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Does terrestrial epidemiology apply to marine systems?

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Most of epidemiological theory has been developed for terrestrial systems, but the significance of disease in the ocean is now being recognized. However, the extent to which terrestrial epidemiology can be directly transferred to marine systems is uncertain. Many broad types of disease-causing organism occur both on land and in the sea, and it is clear that some emergent disease problems in marine environments are caused by pathogens moving from terrestrial to marine systems. However, marine systems are qualitatively different from terrestrial environments, and these differences affect the application of modelling and management approaches that have been developed for terrestrial systems. Phyla and body plans are more diverse in marine environments and marine organisms have different life histories and probably different disease transmission modes than many of their terrestrial counterparts. Marine populations are typically more open than terrestrial ones, with the potential for long-distance dispersal of larvae. Potentially, this might enable unusually rapid propagation of epidemics in marine systems, and there are several examples of this. Taken together, these differences will require the development of new approaches to modelling and control of infectious disease in the ocean.

Although the importance of PARASITES (see Glossary) in terrestrial ecosystems has long been recognized [1], their role in most marine communities is comparatively unknown [2]. DISEASE-causing organisms can have significant impacts on marine species and communities [2], as demonstrated by recent disease outbreaks that have caused mass mortalities over a wide range of marine taxa, including harbour seals *Phoca vitulina* in Europe [3], Florida manatees *Trichecus manatus* [4], coralline algae [5], kelp [6], seagrasses [7], corals [8], other invertebrates [9–12] and fishes [13,14]. Furthermore, for some important marine taxa, diseases and their impacts appear to have increased over the past 30 years. These include turtles, corals, molluscs, urchins and marine mammals [15].

Knowledge of the ecology of disease on land has been driven by a necessity to understand diseases of humans, crops, farm animals and wildlife. Consequently, most epidemiological theory and management methods are based

Glossary

Disease: a condition of a plant or animal that impairs normal function. A disease has a defined set of signs and symptoms, but is not necessarily caused by a transmissible biological agent. Commonly, however, 'disease' is used as shorthand for 'infectious disease'. We use this shorthand in this paper where it does not lead to ambiguity.
Epidemic: an outbreak of a parasite (usually a microorganism) in a population that increases rapidly, reaches a peak and then declines. The etymology (Greek *demos*: people) leads some authors to restrict the term to pathogen outbreaks in humans, with epizootic used for pathogens of non-human animals and epiphytotic used for pathogens of plants. We use the term to refer to outbreaks in either animals or plants.
Macroparasite: a parasite that should be modelled by considering the parasite burden per host and the frequency distribution of parasites amongst hosts. Usually (but not invariably) multicellular metazoans such as helminths that cannot complete an entire life cycle within one individual host.
Microparasite: a parasite that can be modelled (to a first approximation) by considering hosts to be susceptible, infected or resistant, without using information on the number of parasite individuals per host. Usually (but not always) unicellular microorganisms, such as viruses, bacteria and protozoans that can multiply rapidly within a host.
Modular colonial life forms: organisms whose 'individuals' consist of repeated building blocks (such as polyps), which are derived from asexual (clonal) reproduction, often forming colonies. Such organisms are usually sessile, although limited dispersal can occur following colony fission.
Open: an open population or community is one in which most recruitment comes from external sources.
Parasite: an organism that lives in an intimate and durable association with one host individual of another species per life history stage. It has a detrimental effect on the host. Pathogens, parasitoids and parasitic castrators are subsets of parasites.
Parasitic castrator: a parasite that completely prevents host reproduction, but does not normally kill its host.
Parasitoid: a parasite that kills its host as a necessary part of its development
Pathogen: a disease-causing microorganism that multiplies within its host, generally controlled by the host response.
R_0: basic reproductive parameter of a microparasite model; the number of secondary cases per primary case, when the pathogen is first introduced into a population.
Vector: a mobile organism that transmits a parasite from one host to another.
Vertical transmission: transmission of a parasite from parent to offspring
Virulence: the degree of harm caused by a parasite to an infected host. Sometimes, this concept is confused with transmissibility, which is how easily the parasite spreads between hosts.
Zooxanthellae: photosynthetic mutualistic algae that live within the cells of many invertebrates.

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on medical or veterinary examples [16]. There is a parallel, although less developed theory for plant epidemiology [17], which could have much to contribute to our understanding of marine PATHOGEN dynamics, particularly for sessile colonial hosts, such as corals. Here, we explore the extent to which theory and generalizations that have been developed for terrestrial systems can be applied to marine systems.

