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ARTICLE

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Strategies for managing marine disease

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Abstract

The incidence of emerging infectious diseases (EIDs) has increased in wildlife populations in recent years and is expected to continue to increase with global environmental change. Marine diseases are relatively understudied compared with terrestrial diseases but warrant parallel attention as they can disrupt ecosystems, cause economic loss, and threaten human livelihoods. Although there are many existing tools to combat the direct and indirect consequences of EIDs, these management strategies are often insufficient or ineffective in marine habitats compared with their terrestrial counterparts, often due to fundamental differences between marine and terrestrial systems. Here, we first illustrate how the marine environment and marine organism life histories present challenges and opportunities for wildlife disease management. We then assess the application of common disease management strategies to marine versus terrestrial systems to identify those that may be most effective for marine disease outbreak prevention, response, and recovery. Finally, we recommend multiple actions that will enable more successful management of marine wildlife disease emergencies in the future. These include prioritizing marine disease research and understanding its links to climate change, improving marine ecosystem health, forming better monitoring and response networks, developing marine veterinary medicine programs, and enacting policy that addresses marine and other wildlife diseases. Overall, we encourage a more proactive rather than reactive approach to marine wildlife disease management and emphasize that multidisciplinary collaborations are crucial to managing marine wildlife health.

KEYWORDS
disease ecology, marine conservation, marine wildlife

INTRODUCTION

In the last 40 years, wildlife populations have experienced a pronounced increase in emerging infectious disease (EID) occurrence (emboldened terms are defined in Box 1) across terrestrial (Daszak et al., 2000), freshwater (Reid et al., 2019), and marine environments (Tracy et al., 2019). When an EID disrupts ecosystems, causes economic loss, or threatens human health, it becomes a disease emergency (Groner et al., 2016). For marine wildlife in particular, mitigating disease emergencies is critical because of possible direct or indirect

BOX 1 Definition box

Adaptive immunity: Immune response developed in response to specific features of a pathogen. It creates immunological "memory" in case of future exposure to the same pathogen.

Antibodies: Proteins produced in response to and counteracting an antigen by directly or indirectly neutralizing their target. Antibodies form a critical part of immunological memory and can rapidly increase in concentration upon repeated pathogen exposure.

Co-infection: The occurrence of at least two genetically different infectious agents in the same host. Can be defined as simultaneous infection, mixed infection, multiple infections, concomitant infection, concurrent infection, polyinfection, polyparasitism, and multiple parasitism.

Disease emergency: Emerging infectious disease outbreak that disrupts ecosystem and/or ecological community resilience, causes economic loss, or threatens human health.

Emerging infectious disease: Disease associated with infectious agents that are newly identified, have spread to a new population, or whose incidence or geographic range is rapidly increasing.

Fomites: Object or material that carries an infectious agent.

Innate immunity: Systems of the immune response that are not pathogen-specific and do not require extensive development within the host prior to employment.

Marine protected area: A clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values.

Microbiome: The collection of microbes—bacteria, fungi, protozoa, and viruses—that lives on and inside animals and plants.

Non-competent host: Cannot generate new infections in other susceptible hosts, even after pathogen exposure.

Parasitome: The ubiquitous community of parasites—including micro- and macroparasites—found living in close conjunction with animals, plants, and fungi.

Pathogen: Broadly defined as disease-causing micro- and macro-organisms.

Pelagic larvae: Planktonic larval stages that drift in the open ocean until they attain metamorphic competency.

Phage therapy: The use of bacteriophages or bacteria-specific viruses (which are not harmful to the host) to fight off pathogenic bacteria.

Probiotics: Live microorganisms that confer a health benefit to the host.

Reservoir hosts: Hosts that become infected by a pathogen and maintain infections in the ecosystem (with or without disease). They transmit the pathogen to susceptible hosts; often identified in reference to a defined target population.

Trans-generational immunity: Inherited immune resistance of offspring due to exposure of parents to local pathogens.

Vectors: Living organisms that transmit pathogens between their animal or plant host.

effects on fisheries, a US$400 billion dollar industry on which 10% of the global human population depend for their livelihood (FAO, 2020), as well as other negative impacts on marine organisms, which have vast potential to enable technological and biomedical advances (Blasiak et al., 2020).

