CHAPTER 9

Disease ecology in marine conservation and management

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9.1 Introduction

One of the earliest efforts to describe a marine disease began with dermo, caused by the protist *Perkinsus marinus*, which affects both wild and cultured populations of the oyster *Crassostrea virginica* (described in Mackin 1951; Behringer et al. Chapter 10, this volume). The economic importance of this shellfish, whose populations suffered a precipitous decline from both overharvesting and disease, prompted a conversion from harvesting to farming the oysters, as well as one of the most comprehensive disease studies that is known within the marine disease literature (reviewed in Smolowitz 2013). The study of diseases of wild populations has often lagged behind that of aquacultured species, as culture systems are often simplified and thus easier to study, and finding disease control solutions is motived by direct economic loss associated with disease mortality (Behringer et al. Chapter 10, this volume). While we have learned a great deal about the causal agents, etiologies, and control and treatment of cultured marine organisms, culture systems frequently do not mimic open ocean, or even coastal, environments. As the impacts of emerging marine infectious diseases grow, incorporating disease ecology in management and conservation planning becomes paramount.

This chapter discusses what we currently understand regarding the role of diseases in natural marine communities, how anthropogenic stressors drive changes in the host–pathogen balance, options for disease management, and links between aquaculture and natural systems. We present two case studies examining management approaches that have been successful in reducing the impacts of disease.

9.2 Disease as an ecological component

Disease is a natural component of ecological systems, acting as a driver of population dynamics with the capacity to reshape ecosystems. In the last few decades, an increase in disease has been noted (Wilcox and Gubler 2005), including diseases affecting marine organisms (Ward and Lafferty 2004). An important aspect of the ecology of disease is the determination of whether a disease is part of the natural system, or related to a stressor (or multiple stressors). In disease ecology, the factors underlying disease are depicted with a three-part model; the "host–pathogen–environment" paradigm (Figure 9.1).

Within this model, disease outcomes operate dynamically, where a change in the environment (i.e., a temperature increase) can affect both the host (i.e., immune compromise) and pathogen (i.e., increased virulence). Human activities alter ecosystems and can thus act as drivers of disease in marine ecosystems. Anthropogenic change is often linked to emerging infectious disease (EID) (Daszak et al. 2000). EIDs are diseases that have recently and/or rapidly increased in incidence or geographic range, moved

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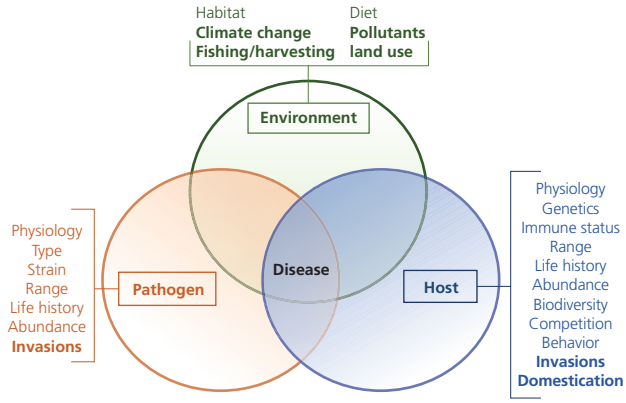

Figure 9.1 Schematic model of the host–pathogen–environment triad of ecological factors to consider in disease management. Factors in bold are those that are linked to anthropogenic activities and, thus, could be easier to control or manage.

into new host populations, or become associated with newly evolved pathogen(s) (Daszak et al. 2000, Burge et al. 2018). Examples of recent marine EIDs include ostreid herpesvirus infections in Pacific oysters (Burge et al. 2018), acroporid serratiosis in *Acropora palmata* (see Box 9.1, Figure 9.2; Burge et al. 2018), and infectious hematopoetic necrosis virus (IHNV) of finfish (Walker and Winton 2010). In the marine environment, disease is often first noted after the system is in an imbalance, characterized by large-scale mass mortalities or increased disease observations (Harvell et al. 1999, Harvell 2019). Increased general disease observations are important but cannot be linked to a specific outbreak without appropriate disease diagnosis, which highlights the need for standardized protocols for disease investigation (Frasca et al. Chapter 11, this volume; Burge et al. 2016b).

To effectively understand the cause of the imbalance in the host–pathogen interaction, the question "*What is normal?*" must first be addressed. Particularly in marine systems, a disease outbreak may occur without knowledge of what constitutes "normal" for the host and its microbiome. For organisms of direct economic importance (i.e., oysters and salmon), an understanding of the normal microbiota associated with an organism may be available, but for species with indirect economic importance (i.e., corals, sea stars), baselines are often not available. Thus, understanding marine disease must begin with determination of "normal" vs "abnormal" (i.e., diseased). If we pause to consider the diversity of ocean habitats, the organisms inhabiting unique niches, and the potential diversity of pathogens that affect them, the lack of understanding of a normal baseline of diseases should not come as a surprise. Often, the first observation of disease will begin with the host organism and/or the population or community to which it belongs. However, first observations must be followed by a consideration of factors across scales, starting at the gene level (i.e., host or pathogen genotype), followed by the cell/tissue affected, the organism, and its population or community, and finally the environment or ecosystem (Burge et al. 2016b). Further, both host and pathogen must be considered across these scales. Though not all diseases will be caused by infectious agents (such as acute domoic acid toxicosis in sea otters; see review in Burge et al. 2016b), the ecological factors contributing to multiple diseases may be similar. A thorough investigation of host and pathogen ecology, including natural history of the host and ecological changes associated with human activities, may be useful for conservation and disease management. Anthropogenic-induced changes can directly (i.e., fishing/harvest or land/habitat use) or indirectly (i.e., climate change; Burge and Hershberger Chapter 5, this volume) impact disease (Burge et al. 2014, Lafferty 2017).

For the host, multiple ecological factors must be considered in conservation and disease management (Figure 9.1; Lafferty 2017). At a basic level, host physiology must be considered. For example, is the

Box 9.1 Acroporid serratiosis: A link between human sewage and coral disease

Acroporid serratiosis, previously known as white pox disease, was first reported in 1996 off Key West, Florida, and has since been observed throughout the Caribbean (Figure 9.2). It exclusively affects the major reef framework-building elkhorn coral *Acropora palmata*, and is characterized by irregularly shaped lesions devoid of tissue, which simultaneously appear on all colony surfaces and progress along the perimeter of lesions at a mean rate of 2.5 cm^2 day^{-1} (Sutherland et al. 2004). It is most prevalent during periods of elevated water temperature. Inoculation experiments, coupled with 16s rDNA sequence analysis and microbiological characterization, identified the human fecal enteric bacterium *Serratia marcescens* as the causal agent, fulfilling Koch's postulates (Patterson et al. 2002). Outbreaks of the disease in 2002 and 2003 were associated with a bacterial strain concurrently found in human sewage. The same strain was also found in the corallivorous snail *Coralliophila abbreviata*, suggesting a possible reservoir and vector of the disease (Sutherland et al. 2011).