The modern theoretical approach to modelling terrestrial EPIDEMICS and determining their impact on host populations was synthesized by Anderson and May [18–21], building from work going back to the beginning of the 20th century [22,23] and even earlier [24]. The basic processes modelled are equally applicable to all host–parasite interactions, whether terrestrial or marine. However, there are major qualitative differences between marine and terrestrial environments, which might have substantial implications for the application of epidemic theory to marine environments. These include:

- Higher taxonomic diversity in marine environments compared with terrestrial ones, both of hosts and parasites;
- Differences in life histories between marine and terrestrial organisms;
- The more open nature of recruitment in marine environments compared with terrestrial ones;
- Differences between terrestrial and marine environments in the modes of parasite transmission;
- Differences in human impacts on marine and terrestrial ecosystems; and
- Differences in potential means of control of infectious diseases in marine and terrestrial environments.

Implications of high diversity in marine environments for host and parasite ecology

The taxonomic, life-history and functional diversity of both hosts and parasites are much greater in marine than in terrestrial environments. Of the 34 animal phyla, only nine are found in terrestrial environments, creating the potential for a more-diverse host–parasite evolutionary milieu in marine environments. In addition, among the phyla present in both habitats, more classes of organism are involved in parasitic relationships in marine than in terrestrial environments ([25], using host range and distribution information from [26]).

In spite of the higher diversity of both hosts and pathogens in marine systems, the range and patterns of host specificity for taxa parasitizing both marine and non-marine hosts appear to be similar. Host specificity varies considerably across stages for parasites with complex multiple-host life cycles and, in general, host specificity is lowest for final hosts and second intermediate hosts.

Differences in life histories between marine and terrestrial systems

For animal hosts, there are three major differences in life histories between terrestrial and marine systems (Table 1) and several differences in transmission and parasitic life styles in the ocean, which have substantial implications for host–parasite dynamics.

Openness and connectivity of marine systems

Perhaps most importantly for the spread of disease, marine populations are often more open than are terrestrial ones (Box 1). Anderson and May [18–21] modelled in the context of closed systems for both parasite and host, but the spatial scale at which populations might be considered closed in marine systems can be different for parasites and hosts [27]. Little attention has been given to how models should be adapted to take this into account. There will be consequences for host–parasite coevolution, as well as host–parasite dynamics, but these are not well understood. For example, it has recently been suggested that parasitism was one of the selective forces leading to the evolution of pelagic larval stages. Parasites are expected to be adapted to the local host genotype [28] and dispersing larval stages with a different genotype arriving into a host population might, therefore, be at a selective advantage [29].

Modular life forms

Among animals, MODULAR COLONIAL LIFE FORMS, such as sponges, corals, bryozoans and ascidians, often form the basis of communities in marine environments, but are completely absent in terrestrial environments (where this role is taken by plants). Functionally, this matters to disease ecology because modular and other clonal species might enable a build-up of more VIRULENT strains, because of the genetic homogeneity of the hosts. Coupled with the relatively rapid evolution of pathogens compared with hosts, this should facilitate the epidemic spread of virulent pathogens. This occurs among clonal terrestrial plants and for farmed animals and plants where genetic variation has been restricted. Sessile organisms are also more apparent and predictable in space. This should also enable higher infection rates than a motile organism will experience for an otherwise similar infectious agent.

Parasitic castrators versus parasitoids

PARASITOIDS are an important natural enemy of insect pests in terrestrial systems [30], but are relatively uncommon in the ocean. PARASITIC CASTRATORS, which are common in the ocean, are similar to parasitoids in that infection of a host reduces its fitness to zero [31]. However, parasitoids remove infected hosts from the population, whereas parasitically castrated hosts remain in the population, potentially to compete with uninfected reproductive hosts [32,33] Compared with parasitoids, parasitic castrators generally parasitize longer lived and larger hosts [31], such as molluscs, decapod crustaceans and echinoderms [33].

