., 2021), brings new perspective to much of this history of oyster diseases. There are important implications for our understanding of the trajectory of *C. virginica* resources; for approaches to their management and restoration; and beyond the *C. virginica-P. marinus* system, for understanding diseases of important marine resource

species world-wide. I describe some of these implications in the paragraphs below.

First, the nadir for *C. virginica* is not exactly what we thought it was. The status of the *C. virginica -P. marinus* relationship between the mid-1980s and the early 2000s did not represent a continuing and deepening failure of the host in its interaction with a long-established pathogen, an assumption behind both the non-native oyster introduction and genetic rehabilitation paradigms that were presented as solutions for the "oyster problem". Rather, it reflected an entirely new interaction between the oyster host and a pathogen that had changed dramatically in its engagement with the host: shortening its life cycle, infecting different tissues, and generally attacking its host far more intensely, and killing its host far more quickly, than it ever had in the past (Carnegie et al., 2021). Clear signs of any evolutionary response by *C. virginica* to this continuing parasitic challenge were absent in those years. Furthermore, physical modeling suggesting lower salinity areas of low infection by both *H. nelsoni* and *P. marinus* were key sources of oyster larval recruitment (North et al., 2005) reinforced earlier suggestions that resistance would be unlikely to develop because of the dominant contributions of low salinity oyster populations with no exposure or adaptation to diseases to reproduction in these systems. We now realise from analyses drawing on long-term monitoring that resistance to *H. nelsoni* was becoming established by the 1990s, if not earlier, even in higher salinity areas of Chesapeake Bay (Carnegie and Burreson, 2011), as it had before in Delaware Bay (Haskin and Ford, 1979). But for *P. marinus*, time, and oyster generations (an oyster generation conceivably being two years, Hedgecock, 1994), would need

to pass before an adaptative response to hyper-virulent *P. marinus* could develop and become widely manifest.

Second, the improvements in oyster populations in recent years should be viewed as at least potentially reflecting resistance and/or tolerance evolution with regard to *P. marinus* compounding the positive effects of increasing resistance to *H. nelsoni*—an adaptive response beginning to be expressed. We know precisely from oyster adaptation to *H. nelsoni* that oyster populations are not functioning in a way that precludes resistance (or tolerance) evolution against *P. marinus*. It is not only oysters in low salinity, disease-free areas that are reproducing; oysters in higher salinity, disease-intense waters must be reproducing as well (Carnegie and Burreson, 2011), and selection should favor those capable of living longer, to greater fecundities, with more opportunities in living longer to pass on genes underlying resistance. Annual surveys indicate that oyster abundance indeed is increasing region-wide (e.g., Maryland Department of Natural Resources, 2018, Southworth and Mann, 2021). While this increase is popularly attributed to success in oyster restoration, particularly the adoption of very large projects conducted at the scale of small tributaries as a preferred strategy, it difficult to imagine a relatively small number of even large restoration projects driving an oyster increase at the vast 300-km scale of the Chesapeake Bay estuary. Other evidence points directly to oyster adaptation, including decreases in oyster mortality despite continued intense *P. marinus* infection pressure that are evident in the long-term monitoring data (e.g., Southworth and Mann, 2021), and indications of increased gonadal area indices

and oocyte densities in *P. marinus-* and *H. nelsoni*-endemic oyster populations in the Virginia part of Chesapeake Bay beginning around 2003 (Huey, 2018). With such signs of oyster adaptation emerging, resource managers should strive to harness this adaptation to greatest effect. Incorporating sanctuaries from harvest, for example, into management paradigms to promote continued adaptation on the part of the oyster should be part of this. However, we should also reconsider the scale of oyster restoration: not just focusing large-scale efforts on a few tributaries at a time, but engaging communities to expand restoration activity as broadly as possible to harness oyster adaptation across the full spatial and geographic extent at which it is occurring.