The disease was implicated as a principal cause of precipitous decline of *A. palmata* throughout the Florida Keys (87 percent loss between 1996 and 2002; Sutherland et al. 2004), which led to the inclusion of *A. palmata* as a candidate species on the Endangered Species List in 1999 (Diaz-Soltero 1999) and its listing as threatened in 2006 (https://ecos.fws.gov). The severity of impacts of this disease has spurred wastewater management changes in the Florida Keys. While sewage treatment plants in Key West were shown to have high concentrations of *S. marcescens* in raw sewage influent water, effluent did not contain the bacterium, demonstrating the efficacy of upgrades of the sewage treatment facility (Sutherland et al. 2010). However, much of the Florida Keys has been serviced via septic tanks, cesspools, and injection wells, which do not remove bacteria. A growing body of evidence showing the impacts of sewage on this essential reef-building coral and extent of contamination of nearshore waters pressured local authorities to devise a plan to convert to wastewater treatment plants throughout the Keys (USEPA 2013), completed in 2017.

Figure 9.2 Putative acroporid serratiosis (white pox disease) affecting *Acropora palmata* in the Florida Keys. (Photo: J. Porter.)

organism an ectotherm or endotherm? Ectotherms (i.e., organisms unable to thermoregulate), such as invertebrates and most species of fish, are more sensitive to changes in temperature, which may lead to enhanced disease expression—a topic that requires more study. Underlying genetic variability may play a role in disease susceptibility: rare, endangered, or domesticated populations may have limited genetic variation and thus less variation in susceptibility. In domesticated populations, host genetics can be leveraged to manage disease (for example, oysters: see Dègremont et al. 2015), where animals more resistant to infection may reduce infection risk. Additional factors that may be important in disease management include host range, habitat (i.e., environment), competition, behavior, and biodiversity (Morton et al. Chapter 3, this volume). Human activities can also affect the host ecology through domestication and invasions; invasions may occur through both direct human-assisted migration, such as movement of cultured organisms (see Section 9.8), and indirect mechanisms such as climate change or transport in shipping ballast water (Doney et al. 2012; Pagenkopp Lohan et al. Chapter 7, this volume).

Pathogens, and potential pathogens, are part of the normal seascape, and are linked to hosts through food webs (McLaughlin et al. Chapter 2, this volume) and the physical environment (see Section 1). A recent literature review indicates there are approximately 102 marine disease agents with notable ecological and/or economic impacts (25 viruses, 33 bacteria, 23 protists, and 21 metazoans) (Lafferty 2017; Bateman et al. Chapter 1, this volume). This is likely an underestimate of disease-causing agents, as their identification is a lengthy process, infections and disease may be cryptic or covert, and an unknown number of diseases are, as yet, undescribed. Pathogens may exist at a low level within a population, (i.e., they are "covert"), and will be undiscovered until an "overt" infection occurs. Potential pathogens may be a ubiquitous part of the environment as constituent members of communities in soils or sediments, air, or water (fresh, brackish, or sea). Each pathogen type and potential pathogen will have variations in life history and physiology (and may be dependent on host physiology) that dictate its range, abundance, strain, and potential to evolve. Important considerations in pathogen life history which may be targeted by management include: type of transmission (horizontal or vertical); reservoirs or vectors of disease; and transmission dynamics, i.e., whether transmission is host density- or pathogen dose-dependent and/or affected by host behavior. An example of pathogen evolution is horizontal gene transfer of either antibiotic resistance or virulence that may occur in common marine bacteria (which may be virulent or benign, depending on the strain) (Little et al. Chapter 4, this volume). A recent emerging disease of shrimp, acute hepatopancreatic necrosis disease (APHD), is caused by a common bacterial species, *Vibrio parahaemolyticus*, which can also be problematic to human health. *Vibrio parahaemolyticus* contains both a plasmid coding for virulence factors (i.e., a 70-kb plasmid containing *pirAB* toxin genes; Lee et al. 2015) and antibiotic resistance (i.e., pTetB-VA1, a plasmid containing a tetracycline resistance gene; Han et al. 2015). Much like their hosts, pathogens may move or invade new populations in a process called "microbial traffic" (Morse 2004), which can occur through movement of infected hosts, vectors, intermediate hosts, or contaminated equipment. Therefore, direct management strategies may reduce pathogen introduction, including both known disease agents and those that are cryptic. Additionally, understanding pathogen ecology can help in management of a disease agent once it arrives, and in rare cases lead to successful eradication of a disease (see Boxes 9.1 and 9.2 for examples). Research focusing on testing disease management strategies is urgently needed, as few marine diseases have associated management strategies with demonstrated effectiveness.

9.3 The unique marine environment

The world's oceans are three-dimensional, open environments, linked by current patterns which can either create transmission pathways or act as barriers to transmission. Additionally, unlike air, ocean water is a microbial soup, similar in constituency to host tissues. This increases the long-term viability of pathogens in a free-living infectious state, as well as the likelihood of their long-distance transport. This capacity for transport and exchange allows for considerable contact and mixing between communities, via larvae or other mobile life stages. These mobile forms frequently serve as dispersal stages

Box 9.2 Introduction and eradication of a "parasite-like" sabellid polychaete epibiont from California

In the 1990s in California, a tiny (2-mm) introduced sabellid polychaete caused an epidemic in cultured red abalone (*Haliotis rufescens*), resulting in domed, brittle shells and deformed respiratory pores, rendering them unmarketable (Oakes and Fields 1996, Kuris and Culver 1999) (Figure 9.3). Shortly after identification within a culture facility, the sabellid was found in the intertidal zone near the outfall of the same farm (< 100 m of shoreline) within a population of susceptible gastropods (*Chlorostoma* (*Tegula*) spp; Culver and Kuris 2000).

The source of the worms was determined likely to be escaped gastropods and empty abalone shells from the culture facility; transmission from the farm was confirmed by a mark recapture "sentinel" study (Culver and Kuris 2000). Linked with sales of abalone seed, the sabellid was also identified across all commercial facilities and in some public aquariums in California (Moore et al. 2013). Previously unknown, the sabellid was named *Terebrasabella heterouncinata*, and has an unusual life history: upon settling on the host shell (typically as a mobile benthic larva) and producing a mucus sheath, the abalone secretes a nacreous layer over the sabellid, resulting in vertical shell growth (Kuris and Culver 1999). The worm then metamorphoses into its adult form: a hermaphrodite capable of self-fertilization. Transmission studies showed that severe infestations lead to the domed, brittle shells first described by farmers (Kuris and Culver 1999, Moore et al. 2007). Prior to introduction to California, *T. heterouncinata* was unrecognized even in its native habitat of South Africa; the worms likely arrived with a shipment of abalone. Though *T. heterouncinata* does not feed on abalone tissue, the sabellid was determined to be a "parasite-like" epibiont (Kuris and Culver 1999), infecting multiple gastropod species (Culver and Kuris 2004, Moore et al. 2007).