There is a well developed body of theory for host–parasitoid population dynamics [34]. In spite of their significance in marine environments, the parallel body of theory for parasitic castrators is not as fully developed, although some models do exist [27,35]. However, standard MICROPARASITE models [20,21] can be modified to model parasitic castrators because a single parasite is usually sufficient to castrate its host [32]. Thus, it is sufficient to characterize a host as being either ‘infected’ or ‘uninfected’. However, the parameter space in which microparasite models are usually investigated is one in

Table 1. Life history characteristics of animal hosts and pathogens in marine versus terrestrial systems

Attribute	Terrestrial	Marine	Implications for marine epidemiology	Refs
Hosts				
Openness of population	Lower	Higher	Buffers local host populations from impact of diseases; facilitates persistence of local diseases; strongly interacts with fisheries management	[27]
Dispersal stage	Usually adult or subadult	Usually eggs or larvae for benthic invertebrates	Host dispersal stages less likely to be infected	[29]
Modular or clonal life forms	Rare	Common	Limited local genetic diversity might lead to locally increased parasitism and patchy transmission	[29]
Parasites and pathogens				
Vertical transmission	Commoner	Rarer	Might increase parasite virulence	None available
Parasitic castration	Rare, but well known for schistosomes	Common in diverse phyla	Might provide infectious control for long-lived hosts; epidemics can occur over longer timescales; might destabilize population dynamics	[32,33,35]
Parasitoids	Common	Rare	Could impact ephemeral marine hosts such as gelatinous zooplankton and algal blooms. Whether other ephemeral marine organisms such as small crustaceans lack this class of natural enemy is unknown	[75]
Vectors	Common	Rarer	Lower searching efficiency, fewer blood-borne pathogens	[41,42]

which infection is of relatively short duration compared with the lifespan of host. Furthermore, these models are usually investigated in cases where the major impact of the pathogen is to increase host mortality rather than to reduce fecundity.

There are major qualitative differences in the dynamics of parasites, which influence fecundity rather than mortality. Most importantly, both coevolutionary [36] and population dynamic arguments [37] suggest that a sterilizing microparasite that does not affect mortality will have a greater effect on its host population than will a parasite that affects only mortality. Therefore, one should expect that parasitic castrators might have particularly severe effects on their host populations, even in cases where the association is relatively old in evolutionary terms. Models of both MACROPARASITES [19] and microparasites [38] show that parasites that reduce fecundity tend to destabilize host dynamics, leading to cyclical behaviour, although this requires further evaluation in the context of open host recruitment (see Box 1).

Box 1. Marine ecosystems as 'open' systems

It has long been dogma that marine systems are 'open', with recruitment uncoupled from local adult density [73]: juvenile or larval stages are frequently highly mobile, with high mortality, whereas adults are often sessile with much lower mortality than the larval stages. At some spatial scale, in any system, it is axiomatic that there must be a relationship, however noisy it might be, between the adult host population size and recruitment to this same population. In marine systems, it has often been argued that the scale at which the population is 'closed' is much larger than in terrestrial systems. Recently, however, it has become clear that, in spite of the potential for long distance dispersal of pelagic larval stages, a high proportion of successful recruits to a population often have originated in that population [29,74]. This is particularly the case in locations where hydrological conditions cause retention of larvae. In such sites, post-settlement density dependent processes might be particularly important in population regulation [29]. Parasitism is one such process.

Modes of transmission

Vertical transmission

VERTICAL TRANSMISSION is important in many terrestrial host–pathogen systems and can have complex effects on the dynamics of the interaction [38]. It is likely to be less important in marine organisms with complex life histories, particularly when small propagules are involved in the host life cycle, simply because it might be difficult for a parasite that infects an adult to also infect a small dispersal stage with a different morphology and physiology. However, mutualists, such as ZOOXANTHELLAE, are often vertically transmitted [39]. Mutualists are similar to parasites in that they have an enduring relationship with one host individual. Given that mutualists are often vertically transmitted, the rarity of known vertical transmission in marine pathogens might merely reflect absence of evidence.

Vectored diseases

Many of the best-known pathogens that cause disease in human and other mammal populations are transmitted by VECTORS [40]. Because vectors increase the efficiency of transmission, particularly from morbid hosts, vector-borne pathogens can evolve to be particularly virulent [41]. Vectored diseases appear to be less common in marine than in terrestrial environments, although this might be due, in part, to the insufficient study of potential marine vectors. However, some have been identified: blood parasites of fishes use leeches and gnathiid isopods [42] as vectors; and fireworms spread an infectious *Vibrio* among corals [43]. Other blood and tissue-feeding micropredators that move from host to host, such as pycnogonids, cymothoid isopods, caligoid copepods, pyramidellid snails and opisthobranch gastropods, merit investigation as potential vectors of marine diseases.