Despite significant recent increases in cases of marine wildlife disease (Harvell et al., 2004; Tracy et al., 2019) and the profound direct and indirect consequences of EIDs, there are few examples of large-scale wildlife management programs or mandates. Accordingly, identifying, developing, and implementing management tools targeted to marine ecosystems is an urgent priority for scientists, managers, and policymakers alike. Furthermore, interdisciplinary collaborations between human, animal, and ecosystem health professionals are essential to effectively understand and manage marine disease emergencies (Groner et al., 2016).

Terrestrial wildlife diseases have been managed for many decades. The successes and challenges in these systems serve as a jumping-off point for developing successful management strategies in marine systems. However, disparate but fundamental features of life in the marine environment can have profound consequences for disease research and management (McCallum et al., 2004). Here, we: (1) briefly describe the relatively unique features of marine compared with terrestrial environments that are pertinent for applying or developing marine disease management strategies; (2) assess the application of terrestrial disease management strategies to marine systems; and (3) make recommendations to improve marine disease management. While we focus on terrestrial and marine disease systems, we recognize that this dichotomy leaves out freshwater habitats. This manuscript does not intend to provide a complete review of marine disease ecology (for a thorough investigation of this topic please refer to Behringer et al., 2020). Rather, we highlight examples of relevant marine disease management strategies and give examples of systems in which they can be useful. Furthermore, although some of our recommendations are focused on the USA, many could be easily applied in any jurisdiction. We aim to identify useful management tools, aid developing strategies fine tuned to marine systems, and facilitate interdisciplinary collaboration between marine and terrestrial disease researchers and managers.

Disease dynamics in the marine environment and implications for management

Pathogen dynamics, host susceptibility, and environmental conditions contribute to an organism entering a disease state (McNew, 1960; Raymundo et al., 2020; Scholthof, 2007; Thrusfield & Christley, 2018). Each of these three variables makes up the disease triad (Figure 1), which can be modulated in turn to prevent or treat disease. We organize the relatively unique effects of life in the marine environment on disease dynamics into these vertices (for a more thorough review of marine versus terrestrial epidemiology please refer to McCallum et al., 2004).

Pathogen dynamics

Pathogen transmission in water fundamentally differs from transmission in air. Airborne pathogens typically desiccate quickly and are transported a few meters at most

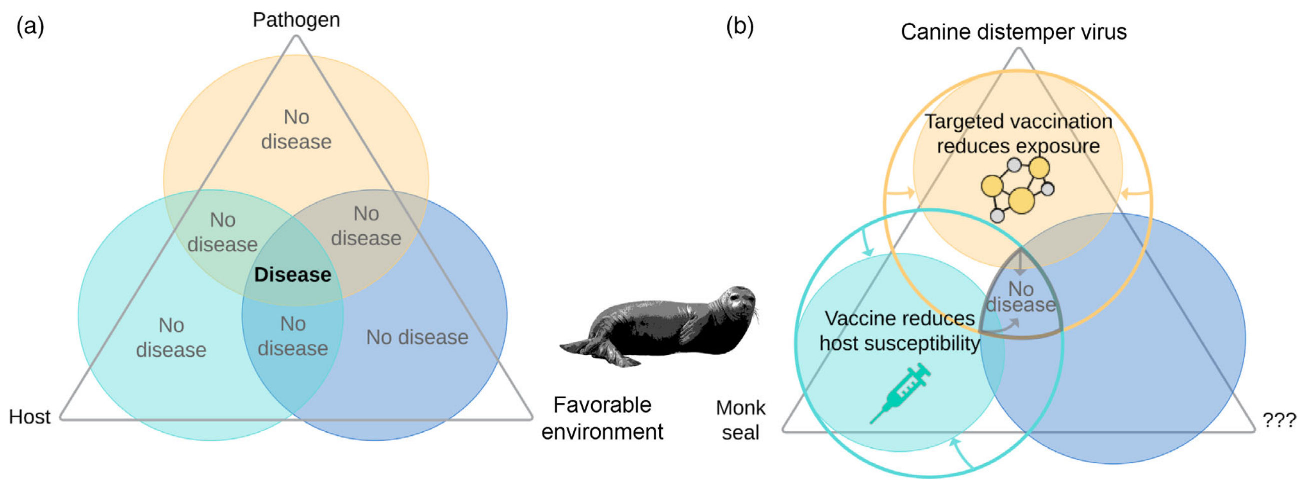

FIGURE 1 (a) A conceptual disease triangle, in which pathogen dynamics, host dynamics, and favorable environments intersect to create disease. (b) Management action reduces overlap of pathogen and host dynamics to reduce disease risk. For example, in Robinson et al., 2018, targeted vaccination of monk seals (host) against canine distemper virus (pathogen) reduced host susceptibility and exposure to pathogens, ultimately reducing disease prevelance.