A rapid, coordinated management response among industry, academia, and regulators led to eradication of the sabellid from the infested intertidal zone and the abalone farms. First, a reduction of new infestations in the intertidal zone occurred through installation of screens in the outfall stream of the farm. In 1996, 1.6 million gastropods (primarily *Chlorotoma* spp.) were removed from the intertidal zone, a number based on the threshold host density

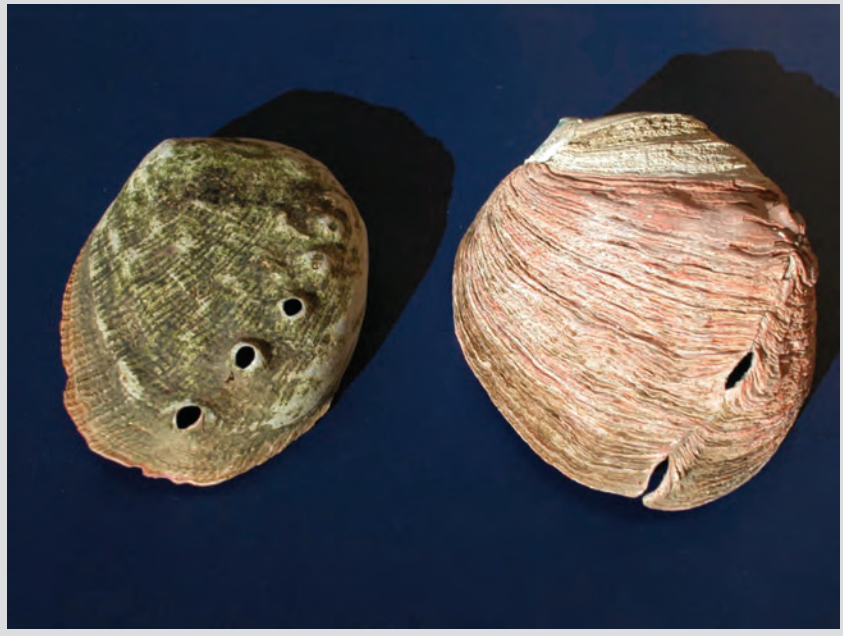

Figure 9.3 Sabellid polychaete disease affecting shell growth of red abalone, *Haliotis rufescens*. (Left) Normal shell; (right) infected shell. (Photo by T. Robbins, California Department of Fish and Game.)

continued

Box 9.2 *Continued*

for transmission (or the Kermack–McKendrick theorem; McKendrick 1940, Stiven 1968) (Culver and Kuris 2000). Early follow-up surveys in 1998 indicated an apparent eradication (Culver and Kuris 2000). These were followed by 9 years of negative findings, indicating eradication of *T. heterouncinata* from the intertidal zone (Moore et al. 2013). Within farms and public aquariums, hygiene practices (i.e., freshwater treatment), first recommended by Culver et al. (1997) and further refined by the California Department of Fish Wildlife (see Moore et al. 2007), were used to eradicate the pest. The last known detection occurred in 2011 (J. Moore, pers. comm.).

for benthic organisms, resulting in large, open populations. Thus, the potential for an infectious disease to become pan-oceanic is far greater than that for terrestrial systems of equivalent size. Lafferty (2017), for example, mentions three scleractinian coral diseases that are global in range: black band disease, caused by a cyanobacterial consortium; bacterial bleaching, associated with multiple species of the ubiquitous marine bacterium *Vibrio* spp.; and white plague, associated with a herpesvirus. Related to this potential for broad geographic range is the possibility for rapid development of epizootics (McCallum et al. 2004; reviewed in Burge et al. 2016b). The 1983–84 Caribbean epizootic of the black-spined sea urchin, *Diadema antillarum*, caused a catastrophic 95 percent reduction in the urchin population throughout its entire range in a matter of weeks (documented in Lessios et al. 1984). While the causal agent of this event was never determined, it resulted in massive and persistent consequences to Caribbean reef systems, many of which shifted from coral-dominated to algae-dominated systems, triggered, in part, by the loss of this dominant herbivore. Twenty years after the epizootic, isolated cases of recovery of urchin populations were recorded in some locations (Edmunds and Carpenter 2001, Miller et al. 2003) but not others (Chiappone et al. 2002).

The influence of marine diseases varies with spatial scale. Large-scale current patterns circulate planktonic larvae, microbes, and parasites across ocean basins, while coastal topography interacting with tidal flow can create localized eddies that can entrain planktonic organisms and restrict water exchange between adjacent communities. The capacity for long-distance dispersal of free-living infectious stages means that infection with a disease may be decoupled from the pathogen source (Lafferty 2017), which poses a challenge for disease management if controlling the source of a pathogen is a desired strategy.

High host density, which is characteristic of many sessile benthic marine communities, is generally associated with higher disease prevalence, as spread of infectious agents between hosts is facilitated by proximity (Lafferty 2004, McCallum et al. 2005, Bruno et al. 2007). This effect may be particularly pronounced if pathogens have a wide host range and can affect multiple species, such as in coral communities, where hosts are sessile and density may be high (Figure 9.4). However, Buck et al. (2017) noted that this general paradigm is not straightforward in its impacts on benthic communities. High host density can actually reduce the risk of infection to individual hosts, providing "safety in numbers." This effect is more pronounced with water-borne pathogens which do not rely on direct transmission. Vectored and vertical transmission are considered more rare in marine systems than in terrestrial (Poulin et al. 2016), though the epidemiology of many diseases has not been fully described.

Diversity in marine organisms takes many forms. For instance, taxonomic diversity of both host and pathogenic agents is higher in marine environments than in their terrestrial counterparts (McCallum et al. 2004). Certain marine pathogens appear able to infect hosts that are taxonomically distant, which can increase their impact on a community. For example, a white syndrome outbreak in Palau in 2005 affected nine scleractinian coral species representing six families. The outbreak, putatively caused by the *Vibrio coralliilyticus* bacterium (Sussman et al. 2008), was localized to a small but diverse patch of corals and resulted in 46 percent mortality

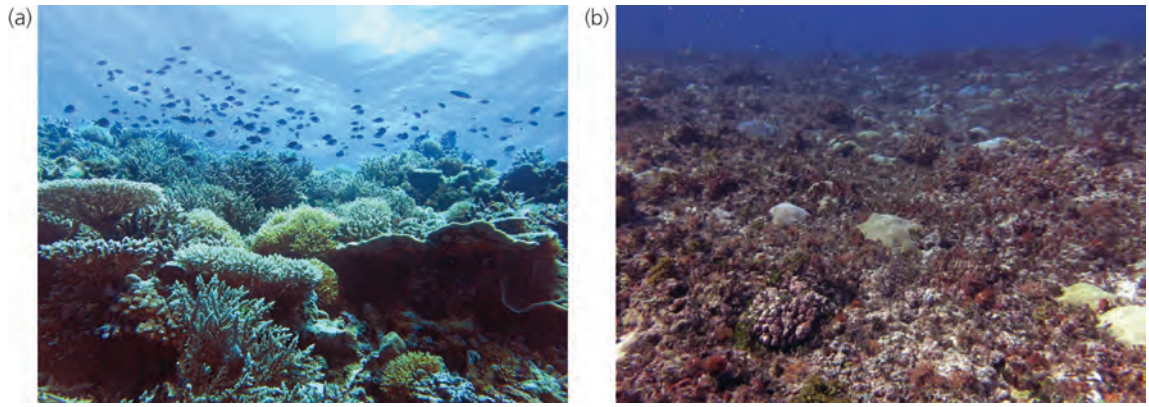

Figure 9.4 High- vs low-density coral reef communities, illustrating high vs low potential for density-dependent pathogen transmission. (A) Tubbataha Reef, Philippines; (B) Rota Island, Micronesia. (Photos by L. Raymundo.)

over a 10-month period. Interestingly, the same bacterium was implicated in white syndrome outbreaks that exclusively targeted *Acropora cytherea* in the Marshall Islands and *Montipora aequituberculata* in the Great Barrier Reef (Sussman et al. 2008). This "plasticity'—the ability of a pathogen to infect a wide range of taxa on one reef during an outbreak, yet target a single species on another reef—is currently poorly understood, but is likely to be influenced by host immune capability, host density, vectors and reservoirs, and environmental drivers (Burge and Hershberger Chapter 5, this volume).