Survival of free-living pathogens and infective stages

Infective stages that persist for extended periods in the environment tend to produce cyclical epidemics [44]. It is

not clear whether, in general, infective stages survive longer in marine or terrestrial environments. Terrestrial bacteria generally do not survive well in marine environments, but estuarine and marine bacteria produce specific compounds that enable growth and metabolism under increased levels of salinity [45]. Other bacteria, including several human pathogens (particularly species within the genus *Vibrio*), can grow and metabolize in the digestive tracts of humans and can also survive for long periods in the marine environment [46].

Rates of epidemic spread in marine and terrestrial systems

Rates of spread of marine epidemics can be higher than those observed for terrestrial pathogens and have led to mass mortalities over vast areas. Examples include the herpes virus that ravaged pilchard populations in the Southern ocean and morbillivirus infections of marine mammals [47]. The only terrestrial counterparts to these rapidly spreading pathogens are the myxomatosis, rabbit calicivirus and West Nile Virus epidemics, all of which were introduced into the area where the epidemic occurred and appear to have flying insect vectors (the vectors responsible for the spread of rabbit calicivirus have not been conclusively identified, but are thought to be flies). Why rates of spread of marine epidemics can be so high is unclear, but it is not merely a result of directional transport in currents. For example, the pilchard epidemics in Australia spread against the prevailing currents [47].

Human impacts and pathogens in marine and terrestrial environments

Reviews of anthropogenic effects on terrestrial and freshwater ecosystems indicate that habitat destruction has the most important impact in terrestrial systems, followed by the impacts of introduced species, overharvesting and eutrophication [48]. In marine environments, overharvesting appears to have the strongest impact, followed by eutrophication and introduced species [49]. Each of these tends to produce different alterations to host–parasite dynamics [50].

Introduced species

Some diseases have been introduced from terrestrial to marine environments (e.g. toxoplasmosis of sea otters [51] and aspergillosis of sea fans [52]) and these sometimes have major impacts on marine populations. The spread of marine exotic species via ballast water and other routes has led to the establishment of many introduced marine pest species, often lacking most of their parasites [53]. There is little evidence, with the possible exception of cholera [46], of introductions of marine diseases to terrestrial habitats. As a generalization, it is likely that models of epidemics in marine systems will need to concentrate more on repeated exogenous inputs than do existing models for terrestrial systems.

Harvesting

Harvesting of wild animals from terrestrial environments is no longer a major source of food for humans, but harvesting from marine environments has increased dramatically over the past 50 years [54] and has reduced populations of many species across the globe [49]. Intensive fishing alters community structure and can have major implications for parasites and pathogens. By decreasing host abundance, fishing will generally reduce transmission rates [27,55] and will thus reduce parasite populations in fished species [56]. Empirical support for this notion is provided by the result that, although disease outbreaks have increased in some taxa of marine organisms since 1970, fishes stand out as having a decreased rate of disease outbreaks [15].

However, fishing might sometimes increase parasite populations [27]. Increased prey and competitor populations might be expected to experience increased transmission and fisheries can spread parasites by returning infected animals that cannot be marketed to places other than where they were caught.

Agriculture and mariculture

In terrestrial environments, the propensity of the high-density populations that are characteristic of agriculture to be subject to disease has been known for many years [57]. For fishes and invertebrates, mariculture similarly provides persistent, stable, high-density populations of hosts, which offers ideal conditions for disease epidemics. Not only has this repeatedly led to the collapse of mariculture operations, but these human-maintained transmission foci act as a source and a reservoir for some infectious agents to spread to wild populations of related organisms. For example, release of viruses from tiger prawn farms has caused high mortality rates in native shrimp populations in the Gulf of Mexico [58].

Pathogen control methods in terrestrial versus marine environments

Endemic infections by parasites and pathogens in farmed or captive terrestrial animals are routinely controlled by chemotherapy, vaccination and breeding for resistance. In addition to these methods, epidemics in farmed animals can also be controlled by broad-scale culling, coupled with quarantine and restrictions on movement [59]. When dealing with epidemics, a standard approach is to use a ring vaccination strategy, in which a control is applied in a ring around the foci of infection. In principle, these same techniques (except for selective breeding) can be, and have been, applied to control of infections in wild terrestrial animals. These technologies cannot be applied in marine habitats other than for mariculture [60] and some fisheries [27], because of the nature of the environment.

