Journal of Invertebrate Pathology 131 (2015) 212–225

Contents lists available at ScienceDirect

Journal of Invertebrate Pathology

journal homepage: www.elsevier.com/locate/jip

Models of marine molluscan diseases: Trends and challenges

Eric N. Powell [a], Eileen E. Hofmann [b,*]

[a] Gulf Coast Research Laboratory, University of Southern Mississippi, 703 E. Beach Drive, Ocean Springs, MS 39564, United States
[b] Center for Coastal Physical Oceanography, Department of Ocean, Earth and Atmospheric Sciences, 4111 Monarch Way, Old Dominion University, Norfolk, VA 23529, United States

ARTICLE INFO

Article history:
Received 30 June 2015
Revised 29 July 2015
Accepted 30 July 2015
Available online 31 July 2015

Keywords:
Marine disease models
Pathogen proliferation models
Gene-based models
Marine disease transmission models
Marine disease management models

ABSTRACT

Disease effects on host population dynamics and the transmission of pathogens between hosts are two important challenges for understanding how epizootics wax and wane and how disease influences host population dynamics. For the management of marine shellfish resources, marine diseases pose additional challenges in early intervention after the appearance of disease, management of the diseased population to limit a decline in host abundance, and application of measures to restrain that decline once it occurs. Mathematical models provide one approach for quantifying these effects and addressing the competing goals of managing the diseased population versus managing the disease. The majority of models for molluscan diseases fall into three categories distinguished by these competing goals. (1) Models that consider disease effects on the host population tend to focus on pathogen proliferation within the host. Many of the well-known molluscan diseases are pandemic, in that they routinely reach high prevalence rapidly over large geographic expanses, are characterized by transmission that does not depend upon a local source, and exert a significant influence on host population dynamics. Models focused on disease proliferation examine the influence of environmental change on host population metrics and provide a basis to better manage diseased stocks. Such models are readily adapted to questions of fishery management and habitat restoration. (2) Transmission models are designed to understand the mechanisms triggering epizootics, identify factors impeding epizootic development, and evaluate controls on the rate of disease spread over the host's range. Transmission models have been used extensively to study terrestrial diseases, yet little attention has been given to their potential for understanding the epidemiology of marine molluscan diseases. For management of diseases of wild stocks, transmission models open up a range of options, including the application of area management, manipulation of host abundance, and use of scavengers and filter feeders to limit the concentration of infective particles. (3) The details of host population processes and pathogen transmission dynamics are blended in models that evaluate the effects of natural selection and/or genetic modification in developing disease resistance in the host population. Application of gene-based models to marine diseases is only now beginning and represents a promising approach that may provide a mechanistic basis for managing marine diseases and their host populations. Overall disease models remain both uncommon and underutilized in addressing the needs for managing molluscan diseases and their host populations.

1. Introduction

Understanding the transmission of pathogens, the progression of disease epizootics, and the response of host populations are three of the primary challenges limiting the development of informed and effective policies for management of shellfish resources that are affected by disease (Lafferty et al., 2015). Managing and mitigating the effects of disease requires the ability to evaluate outcomes under conditions not yet observed and to understand how observed outcomes came to be. Mathematical models, coupled with experimental and observational studies, provide a quantitative framework for investigation of biological and environmental controls on the disease process, scenario testing, and development of projections and predictions of future states in response to changing biological, environmental, and regulatory conditions.

Unlike models of terrestrial disease, which have been developed for a wide range of organisms and systems (e.g. human, mammalian, lacustrine), models for marine diseases are more limited in the organisms and environments studied, with the majority of models for marine invertebrates being developed for diseases of

---

* Corresponding author.
E-mail address: hofmann@ccpo.odu.edu (E.E. Hofmann).

http://dx.doi.org/10.1016/j.jip.2015.07.017

molluscs, corals, and decapod crustaceans. Molluscan diseases, the focus of this review, have received particular attention due to the keystone position of certain molluscs in marine communities (e.g., Bruno and Bertness, 2001; Gutiérrez et al., 2003), their use as sentinel taxa in ecosystem monitoring (e.g., Kim et al., 2001, 2008), and the widespread importance of molluscs for marine fisheries and aquaculture (e.g., Guo et al., 1999; Lafferty et al., 2015). In the terrestrial realm, disease models frequently have considered host populations without specification of detailed host population dynamics beyond mortality or of the influence of environmental drivers, although spatial interactions between host population centers in simple or complex landscapes have received considerable attention (Dobson and Hudson, 1992; Fenton et al., 2002; Hufnagel et al., 2004; Mundt et al., 2009; Youssef and Scoglio, 2011) and climate cycles have received some notice (Adler et al., 2008). In contrast, models of marine diseases commonly focus on pathogen proliferation in the host once the host is infected, and this is particularly true for models of molluscan diseases. These models simulate the proliferation process as modified by host population processes and environmental conditions; they often include environmental drivers such as temperature, salinity, and host food supply as inputs and permit simulation of host population dynamics with and without disease. In these models, the intensity of infection is a principal metric in addition to host mortality because infected individuals rarely recover and the disease's influence on host population dynamics typically is a function of pathogen infection intensity.