Life-history strategies reflect the complexity and variety of habitat and environmental choices available to marine organisms. Both coloniality and clonality are common, particularly among lower invertebrates (Shields 2017). Coloniality can create large, clonal mega-organisms lacking in genetic diversity but with the capacity to partially die, to then recover by asexually iterating their individual units (zooids, polyps), and to grow indeterminately. Older colonies are generally larger (but not always; see Hughes and Jackson 1980), which increases the probability of contact with pathogens. Thus, coloniality allows an infected host to potentially remain so for a long time, or to become re-infected seasonally, thus continuing to transmit pathogens to surrounding susceptible hosts. Likewise, colony morphology can influence contact with pathogens; highly branched, complex growth forms may entrain water and suspended particles within the colony, increasing the chances of contact with host tissues (Kim and Lasker 1998). These factors require consideration when either modelling disease processes or formulating management strategies for disease outbreaks.

9.4 Environmental drivers and anthropogenic forcing

Marine disease processes are influenced by the environment, which encompasses both natural variability and anthropogenic change (reviewed by Burge et al. 2014). Natural variability in the environment may include connected abiotic (i.e., water quality: Bojko et al. Chapter 6, this volume) and biotic (i.e., food web: McLaughlin et al. Chapter 2, this volume) characteristics that a host and pathogen are exposed to. Disease is thus often seasonal, as specific environmental attributes that vary seasonally lead to disease expression. Water quality includes factors such as temperature, salinity, dissolved oxygen, carbonate chemistry, dissolved and particulate organic material, and nutrients. Temperature is the most understood driver of disease outbreaks, associated with outbreaks in plants, marine invertebrates (abalone, oysters, and corals), fishes, and marine mammals (Burge et al. 2014). Most diseases are linked with warmer summer temperatures. Rarer are the so-called cold-water diseases, such as Denman Island disease, a Pacific oyster disease caused by the microparasite *Mikrocytos mackini*, which needs winter temperatures less than 10°C for three to four consecutive months

for disease outbreaks to occur (Hervio et al. 1996). Similarly, in an analysis of global coral disease prevalence, Ruiz-Moreno found that both warm and cold temperatures are linked to disease outbreaks (Ruiz-Moreno et al. 2012). Anthropogenic nutrient loading has also been associated with increases in coral disease prevalence and severity (Bruno et al. 2003, Redding et al. 2013, Vega-Thurber et al. 2014). Human-induced change often leads to shifts in both abiotic and biotic characteristics of a system, and can act on both a local (i.e., nutrient inputs or other water quality parameters, sedimentation, or overharvesting) and a global or regional level (climate change, weather pattern shifts, ocean acidification).

In an era of rapid change, attributing causation to unknown mass mortalities can be tricky, as both a pathogen and an environmental stressor can contribute to mortality. In reality, some diseases may be multistressor syndromes (i.e., summer mortality syndrome of Pacific oysters), which are typically non-infectious. Such complexity can make both management of symptoms and determination of disease causation difficult. For a presentation of these issues, Frasca et al. (Chapter 11, this volume) discusses diagnostic processes.

When we consider disease management in this era of change, questions related to environmental drivers of disease that may guide future research efforts include (but are not limited to) the following: How do both subtle and drastic changes in environmental parameters influence disease processes? What are tipping points or thresholds of these parameters, and how might they interact with each other to influence disease processes? How is climate change likely to influence marine disease? And finally: Do we currently know enough to predict answers to these questions?

9.5 Consequences for conservation and management

Diseases have emerged as a global threat to the conservation of many species (Altizer et al. 2013), at least partly because environmental conditions altered by human activities have compromised immune defenses or enhanced the virulence of pathogens (Harvell et al. 2009; Harvell and Lamb Chapter 8, this volume). Although diseases may not immediately kill their hosts, they often reduce their fitness by deleteriously affecting fecundity, growth, behavior, and resistance to other climate-driven impacts (Harvell et al. 2009, Wobeser 2013). The need to evaluate the veracity of management practices designed to protect ecosystem health is becoming increasingly urgent, given that diseases often impact habitat-structuring species and are likely to have cascading and indirect impacts on a multitude of associated marine populations.

Disease epizootics have been linked to both anthropogenic (Bojko et al. Chapter 6, this volume) and climatic (Burge and Hershberger Chapter 5, this volume) stressors. For example, numerous studies have associated the passage of intense tropical storms with subsequent elevated levels of disease in organisms as diverse as plants (Irey et al. 2006), sea urchins (Scheibling and Lauzon-Guay 2010), and reef corals (Brandt et al. 2013). Furthermore, marine disease outbreaks are often linked to chronic exposure to pollutants such as sewage (Wear and Thurber 2015), terrestrial sediment or agricultural herbicides (Pollock et al. 2014, Renault 2015), nutrients and fertilizers (Gochfeld et al. 2012, Vega Thurber et al. 2014), and aquaculture (Lafferty et al. 2015). Relationships between marine disease and the multitude of environmental parameters that are influenced by a changing climate and increasing levels of anthropogenic activities are often complex (Altizer et al. 2013). Our understanding of the pathogens that cause most marine diseases is still unclear, particularly when compared to diseases that occur on land. Thus, developing management strategies for marine diseases has often had to occur with little or no knowledge of the causal organism, drawing heavily on experiences from terrestrial systems, which may or may not be appropriate.

9.6 Managing marine disease outbreaks

Managing local stressors more effectively may build disease resistance and resilience to global stressors. However, reducing the effects of escalating disease threats is particularly challenging in marine environments (McCallum et al. 2003, Harvell et al. 2009, Altizer et al. 2013). Managers confronted with controlling terrestrial disease outbreaks have multiple tools available, such as vaccination, quarantine, and culling, to restrict contact between healthy and infected individuals, biological and chemical

controls, elimination or regulation of vectors, and genetic breeding for disease resistance or tolerance (Daszak et al. 2000). However, inherent difficulties associated with executing such disease control methods in fluid environments limit their applicability for marine species (McCallum et al. 2003). There is an increasingly critical need to apply ecological theory to practical management solutions for alleviating disease impacts on marine populations. In Table 9.1, we present examples from the available literature of tools that have been tested to incorporate disease ecology in marine conservation and management strategies. The potential role of managing food webs (McLaughlin et al. Chapter 2, this volume) to control disease outbreaks has not been investigated (hence, there is no reference to this in Table 9.1). This suggests a line of future research that could result in an additional management tool for diseases and parasitic infections for which vectors, reservoirs, or causal agents are known.

Table 9.1 Examples of tools that have been tested to incorporate disease ecology in marine conservation and management strategies.