(e.g., Booth et al., 2005; Olsen et al., 2003; Wells, 1934). As such, many terrestrial pathogens instead use different modes of transmission, such as transmission by direct contact, **fomites** (e.g., soil, vegetation), or **vectors** (e.g., mosquitoes), to increase dispersal and dissemination. Still, these pathogens are constrained by the relatively limited mobility of terrestrial hosts, fomites, and vectors. In contrast, marine pathogens are believed to be largely waterborne, either transmitted as free-living organisms or by free-living non-motile vectors (e.g., algae) or fomites (e.g., marine snow, sediment), remaining viable in seawater for weeks to days and traveling hundreds of miles in ocean currents (Ben-Horin et al., 2015; Hawley & Garver, 2008; Kramer et al., 2016; McCallum et al., 2003; Oidtmann et al., 2018; Shore & Caldwell, 2019). Extended viability coupled with current-mediated long-distant transport facilitates rapid transmission. Consequently, marine diseases can spread an order of magnitude faster than those on land (Cantrell et al., 2020). Altogether, extended viability, long-distance transport, and rapid transmission complicate managers' abilities to contain waterborne pathogens (Raymundo et al., 2020).

Marine pathogens may also be transmitted via direct transmission or motile vectors (Certner et al., 2017; Frada et al., 2014; Shore & Caldwell, 2019). However, vector competency and contribution to transmission have yet to be confirmed for most marine disease systems. Overall, there is still much to learn about pathogen biology and transmission in the ocean and, accordingly, how to modulate pathogen dynamics for marine disease management.

Host dynamics

Several characteristics of marine hosts contribute to the complexity of understanding marine disease dynamics, including abundant colonial and sessile species, the importance of pelagic larvae, and variation in host immune systems. Both colonial and sessile life stages are more common in marine environments, and many foundational species exhibit one or both of these traits (e.g., corals, sponges, and bivalves, Costello & Chaudhary, 2017). Behavioral strategies used by more mobile species, such as avoiding sick individuals, are not employable by sessile organisms (Behringer et al., 2018), and the tendency of many species to grow in proximity may facilitate rapid pathogen transmission. However, if measures are taken before an outbreak causes infection of all hosts, these organisms are typically easier to capture, quarantine, or even breed in captivity. Many sessile and colonial animals are also filter feeders that can sequester rich assemblages of pathogenic microbes, offering a management tool unique to aquatic systems (Burge, Closek, et al., 2016).

Furthermore, many marine taxa have pelagic larval phases, in which propagules travel long distances before settling into adult habitats (Cowen & Sponaugle, 2009). Except for some terrestrial plants, this strategy is uniquely common among marine taxa, including fish, corals, crustaceans, mollusks, and echinoderms. Movement of highly mobile **pelagic larvae** between populations has two potential outcomes for disease transmission: (1) transport can allow offspring to escape infected hotspots; or (2) larvae can act as vectors, spreading pathogens to new communities (Kough et al., 2014). Advantageously, larval export can repopulate or establish new host populations (Carr et al., 2003). These larvae may be protected from pathogens that affect their parents if larvae acquire **trans-generational immunity**, possibly promoting survival and mitigating the negative consequences outlined here (Yue et al., 2013). Furthermore, pelagic larval strategies are often coupled with very high numbers of offspring, which increases the adaptation potential at the population level (e.g., Schiebelhut et al., 2018). However, if the pathogen remains in the population, the consistent recruitment of larvae to an infected population may fuel outbreaks by repopulating pools of susceptible hosts (Behringer et al., 2020b).