The concept of 'herd immunity' is important in the control of epidemics: if a sufficiently high proportion of individuals can be vaccinated, not only are those individuals protected, but the basic reproductive number R_0 of the parasite is reduced to below unity, and it can not invade the 'herd' or population as a whole [61]. Similarly, culling might not only remove infected individuals, but can also reduce the local population density sufficiently so that it falls below the threshold for disease maintenance.

Vaccination and chemotherapy

These techniques for disease control are often used in aquaculture, as they are in terrestrial systems, although aquatic environments can make their use more difficult. For example, spillover of antibiotics from fish pens can lead to low doses of antibiotic being delivered into the wider marine ecosystem, with resulting selection for antibiotic resistance [62]. Vaccination has been used to control rabies in wild foxes in Europe [63], using vaccine in chicken heads, but we know of no attempt to control a pathogen in a wild marine population using vaccination. However, using canine distemper virus vaccine to control morbillivirus infections in seals has been suggested [64].

Culling

Provided transmission is not frequency dependent [65], there is a threshold host density below which parasites and pathogens cannot be maintained in the host population. Culling of wild terrestrial hosts to eradicate disease is widely practiced (e.g. the culling of badgers in the UK and brushtail possums in New Zealand to control bovine TB), although direct evidence that it has been successful is limited [66]. There are some examples where culling has been successful in marine systems. For example, a sabellid polychaete that infested and stimulated shell deformation in abalone and other gastropods was accidentally introduced via aquacultured abalone from its native South Africa to California. Hosts of the most susceptible species and sizes were removed, reducing transmission of the sabellid worms to the surviving gastropods to below the replacement rate until no more infected gastropods were recorded, effectively eliminating the parasite [67].

An approach analogous to culling is for a fishery to 'fish out' a parasite by reducing the host population below the density threshold for parasite persistence. This might be profitable if the host threshold density is higher than the density for maximum sustainable yield [55]. Fishing out a parasite at a local scale is most probable for host–parasite interactions where the parasite has a recruitment system that is relatively closed compared with the open recruitment of its host [27]. For example, in the Alaskan red king crab *Paralithodes camtschatica* fishery, nemertean worms can consume most crab eggs in some areas. Because nemerteans develop rapidly, are probably transmitted locally and king crab larvae disperse widely, fishing king crabs intensively (including females) in certain fjords has the potential to extirpate the nemertean locally [68].

Epidemics in aquaculture are often controlled by the culling of infected populations. However, the increased connectivity of marine ecosystems relative to terrestrial ecosystems means that culling is often less effective at halting epidemic spread.

Novel methods of control for marine systems

The use of cleaning symbionts is a method of parasite control that has been applied in mariculture, but not in terrestrial farming systems. Cleaner fishes have been used effectively to reduce densities of fish lice (caligoid copepods) in penned fish farms [69], and cleaning symbioses are known in terrestrial environments (e.g. oxpeckers). However, we know of no attempts to introduce them deliberately to farmed populations.

For some high-value fisheries, particularly of crabs, lobsters and abalone, fishers might inspect each animal individually at the time of harvest, and make a decision about whether to harvest it or return it to the population. This allows for a range of potential disease management strategies. For example, the tanner (snow) crab fishery is affected by bitter crab disease (a dinoflagellate) [70], which renders the meat unpalatable. Fishers used to discard infected animals, often in places other than where they had been collected, spreading the infection [71]. Implementing a strategy of not discarding infected hosts has the potential to reduce disease spread and impact.

Conclusion

The basic principles of epidemiology remain the same, whether on land or in the ocean. However, a crucial issue that requires urgent consideration is the spatial scale at which host processes occur, compared with those of parasites. Most existing models of terrestrial animal host–parasite interactions do not explicitly include space and, therefore, assume implicitly that host and parasite dynamics occur on similar spatial scales. Plant epidemiological and coevolutionary models usually deal with parasites that disperse more widely and rapidly than do their hosts [72]. Both of these situations can occur in marine systems, but it will often be the case that host dispersal, particularly in the larval stage, occurs more widely than the dispersal of the parasites. Few existing models deal with this context. The consequences for host–parasite coevolution resulting from these differences in life histories between terrestrial and marine environments are also poorly understood, but recent work suggests that they are important. Finally, the differences in human impacts and potential control strategies between land and sea will require a new generation of models to manage disease threats in the ocean.

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