Taxa affected	Diseases	Causative agent(s)	Management strategy examined	References
Corals	Black band disease	Cyanobacteria-based consortium	Stopping progression of band disease in corals with epoxy plugs	Aeby et al. 2015
Shellfish, salmon	Various	Bacteria, viruses, parasites	Using benthic filter feeders to "clean" water and reduce pathogen load	Reviewed in Burge et al. 2016a, Lamb et al. 2017
Corals	White syndromes Skeletal eroding band Brown band disease	*Vibrio* spp. and others Halofolliculinid ciliate *Porpostoma* ciliates	Establishment of marine protected areas and reserves	Raymundo et al. 2009, Page et al. 2009, Lamb et al. 2015, 2016
Corals, sea turtles	White syndromes Skeletal eroding band Brown band disease (corals)	*Vibrio* spp. and others Halofolliculinid ciliate *Porpostoma* ciliates	Reducing physical injury from human activities—including fishing gear, concentrating tourism, ship groundings	Lamb and Willis 2011, Lamb et al. 2014, 2015, 2016, Work et al. 2015, Raymundo et al. 2018
Shrimp, fish	AHPND	*Vibrio parahaemolyticus*	Biological control	Reviewed in Shields 2017
Shrimp	TSV MSGS IHHNV	Virus Unknown Virus	Selective breeding for resistance; specific pathogen-free stocks	Thitamadee et al. 2016, reviewed in Shields 2017
Shellfish	Various	Various	Culling	Elston and Ford 2011, reviewed in Shields 2017
Shrimp	WSSV, TSV, YHV	Viruses	Vaccination	Reviewed in Shields 2017
Bivalves, crustaceans	Various	Various	Quarantine	Reviewed in Shields 2017
Shrimp	Viral diseases	Viral pathogens	Elimination of vector species in culture	Thitamadee et al. 2016
Shrimp	WSSV, YHV, TSV	Viral pathogens	Increasing biosecurity monitoring and surveillance	Flegel 2012, reviewed in Shields 2017
Corals	White syndromes	*Vibrio* spp. and others	Increasing forecasting and predictive power using satellite imagery—temperature, sediment exposure, plastic waste from terrestrial sources	Maynard et al. 2011, 2015a, 2016, Pollock et al. 2014, Lamb et al. 2016, 2018
Corals	Serratiosis	*Serratia marcescens* bacterium	Improving sewage treatment and waste water discharge	Sutherland et al. 2010, Sutherland et al. 2011

(continued)

Table 9.1 Continued

Taxa affected	Diseases	Causative agent(s)	Management strategy examined	References
Corals	Bacterial diseases	Bacterial pathogens	Probiotics	Teplitsky and Ritchie 2009
Corals, lobsters	White syndromes	Bacterial pathogens	Disease surveillance, monitoring	Maynard et al. 2011, Shields 2017
Corals	Black band disease	Cyanobacteria-based consortium	Rapid pathogen tests	Discussed in Pollock et al. 2011
Abalone, oysters, shrimp	Abalone herpesvirus, oyster dermo, shrimp AHPND	*Perkinsus marinus; Vibrio parahaemolyticus*	Improving health certification protocols for transported animals	Thitamadee et al. 2016
Corals	Bacterial bleaching	*Vibrio coralliilyticus*	Phage therapy	Efrony et al. 2007, Teplitsky and Ritchie 2009
Corals	Florida Reef Tract white disease	Unknown, possible bacterium	*In-situ* chiseled trench in skeleton behind disease progression front, amoxicillin, amoxicillin + trenching	Neely and Lewis 2018
Corals	Florida Reef Tract white disease	Unknown, possible bacterium	UV radiation applied to lesions	Enochs and Kolodziej 2018
Corals	Florida Reef Tract white disease	Unknown, possible bacterium	*Ex-situ* testing of antibiotics, chlorine with various barriers (epoxy, clay), with and without trenching	Neely 2018

9.7 Managing human impacts on natural systems

Terrestrial disease management strategies are not necessarily directly transferrable to the marine environment. Marine disease control is challenging due to the fluidity of open ocean systems; options such as quarantine, culling, and vaccination are not viable in most situations. Thus, diseases affecting marine communities require the development of innovative approaches and novel tools that integrate marine and terrestrial management areas. In this section, we discuss three promising strategies for the management of marine diseases: the use of marine protected areas, the development of early warning systems for disease outbreaks, and the use of natural systems as pathogen "filters."

9.7.1 Marine protected areas and spatial management

Tissue damage has been shown to promote disease development by providing a site for pathogen invasion in many taxonomic groups, including humans and megafauna (Wobeser 2013), insects (Ferrandon et al. 2007), plants and trees (Underwood 2012), fishes (Austin and Austin 2007), and marine invertebrates such as sponges and corals (Mydlarz et al. 2006). Moreover, invertebrate immune responses are depleted during wound regeneration, resulting in reduced capacity to develop an immune response following exposure to a foreign substance, further increasing the likelihood of disease development (Mydlarz et al. 2006). Protecting flora and fauna from physical disturbances associated with human use has prompted spatial management solutions, such as restricting site access or activities allowed within designated areas (De'ath et al. 2012, Newsome and Moore 2012).

Protected areas have been instrumental in reducing damage in terrestrial and aquatic environments (Leung and Marion 2000, Sobel and Dahlgren 2004), yet links between damage reduction and disease mitigation have only been assessed in a handful of studies. The efficacy of marine reserves as management tools for preventing disease outbreaks has

been assessed numerous times in coral populations, though results vary. For example, no-take marine reserves have been shown to mitigate coral disease by maintaining functionally diverse fish assemblages (Raymundo et al. 2009) and by reducing physical damage associated with fishing activities and derelict gear (Lamb et al. 2015, Lamb et al. 2016). It is postulated that high densities of herbivorous fish within marine reserves could limit the growth of algae (Bellwood et al. 2003), which can act as reservoirs of pathogens (Nugues et al. 2004, Smith et al. 2006). Moreover, exclusion of activities that injure corals inside marine reserves, such as destructive fishing methods and gears (e.g., Asoh et al. 2004, Yoshikawa and Asoh 2004), and high-intensity tourism (Lamb and Willis 2011, Lamb et al. 2014), is likely to mitigate disease by reducing entry points for opportunistic coral pathogens (Page and Willis 2008, Nicolet et al. 2013, Katz et al. 2014, Lamb et al. 2014). Other studies have found little evidence that protected areas mitigate coral disease (Coelho and Manfrino 2007, McClanahan et al. 2009, Page et al. 2009), although authors cautioned that either poor compliance with fishing restrictions or the presence of environmental influences that permeate reserve borders could have negated reserve effectiveness in their studies. It is also plausible that protected areas might facilitate the spread of disease by increasing densities or cover of susceptible coral hosts (McCallum et al. 2005, Bruno et al. 2007, Myers and Raymundo 2009), or by increasing densities of fishes that are either vectors for coral pathogens or cause feeding injuries that increase coral susceptibility to opportunistic pathogens (Aeby and Santavy 2006, Raymundo et al. 2009).

Well-managed marine reserves may assist adaptation to impacts of climate change by increasing community resilience (Figure 9.5a; Roberts et al. 2017); however, there is mounting evidence that climate-related stressors may undermine resistance to disease afforded by reserve protection. For example, although marine reserves mitigated coral disease following a severe cyclone, they were ineffective in moderating disease when sites were exposed to higher than average terrestrial runoff from a degraded river catchment (Lamb et al. 2016). This is further supported by Hughes et al. (2017), who reported that water quality and marine reserves had no influence on the unprecedented bleaching on the Great Barrier Reef in 2016, suggesting that local protection may provide little or no protection from coral diseases associated with temperature.

The capacity of spatial closures and marine reserves to ameliorate disease will also depend upon the mechanism of disease pathogenesis. Reserves are likely inadequate for mitigating marine disease under several conditions. They may not, for example, protect highly mobile mega-fauna and fishes that traverse boundaries. Frequently, impacts are displaced outside protected area boundaries (Agardy et al. 2011) and could thus further degrade adjacent ecosystems, overriding the management benefits. Furthermore, range shifts due to anthropogenic and climate-driven processes may cause both pathogens and hosts to move out of protected areas (Hannah et al. 2007), potentially reducing the relevance of fixed spatial locations as conservation strategies for moderating disease. The benefits and limitations presented here represent only some of the considerations needed to inform the development of spatial management strategies for moderating marine disease.