Finally, there are two overarching classes of the immune response, the presence and complexity of which vary among taxa. All organisms utilize **innate immunity**, a non-specific immune response that is widely activated upon detection of pathogen invasion (Cooper, 2018; Mydlarz et al., 2006). Vertebrates also use **adaptive immunity**, in which **antibodies** are created to establish rapid, pathogen-specific immunological memory (Pastoret et al., 1998). As most terrestrial wildlife disease management has focused on vertebrates, some of the most effective and commonly used strategies capitalize on antibody responses for disease diagnostics (e.g., serological assays) and prevention (e.g., vaccination). Yet, invertebrates make up most animal taxa in the ocean (Mather, 2013) and, at least partly due to considerable differences in the biomass of marine invertebrates versus terrestrial taxa (Bar-On et al., 2018), are more affected by disease than terrestrial invertebrates. These differences require fine tuning of management strategies to improve mitigation of marine disease emergencies, such as prioritizing the development of natural therapeutics (e.g., probiotics) that enhance innate immunity.

A changing environment: Climate change and disease dynamics in the sea

Due to anthropogenic climate change, organisms in marine and terrestrial environments are experiencing changing average temperatures and increased variability in local weather patterns, with marine organisms experiencing additional stressors such as hypoxia and ocean acidification. Across systems, elevated temperatures can sometimes increase virulence, growth rates, reproductive window, and overwintering success of pathogens (Harvell et al., 2002;

Shields, 2019; reviewed in Burge & Hershberger, 2020). Furthermore, while temperature stress in host organisms may bolster some innate immune functions, temperature stress could also increase the amount of energy devoted to other metabolic demands and respiration, leaving fewer resources for immunological function (please refer to Table 1 in Burge et al., 2014; Shields, 2019). Ocean acidification and hypoxia further deplete marine host energy reserves, damage tissue, and compromise various immune functions, which could increase susceptibility to infection (Burge & Hershberger, 2020; Hernroth & Baden, 2018; Schwaner et al., 2020; Shields, 2019). These stressors often co-occur, with consequences ultimately compounded (Burge et al., 2014; Gobler & Baumann, 2016). Multiple stressors are especially threatening for sessile marine species that cannot escape their habitat when faced with water quality changes due to rising temperatures, ocean acidification, or hypoxia. However, mobile animal populations may be threatened by novel host–pathogen interactions resulting from climate-induce range shifts. Therefore, although linking causality between climate change and disease dynamics is challenging (Burge & Hershberger, 2020), the immediate study of the effects of climate change on marine disease dynamics is critical and ongoing. Improving our understanding of host–environment and pathogen–environment interactions and long-term monitoring will be critical for forecasting and proactively managing disease emergencies (Burge & Hershberger, 2020; Cantrell et al., 2020).

Limited access

Humans do not inhabit marine ecosystems and are always temporary visitors. Certainly, many terrestrial systems are quite inaccessible (e.g., jungles, polar environments, deserts), but this is a nearly universal feature of marine environments, rendering marine disease systems understudied compared with terrestrial systems (Lafferty & Hofmann, 2016). Creative sampling techniques are starting to improve accessibility to some marine environments, for example using drones to sample the respiratory viromes of whales (Geoghegan et al., 2018). However, the feasibility of managing disease is generally diminished because disease emergencies are typically harder to detect and because accessing populations or individuals for disease management is commonly limited or nigh impossible (e.g., the deep sea).

MANAGEMENT STRATEGIES FOR MARINE DISEASE EMERGENCIES

In light of the fundamental differences in disease dynamics and the implications for management covered above, we now assess the application of numerous terrestrial disease management strategies to manage marine disease emergencies. For each management strategy, we assigned a score between 1 and 4 based on potential utility in marine disease systems (Figure 2a). Our goal for these scores is not to discount or advocate for a particular strategy for all marine diseases but to identify which management tools may be particularly useful in marine environments and may merit more resources or development. A score of 1 means the strategy is likely not to be useful in most marine disease systems, a 2 means it may be useful in some marine disease systems (e.g., some taxa or circumstances), a 3 is potentially useful in most marine systems with more research and/or resources, and 4 is useful in most marine disease systems (Figure 2a). We also group each marine disease strategy into