Finally, the *C. virginica-H. nelsoni-P. marinus* system highlights the importance of long-term monitoring for understanding ecological and evolutionary dynamics in all our disease systems as they play out over decades. This is a point that was made earlier in another recent forum, the ICES Workshop on Emerging Mollusc Pathogens (ICES, 2019), but it deserves mention here too as an area warranting priority attention. Without long-term perspective on key disease metrics such as prevalence and intensity profiles over some degree of space, it is impossible to ascertain patterns of change that could be relevant to control of important diseases. Without additional perspective on relevant host and environmental factors that may be important, such as host abundance or density or demographics, and water temperature, salinity, and so on, it may be difficult to interpret, and construct hypothesis concerning, epizootiological

patterns that may emerge. Yet the lesson of the oyster disease system in the eastern USA is that these relationships are dynamic, and important changes may be occurring that we should understand if we are to successfully manage aquatic diseases as effectively as we must. While it is just not feasible to collect highly granular data across all our important host-pathogen systems wherever they occur, we might envision identifying networks of key populations or sites that can be more intensively evaluated over time; partnering more effectively with fisheries agencies and other resource managers and with commercial interests to pursue and integrate key perspective on host populations; and integrating environmental data collection with oceanographic and meteorological observations at different scales to allow for modelling of system function under changing climate. This will allow the relative roles of environmental drivers of change to be better understood, providing an important backdrop against which evolutionary dynamics might be inferred.

As aquaculture in particular grows in importance as a source of sustenance for growing human populations, and as global change including to marine and freshwater aquatic environments intensifies, we are not expanding efforts fast enough to understand disease dynamics in cultured and wild systems under this dynamic change. In fact, disease surveillance often has eroded relative to activity in the past. The case study of *P. marinus* and *H. nelsoni* in *C. virginica* is useful in underscoring the importance of intensive and long-term disease surveillance, and in providing a template for how we may similarly view other systems.

References

Allen SK, Brumbaugh R and Schulte D (2003). Terraforming Chesapeake Bay. *VA Marine Resource Bulletin* **35(1)**, 2-8.

Andrews JD (1962). Oyster mortality studies in Virginia IV. MSX in James River public seed beds. *Proceedings of the National Shellfish Association* **53**, 65-84.

Burreson EM and Andrews JD (1988). Unusual intensification of Chesapeake Bay oyster diseases during recent drought conditions. Proceedings of the Oceans '88 Conference, Baltimore, Maryland, USA, pp. 799-802.

Carnegie RB and Burreson EM (2011). Declining impact of an introduced pathogen: *Haplosporidium nelsoni* in the oyster *Crassostrea virginica* in Chesapeake Bay. *Marine Ecology Progress Series* **432**, 1-15.

Carnegie RB, Ford SE, Crockett RK, Kingsley-Smith PR, Bienlien LM, Safi LSL, Whitefleet-Smith LA and Burreson EM (2021). A rapid phenotype change in the pathogen *Perkinsus marinus* was associated with a historically significant marine disease emergence in the eastern oyster. *Scientific Reports* **11**, 12872.

Ford SE (1996). Range extension by the oyster parasite *Perkinsus marinus* into the northeastern United States: response to climate change? *Journal of Shellfish Research* **15**, 45-56.

Haskin HH and Ford SE (1979). Development of resistance to *Minchinia nelsoni* (MSX) mortality in laboratory-reared and native oyster stocks in Delaware Bay. *Marine Fisheries Review* **41**, 54-63.

Haskin HH, Stauber LA and Mackin JA (1966).

Minchinia nelsoni n. sp. (Haplosporida, Haplosporidiidae): causative agent of the Delaware Bay oyster epizootic. *Science* **153**, 1414-1416.

Hedgecock D (1994). Does variance in reproductive success limit effective population size of marine organisms? In: Genetics and evolution of aquatic organisms (Beaumont, A. R., ed.). Chapman & Hall, London, pp. 122-134.

Huey LI (2018). Reproductive Investment in *Crassostrea virginica* as an Indicator of a Tolerance Response to *Perkinsus marinus*". *Dissertations, Theses, and Masters Projects,* William & Mary. Paper 1550153640.

ICES (2019) Workshop on Emerging Mollusc Pathogens (WKEMOP). *ICES Scientific Reports* **1**, 57. 19 pp.

Maryland Department of Natural Resources (2018) A stock assessment of the eastern oyster, *Crassostrea virginica*, in the Maryland waters of Chesapeake Bay. 359 pp.

National Research Council (2004). Nonnative Oysters in the Chesapeake Bay. The National Academies Press, Washington, DC, USA. 344 pp.

North EW, Schlag Z, Hood RR, Li M, Zhong L, Gross T and Kennedy VS (2008). Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. *Marine Ecology Progress Series* **359**, 99-115.

Southworth M and Mann R (2021). The status of Virginia's public oyster resource, 2020. Molluscan Ecology Program, Virginia Institute of Marine Science, Gloucester Point, Virginia. 52 pp. See https://scholarworks.wm.edu/reports/2326/.