Placement of protected areas is a key consideration for maximizing their effectiveness (Halpern 2003). Exposure to disturbances is an essential determinant of the vulnerability of marine ecosystems (Marshall and Johnson 2007) and such disturbances are not often spatially uniform (Devlin et al. 2013). Therefore, it is imperative to consider local patterns of exposure to disturbances when establishing protected areas for disease management. However, exposure to disturbance is rarely considered in marine protected area planning (Game et al. 2008) (but see Maynard et al. 2015b), and considerable debate is generated regarding the efficacy of protecting high- versus low-risk areas (Game et al. 2008).

9.7.2 Early warning systems and forecasting marine disease outbreaks

Early warning systems can potentially form an important component of management options of disease outbreaks, particularly in locations that are very difficult to access (Lamb et al. 2016). For example, a forecasting system linking global ocean and atmospheric climate models to malaria risk in

Botswana enabled the prediction of anomalously high probability areas so that strategies for mitigation could be initiated (Thomson et al. 2006). Forecasting is well established in crop disease management and leads to improved timing of pesticide application and deployment of planting strategies to lower disease risk (Schaafsma and Hooker 2007). On coral reefs, forecasting programs for coral bleaching are core to marine resilience programs (Eakin et al. 2010) and are guiding the development of climate-driven disease forecasting algorithms for white syndromes in reef-building corals (Maynard et al. 2011, Maynard et al. 2015a) and shell disease of American lobsters (Maynard et al. 2016). However, temporal and spatial variability in thermal anomalies could complicate efforts to predict disease outbreaks, due to uncertainty pertaining to future patterns and trajectories of stress, as well as a general lack of knowledge regarding the role of temperature stress in disease etiologies.

Satellite-derived water quality data have been critical in assessing the drivers of coral disease following acute sediment exposure from seafloor dredging (Pollock et al. 2014) and chronic exposure to terrestrial runoff (Lamb et al. 2016). Such data offer the potential for identifying and forecasting locations at increased risk of outbreaks triggered by poor water quality. Likewise, algal blooms cause mass mortality via anoxia or toxic exposure, which has an obvious immediate impact on marine populations; chronic hypoxia or exposure to algal toxins could be equally detrimental in the development of disease. For instance, nutrient-enriched primary productivity is linked with increases in the severity of amoebic gill disease of fish (Nowak 2001) and the promotion of the debilitating tumor-forming disease fibropapillomatosis in sea turtles (Van Houtan et al. 2010). Nutrient enrichment increases the prevalence and severity of multiple coral diseases in controlled laboratory and field settings (Bruno et al. 2003, Redding et al. 2013, Vega Thurber et al. 2014). Recent research found that plastic waste increased disease likelihood on coral reefs and used estimates of plastic waste entering the oceans to predict and forecast disease levels across Asia Pacific (Lamb et al. 2018). These studies suggest that established links between environmental drivers and disease outbreaks may be useful in developing forecasting tools across larger spatial scales, thus improving the use of targeted surveillance and management action.

9.7.3 Natural ecosystem "filters"

Marine and terrestrial environments are often regarded as two separate ecosystems, and managed as independent entities (Alvarez-Romero et al. 2011). Significant benefits to the health of marine

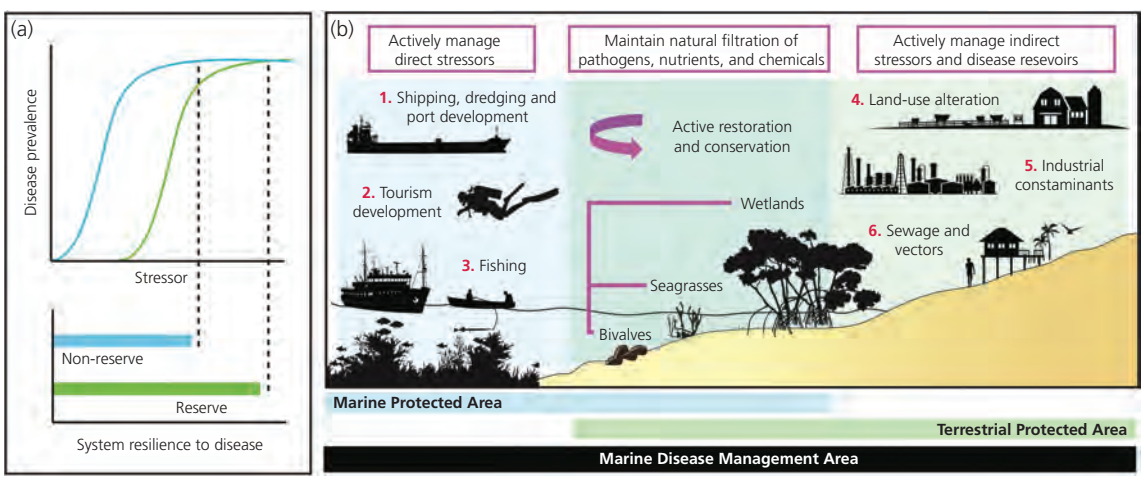

Figure 9.5 Conceptual diagram illustrating active strategies for mitigating marine disease outbreaks by increasing ecosystem resilience to disease (see also Table 9.1). (a) Effect of marine reserves on resilience to disease; (b) linkages between terrestrial and marine systems and management options for each. (Diagram from Lamb et al. (2016).)

Figure 9.6 A seagrass bed adjacent to a coastal fishing village in Indonesia. The seagrass bed acts as a filter, mitigating the delivery of human pathogens and nutrients to nearshore coral reefs. (Photo by J. Lamb.)

organisms may arise from investing conservation efforts in connecting marine and terrestrial systems (Figure 9.5b; Lamb et al. 2016). For example, ecosystem sequestration of pathogens by healthy marine habitats is a novel tool to mitigate disease outbreaks in the ocean. Lamb et al. (2017) found that seagrass ecosystems reduced sewage-sourced bacterial pathogens of humans, fishes, and invertebrates by 50 percent and coral diseases were reduced two-fold where reefs were adjacent to seagrasses (Figure 9.6). Similarly, filter feeders, such as bivalves, sponges, and polychaetes, have huge potential for reducing disease transmission to the marine environment from terrestrial sources, by filtering out pathogenic micro-organisms from the water column (Faust et al. 2009, Burge et al. 2016a). Mangroves and constructed wetlands have also been used as biofilters for natural sewage control and are effective filtration systems for excess sedimentation, nutrients, and organic matter (Yang et al. 2008). Therefore, conserving marine littoral zones may reduce levels of disease-causing pollutants entering coastal environments. An important area for future research would be to assess the mechanisms by which these habitats sequester pollutants and alleviate marine disease outbreaks.

9.8 Managing aquaculture systems and their interactions with natural systems

The human global population continues to expand as fish stocks dwindle, many to the point of collapse (Worm et al. 2009). Many countries are turning to aquaculture to address food security issues (Goldberg and Naylor 2005). While this can alleviate overharvesting, increase protein availability,

and boost income, ecological and biosecurity issues associated with aquaculture are of concern, as many practices are poorly regulated and can have disastrous consequences for local coastal ecosystems (Naylor et al. 2000). Behringer et al. (Chapter 2, this volume) explores the topic of aquacultured fisheries in detail; here, we focus on interactions between aquaculture and natural systems.