The objectives of this review are to provide an overview of models applied to diseases of marine molluscs and to evaluate the strengths and weaknesses of a range of model applications in population dynamics and epidemiology, the role of climate change in forecasting future trends, resource management, and the management of marine diseases. This overview is organized around models developed for pathogen proliferation, gene-based models of disease resistance, models for management of diseased populations, and those developed for disease transmission. Excluded are simple to complex regression and spatial statistical models that relate environment to observed trends in prevalence or infection intensity or examine pathogen patchiness or population distribution functions (e.g., Powell et al., 1987; White et al., 1989; Jolles et al., 2002; Bottger et al., 2013; Vázquez et al., 2013; Granovitch and Maximovich, 2013).

2. Molluscan pathogen proliferation models

Many diseases of marine molluscs are characterized by high prevalence over large geographic regions, are caused by unicellular pathogens capable of proliferating to high *in vivo* cell density, are strongly influenced by environmental conditions, and are marked by widespread and rapid transmission. The latter characteristic minimizes the importance of transmission in the population dynamics of the diseased host population. The impact of these diseases on the host population is manifested by the intensity of infection and the accompanying increase in mortality and this is influenced most often by environmental and more rarely by population controls on the rate of pathogen proliferation inside the host.

Diseases of this type that have been considered in modeling studies include the oyster diseases MSX (pathogen: *Haplosporidium nelsoni*) and Dermo (pathogen: *Perkinsus marinus*), and the clam disease BRD (pathogen: *Vibrio tapetis*). Models of these diseases have focused on proliferation and consider the host–pathogen system from the standpoint of the host and its population dynamics (Fig. 1). The most common and simplest models subsume the host population and pathogen proliferation dynamics into a mortality term that may be influenced by environmental conditions or simply be described by a time-varying term (solid arrow in Fig. 1). These models will be considered in a later section of this review. More complex models typically relate environmental conditions to host population dynamics in terms of the energy budget (dotted arrow in Fig. 1): specifications normally describe the processes of ingestion, assimilation, respiration, and the division of net production into somatic and reproductive growth. Many of these processes are relatively easily specified because the allometric relationships of most components of the molluscan energy budget and the influence of environmental conditions on these processes tend to be conserved traits across a range of molluscan taxa (e.g., Powell and Stanton, 1985; van der Veer et al., 2006). Challenges routinely involve the two most notably variable

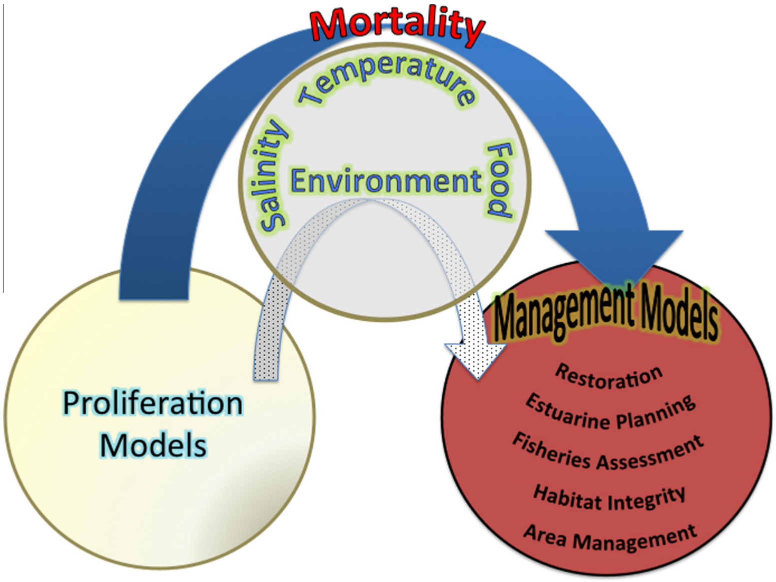

Fig. 1. Proliferation models normally use time series of environmental variables to provide information pertinent to management models associated with sustainable habitat management and habitat restoration and fisheries management, including area management options. The bold arrow shows the common information transfer route in the form of a disease mortality term as the disease increases the mortality rate of the host. The stippled arrow shows the rarer case where the model of the population dynamics of the host and pathogen is specified in detail, directly incorporates time-varying environmental conditions, and is coupled directly to or is used as the management model.