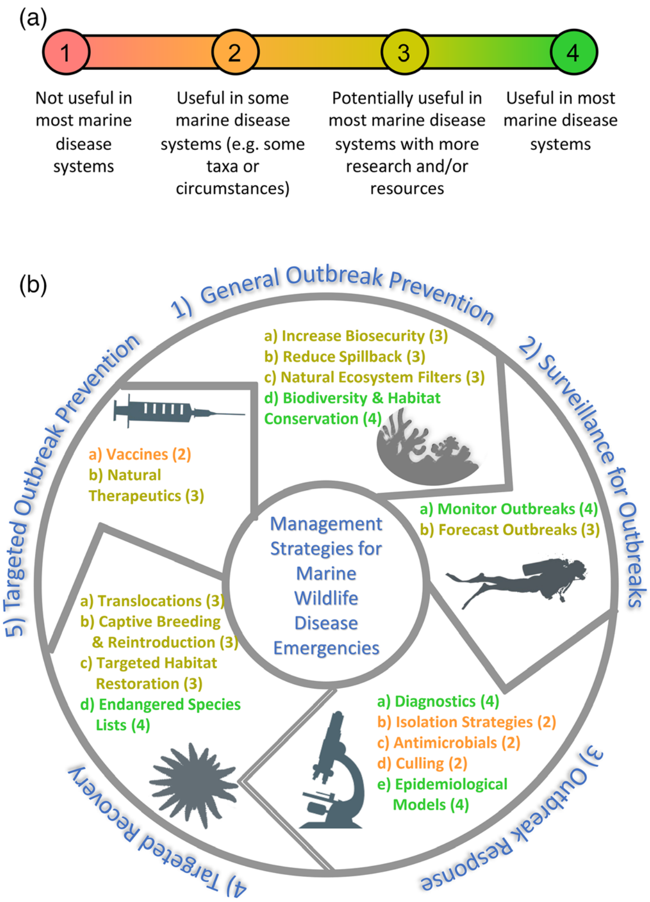

FIGURE 2 (a) The scale used to classify a given management strategy according to its utility in managing marine disease emergencies. A high score of 4 (green) indicates that the strategy is useful in most marine disease systems. 3 (yellow) indicates the strategy is potentially useful in most marine disease systems with more research and/or resources. 2 (orange) indicates the strategy is useful in some marine disease systems depending on the taxon or circumstances, and 1 (red) indicates the strategy is not useful in most marine disease systems. (b) Summary of management strategies and their utility score, according to color and scale in (a) in marine disease emergencies. Management strategies are grouped by the time frame during which they may be useful and the specificity to a given disease system in blue

one of five stages according to the timeframe during which they may be useful, including (1) General outbreak prevention to promote resilience to multiple or unknown marine diseases, (2) Outbreak surveillance to detect disease outbreaks, (3) Outbreak response once a disease emergency is detected, (4) Targeted recovery of a host after a disease-induced decline, and (5) Targeted outbreak prevention to prevent repeated outbreaks of a particular disease of known etiology (Figure 2b).

Stage 1: General outbreak prevention

Strategy 1a: Increase biosecurity

Score: 3. Anthropogenic movement of microbes and animals (i.e., invasive species) are commonly associated with novel disease introductions (Vilcinskas, 2019). Biosecurity measures aim to prevent these occurrences. Two primary sources of pathogen introduction in marine environments include the wildlife trade and ballast water. The movement of popularly-traded ornamental species is a common source of pathogen introduction, even in systems with strict quarantine regulation (Whittington & Chong, 2007). Furthermore, release of ballast (water held in tanks and cargo ships and released in harbors) is a well known point source of invasive species, novel pathogens, and pollutants (Aguirre-Macedo et al., 2008). For example, irresponsible discharge of ballast water most probably introduced the pathogens causing the devastating stony coral tissue loss disease to the Bahamas (Dahlgren et al., 2021).

Biosecurity in terrestrial and freshwater systems has been most effectively managed through policy, legislation, and informal campaigns (e.g., enforced border management of overseas goods in New Zealand, Champion, 2018; firewood restrictions for fungal pathogens, Diss-Torrance et al., 2018). These same biosecurity measures are likely to be equally effective in marine ecosystems. For example, in 2018, New Zealand adopted a policy that mandated specific protocols for dumping ballast water, including keeping a detailed record on volumes, locations and dates of ballast water exchange, and inspection of ballast water by government officials prior to dumping ballast water in New Zealand waters (Marine Protection Rules Part 300, 2016; Table 1). Currently, challenges are posed by the overall fragmented nature of both ballast water and wildlife trade regulation and documentation among countries. Increased efforts to develop universal and standardized policies have a high potential to reduce biosecurity risk globally (Smith et al., 2017). Increasing biosecurity is a feasible, if challenging, strategy broadly applicable to disease systems in which humans contribute to transmission.