Cultured organisms are often grown in artificial, high-density monocultures with greatly altered water quality, which stresses organisms and reduces their immune function. Regular prophylaxis, such as treatment with antibiotics, may be necessary to prevent infectious disease outbreaks. Food provisioning is often unregulated, as are the means by which prophylactics and growth hormones are delivered. Excess food and waste are released in effluent, impacting coastal water quality. Water exchange between culture systems and adjacent nearshore marine communities provides an avenue for pathogens, species invasions, and degraded water (Murray 2013). Further, many aquaculture facilities are built on converted or reclaimed wetlands, mangroves, seagrass, or coral communities, which can alter local hydrodynamics and water quality, and remove the innate microbial filtering capacity of these ecosystems (Lamb et al. 2017). Lastly, cultured organisms are frequently traded between facilities and may not be native to the area where they are cultured. This facilitates interactions between cultured and native organisms that can have deleterious consequences for either or both, but certainly constitutes an invasive species risk, referred to as "biological pollution" by Naylor et al. (2001).

Nonetheless, though unregulated aquaculture can wreak havoc on nearshore marine communities, much of what we know about marine diseases developed via experiences with cultured species (reviewed in Shields 2017). Economic losses from disease are estimated in billions of dollars, providing a strong incentive to understand disease epizootiology and develop effective control measures (Lafferty et al. 2015). Most diseases of cultured finfish originated from wild stock, due to high connectivity between aquatic environments and multiple transmission pathways (Kurath and Winton 2011). Pathogens may be latent in a natural population, but become infectious when an unusually stressful event occurs or when introduced to the artificial and dense stocking conditions of aquaculture. This appears to be the case with aquarium corals, which are susceptible to heavy infestations of microcrustaceans and worms, yet these organisms are not reported to infest wild corals in significant densities (Sweet et al. 2011). Complex transmission dynamics may develop over time between farmed and wild populations. For instance, sea lice are a common ectoparasite of adult salmon, but rarely infect wild juveniles due to a life-history stage that prevents contact with infected adults. However, the presence of salmon farms altered the transmission dynamics of sea lice by increasing exposure of wild juveniles. This increased their mortality from predation, as predators selectively consumed infected prey (Krkosek et al. 2005). More rarely, aquaculture may introduce pathogens to wild naïve populations, with devastating effects. Non-native cultured red drum, for example, were the source of the bacterial pathogen *Streptococcus iniae* which infected two species of wild fish in the Red Sea (Corloni et al. 2002). Changing climate patterns are predicted to influence disease dynamics as well. *Perkinsus marinus*, the protist parasite causing dermo in the oyster *Crassostrea virginica*, is favored under a warming environment; parasitic infection intensity increases, and host survival decreases, with higher temperatures, suggesting a long-term increase in the impact of this disease (Malek and Byers 2018).

While managing diseases within aquaculture facilities involves well-established best-management practices for controlling water quality, inoculation, quarantine, and culling (Sindermann 1984, Tucker and Hargreaves 2008), the challenge for reducing spillover impacts on wild communities remains, as ineffective or non-existing regulations plague many facilities. In Lingayen Gulf, the Philippines, unregulated culture of the milkfish *Chanos chanos* has resulted in construction of over 1,170 fish pens within an 8-ha area of shallow estuarine water (Figure 9.7) (Travaglia et al. 2004). Water quality has degraded, with resultant increases in eutrophication in both coastal and river waters (Aban et al. 2008; Garren et al. 2008). Controlling or treating effluent should be a priority, as wastewater transports microbes, excess nutrients, and organic matter,

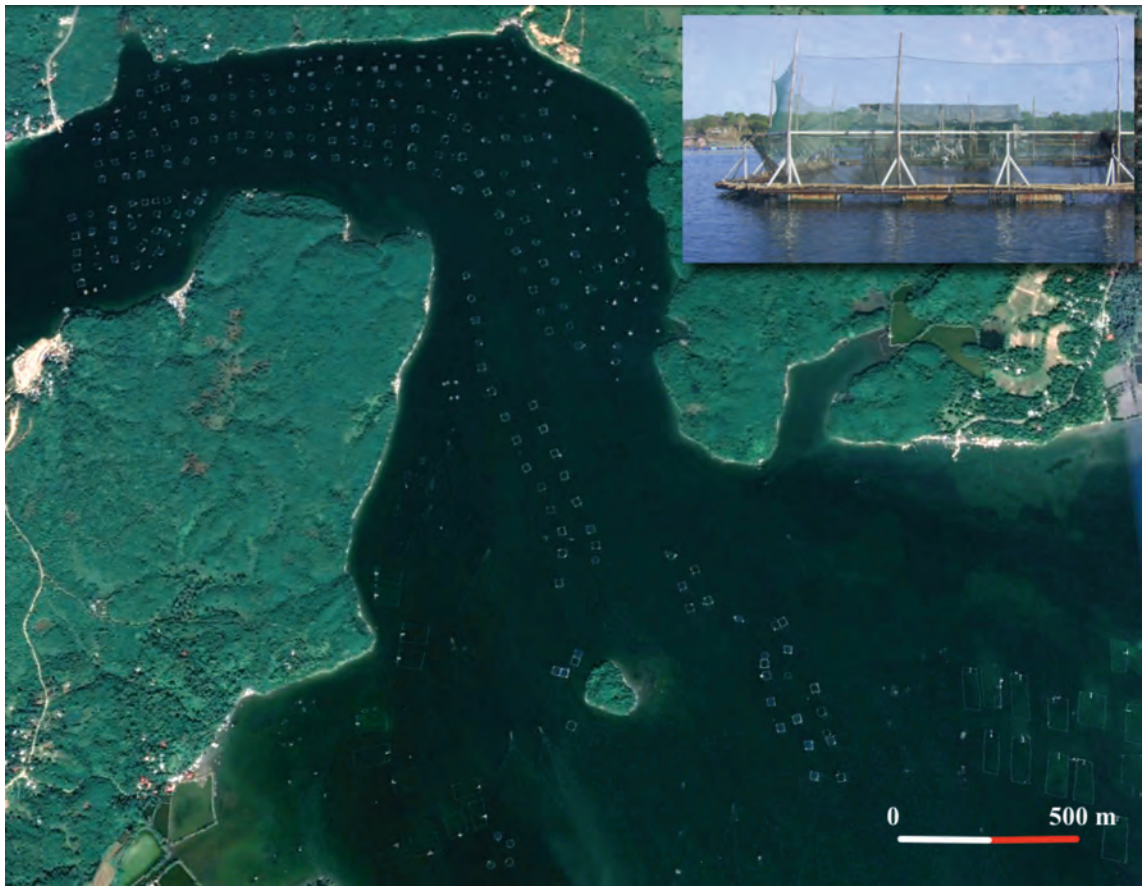

Figure 9.7 Aerial view of unregulated proliferation of fish pens of cultured milkfish, *Chanos chanos*, in Bolinao, Lingayen Gulf, the Philippines. Inset shows a single fish pen. (Aerial view taken from Google Earth; inset photo by L. Raymundo.)

antibiotics, sediment, and fecal waste (LaPatra 2003). Aside from the direct impact of introduction of pathogenic microbes into wild systems, degrading water quality can further stress organisms, increasing their susceptibility to opportunistic pathogens.

