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Review article

The ecology, evolution, impacts and management of host–parasite interactions of marine molluscs

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ABSTRACT

Molluscs are economically and ecologically important components of aquatic ecosystems. In addition to supporting valuable aquaculture and wild-harvest industries, their populations determine the structure of benthic communities, cycling of nutrients, serve as prey resources for higher trophic levels and, in some instances, stabilize shorelines and maintain water quality. This paper reviews existing knowledge of the ecology of host–parasite interactions involving marine molluscs, with a focus on gastropods and bivalves. It considers the ecological and evolutionary impacts of molluscan parasites on their hosts and vice versa, and on the communities and ecosystems in which they are a part, as well as disease management and its ecological impacts. An increasing number of case studies show that disease can have important effects on marine molluscs, their ecological interactions and ecosystem services, at spatial scales from centimeters to thousands of kilometers and timescales ranging from hours to years. In some instances the cascading indirect effects arising from parasitic infection of molluscs extend well beyond the temporal and spatial scales at which molluscs are affected by disease. In addition to the direct effects of molluscan disease, there can be large indirect impacts on marine environments resulting from strategies, such as introduction of non-native species and selective breeding for disease resistance, put in place to manage disease. Much of our understanding of impacts of molluscan diseases on the marine environment has been derived from just a handful of intensively studied marine parasite–host systems, namely gastropod–trematode, cockle–trematode, and oyster–protistan interactions. Understanding molluscan host–parasite dynamics is of growing importance because: (1) expanding aquaculture; (2) current and future climate change; (3) movement of non-native species; and (4) coastal development are modifying molluscan disease dynamics, ultimately leading to complex relationships between diseases and cultivated and natural molluscan populations. Further, in some instances the enhancement or restoration of valued ecosystem services may be contingent on management of molluscan disease. The application of newly emerging molecular tools and remote sensing techniques to the study of molluscan disease will be important in identifying how changes at varying spatial and temporal scales with global change are modifying host–parasite systems.

Contents

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1. Introduction

"Most biological studies, especially in ecology and evolution, have been done on free-livers. That is, the great bulk of our knowledge of biology comes from studying the minority of species!."

[Windsor, 1998]

1.1. Host–parasite ecology

The study of diseases and related epidemiological theory in aquatic, and especially marine ecosystems is relatively new, when compared to terrestrial ecosystems (e.g., Harvell et al., 1999, 2002), and the foundation of a lot of the relevant general ecological theory is derived from our long-standing overlap between human and animal hosts (either hunted or later cultivated) and our need to comprehend related diseases (e.g., Harvell et al., 2002; McCallum et al., 2004).

It took till the 1960s for ecologists, and behavioral and evolutionary biologists to begin to embrace the existing parasite literature and to couch the existing observations more broadly, in terms of mounting ecological and evolutionary hypotheses and theory. As this science on host and parasite interactions in the above perspective grew, the perspective expanded, not just on single species parasite–host systems where the host is in essence the 'habitat' (or island, Kuris et al., 1980; but see Lawton et al., 1981) for the parasite, but an ever increasing vision of higher ecological levels of complexity from individuals to even ecosystems. With this expanding interpretation the perspective also expanded spatially, from a single host as a parasite's 'world' to metapopulations, populations, expanding from meters to kilometers and even greater spatial ranges from continents or oceans to global terrestrial, freshwater, and marine biogeographical provinces (e.g., Lafferty et al., 2005, 2010; Morand and Krasnov, 2010; Poulin et al., 2011; Byers et al., 2014; Hopper et al., 2014; Wood et al., 2015). These patterns have been exacerbated significantly by global parasite and host introductions (e.g., Thieltges et al., 2009; Sorte et al., 2010; Sousa et al., 2014). Furthermore studies across natural (e.g., productivity), and anthropogenic gradients of eutrophication, fishing, and disturbance often suggest strong positive relationships between environmental gradients and parasite abundance (e.g., Johnson and Carpenter, 2008; Morand and Krasnov, 2010; Poulin et al., 2011; Lafferty and Harvell, 2014; Wood et al., 2015).

Since the 1950s and particularly in the early 21st century, marine research on host–parasite interactions, and related diseases, has rapidly advanced in scope. Initially, marine host–parasite ecology was to a large extent generally descriptive. It emphasized parasite and host abundance patterns, without directly addressing more complex and often difficult 'ecology' within- or among-hosts and parasite communities (e.g., Ricklefs, 2010; Lafferty and Harvell, 2014; Lafferty et al., 2015). With time, however, marine research has expanded to address:

(1) The biodiversity of marine parasites and their hosts (e.g., Mouritsen and Poulin, 2002a; Hechinger and Lafferty, 2005; Kim et al., 2005; Lafferty and Harvell, 2014).
(2) The role of parasites in food webs (e.g., Lafferty et al., 2008; Byers, 2009; Sonnenholzner et al., 2011; Dunne et al., 2013; Lafferty, 2013; Thieltges et al., 2013; Lafferty and Harvell, 2014).
(3) The relationship between environment, both current and future (climate change), and parasitism and disease (e.g., Harvell et al., 1999; Kim and Powell, 2009; Soniat et al., 2009; Burge et al., 2014).
(4) The relationship between parasites and disease and other natural and anthropogenic stressors (i.e. hurricanes and