Finally, unregulated transport and trading of farmed animals provides another avenue for introduction of exotics and micro-organisms transported with them. Exotic mollusc aquaculture, in particular, has existed for hundreds of years, constituting what may be the greatest mode of introduction of any taxon worldwide (McKindsey et al. 2007). Failure to manage exotic introductions can be disastrous for both aquaculture ventures and natural populations; transport of South African abalone into California in the 1980s unwittingly introduced a parasitic polychaete that deforms shells. This introduction impacted market prices and caused the failure of several farms. An infection of a population of gastropods was detected soon after but was successfully eradicated (Kuris and Culver 1999; see Box 9.2, Figure 9.3). Impacts of the abalone herpes-like virus (AbHV), which causes a highly lethal disease, abalone viral ganglioneuritis (AVG), was devastating to both cultured and wild populations in Australia between 2006 and 2012. The disease first emerged in farms and was later found in nearby wild populations, resulting in devastating population reductions and economic loss. Strict regulation of the transport of animals between farms is the current most effective management option (Corbeil et al. 2010).

Health certification programs exist for the movement of cultured animals, though these programs

are predicated by knowledge of specific diseases/pathogens. Additionally, it is prudent to develop protocols for transport of aquatic organisms, such as the health certification procedure outlined by Humphrey et al. (1988) for cultured giant clams. These clams were transported throughout the western Pacific as part of a reintroduction program in the 1980s, sponsored by the Australian Centre for International Agriculture Research. Such protocols exist for many cultured species and/or industries. For some infectious diseases (of both terrestrial and marine vertebrates and invertebrates), the World Organisation for Animal Health (OIE; acronym based on a previous name: Office International des Epizooties) requires reporting of 117 OIE-Listed Diseases (OIE 2019). To date, the OIE has focused on diseases of economically important organisms, though a portal for reporting non-listed wildlife diseases also exists. Additionally, the OIE provides diagnostic manuals, treatment options (where they exist), and reference laboratories for listed diseases (e.g., "White spot disease in shrimp") and other specific pathogens of interest (e.g., "Infection with ostreid herpesvirus 1 microvariants"). In the USA, the USDA-APHIS is the governing body for movement of cultured animals for international import and export; for non-cultured animals, agencies such as NOAA and the US Fish & Wildlife Service are the equivalent. Movement between US states is based on the laws and regulations of the individual state; states may, in fact, share bodies of water, with laws regulating transfer of animals across state lines via the body of water. Before a culturist or researcher moves animals (either within the state or across state lines), it is important to contact the appropriate authorities (e.g., the California Department of Fish & Wildlife, Maryland Department of Natural Resources) to determine the necessary health examinations and health history required prior to the movement of animals.

9.9 Managing disease for restoration

Ecological restoration has rapidly become an essential management option to reverse the decline of marine systems, as it has been for terrestrial systems for decades. At present, disease outbreaks in restored marine populations, particularly corals, pose a threat to the success of many efforts, as restoration may involve introducing naïve organisms to new environments. Thus, disease management should be a necessary consideration in the development of restoration science. Managing and treating disease, as well as building resistance, have historically been necessary foci of aquaculture ventures, to ensure continued financial benefits (discussed in Section 9.8). Developing strategies that apply to restoration could naturally progress from this, drawing on lessons learned from culturing organisms for food and trade. For instance, Carnegie and Burreson (2011) reported increased natural resistance in wild *Crassostrea virginica* populations to *Haplosporidium*, which causes MSX and has hampered restoration efforts for the oyster. The disease is enzootic but decreasing in wild oysters growing in polyhaline conditions, while still very lethal in naïve sentinel populations growing in low-salinity environments. The authors recommended using this naturally resistant population as a source of restoration efforts; Lipcius et al. (2015) further recommended selecting polyhaline sites for restoration. Thus, lessons learned from disease management of the economically important cultured oyster is informing a re-establishment strategy in wild populations.

Disease management in marine restoration is likely to require a diverse toolkit. This may include managing environmental quality, reintroducing organisms, tracking the disease history of source populations and reintroduced organisms, and selectively breeding for disease resistance. *Ex-situ* facilities used to culture organisms for reintroduction are well equipped to monitor and control disease using traditional practices such as culling, quarantine, and active intervention. Care should be taken to use only clinically healthy organisms in restoration in order to reduce the risk of introducing pathogens to naïve populations and reduce post-introduction stress, as transplantation itself is a stressful event which may increase disease susceptibility.

Corals, which are currently a focus of restoration, may benefit from the concept of assisted evolution (van Oppen et al. 2015). This technique uses genetic tools to culture colonies that are resilient to a changing climate, with the goal of reintroducing them to natural reef habitat where it is hypothesized they

will survive better than their predecessors. While the main thrust of such efforts has been producing corals that are resistant to increasing temperatures, disease resistance must be considered as well, as temperature stress and subsequent disease outbreaks may be linked (Bruno et al. 2007, Brandt and McManus 2009). Further, coral taxa may vary in susceptibility to temperature stress and disease; certain taxa show low-temperature resilience but high subsequent disease susceptibility, or vice versa (Smith et al. 2013). This suggests evolutionary trade-offs in coping with these two major stressors. Differences in susceptibility may even vary between genotypes, highlighting the importance of genetic analysis of cultured populations and applying this information to identify potentially resistant strains for restoration (Miller et al. 2019). Thus, a focus for restoration research should encompass population genetics tools to understand how these stress-coping strategies manifest in species selected for culture. Protocols could then be incorporated that reduce stress, such as timing outplanting to avoid heat stress during the recovery phase, and selective breeding for disease resistance.

9.10 Summary

- Disease is a natural part of ecosystems and communities. However, marine diseases are on the rise, so it is essential to establish what is considered a normal level of disease for a given species or community in order to assess disease risk. Anthropogenic stress is associated with many emerging infectious diseases (EIDs) and current marine disease ecology research efforts involve understanding the influence of such stressors on the three interacting components of disease: the host, the pathogen, and their environment.
- Marine systems differ fundamentally from terrestrial systems in that they are more open and connected; sessile, clonal colonial forms with larval dispersal stages are ubiquitous; host density and diversity may be very high; and microbes are diverse and abundant in ocean water.
- Marine disease processes are influenced by the environment, which includes both natural variability and anthropogenic change, as well as both biotic (species and community interactions) and abiotic factors (temperature, water quality).
- Managing marine diseases requires novel approaches, as terrestrial strategies may not be applicable. Three novel approaches—establishment of marine protected areas, development of early warning or forecasting tools, and the maintenance and use of natural ecosystem filters—are promising strategies.
- Aquaculture can have significant negative impacts on wild ecosystems via introduction of pathogens and exotic species, degraded water quality, and conversion of coastal habitats. The reverse—impacts of wild species on farmed organisms—can also have deleterious consequences for cultured animals, though more rarely.
- Disease management and regulatory procedures have been developed, but implementation is still an issue. This is particularly challenging when international transport and exchange occur with cultured organisms.
- Ecological restoration is a growing field in conservation which would benefit from a consideration of disease susceptibility and resistance. Genotyping to identify distinct cultured populations should become standard protocol in restoration, to examine natural differences in resistance to disease and other stressors and to provide guidance in selective breeding for resistance.

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