Strategy 1b: Reduce spillback

Score: 3. In marine systems, aquaculture and wastewater are sources of pathogen spillback to adjacent natural populations (Raymundo et al., 2020; Sutherland et al., 2010, 2011). In land-based aquaculture facilities, vaccination and sterilization of outflow water decrease spillback and are effective, feasible management tools (Sung et al., 2011). However, many aquaculture facilities are in open water or coastal systems (e.g., net pens) where uncontrolled water exchange occurs between facilities and the environment. This exchange can facilitate transmission of novel pathogens to native species, especially when non-native species are being cultured, so may cause increased pathogen prevalence in the area around facilities (Klinger et al., 2017; Krkošek, 2017; Lafferty & Hofmann, 2016). As in terrestrial systems, preventive treatment such as vaccination (which is only feasible for some species, such as fishes), antimicrobials, natural therapeutics, or targeted culling may reduce spread from aquacultured animals to wildlife (please refer to Stage 5: Targeted prevention). Mainly unique to marine systems is the potential to control pathogen abundance by co-culturing filter feeders that can consume pathogens but do not serve as reservoirs (Burge, Closek et al., 2016; please refer to "*Natural ecosystem filters*"). For example, the common Mediterranean filter-feeding polychaete *Sabella spallanzanii* effectively reduces the accumulation of bacteria in fish aquaculture (Stabili et al., 2010; Table 1). Management and reduction of spillback are challenging in open marine systems, but successful large-scale aquaculture of many species is contingent upon improving the understanding of and reducing spillback.

Furthermore, pollutants to the marine environment, whether biological, chemical, or physical, due to human activities, have wide-ranging impacts on marine disease dynamics, including introducing pathogens (e.g., *Toxoplasma gondii* in southern sea otters) as well as increasing host susceptibility and disease-induced mortality to ultimately worsen disease outcomes (Baskin, 2006; Lamb et al., 2018; Randhawa et al., 2015; reviewed in Bojko et al., 2020; please refer to figure 6.1). Increased regulation of wastewater through local policy and informational campaigns paired with restoration or conservation of *Natural ecosystem filters* at the intersection of the human–wildlife interface are feasible strategies for reducing spillback. Reducing spillback is a logical strategy that should be prioritized in systems where aquaculture waste and wastewater are containable.

Strategy 1c: Natural ecosystem filters

Score: 3. Natural filtering processes in aquatic ecosystems can reduce pathogen abundance (Buck et al., 2018;

TABLE 1 Examples of successful applications of management strategies in marine systems

Management strategy	Score	Example	Associated recommendation	Further references
Stage 1: General outbreak prevention				
1a: Increase biosecurity	3	New Zealand policy (Marine Protection Rules Part 300, n.d.) enforces control safe handling of ballast water to prevent introduction of pathogens and invasive species.	Improve marine ecosystem health.	**Marine Protection Rules Part 300**, 2016 ; Miller et al., 2002; Whittington & Chong, 2007; Aguirre-Macedo et al., 2008; Sutherland et al., 2010, 2011; Flegel, 2012; reviewed in Shields, 2017; McDonald et al., 2020
1b: Reduce spillback	3	The filter-feeder polychaete *Sabella spallanzanii* reduces accumulation of bacteria from aquaculture.	Improve marine ecosystem health.	**Stabili et al.**, 2010; Burge, Close, et al., 2016; Lamb, van de Water, Bourne, Altier, Hein, et al., 2017; Vaughn & Hoellein, 2018; Ben-Horin et al., 2018
1c: Natural ecosystem filters	3	Seagrass meadows protect coral reef invertebrates and fish from bacteria pathogens in human sewage.	Improve marine ecosystem health.	Yang et al., 2008; Faust et al., 2009; Stabili et al., 2010; Onishi et al., 2014; Wu et al., 2016; **Lamb, van de Water, Bourne, Altier, Hein, et al.,** 2017; Zamora et al., 2019
1d: Biodiversity and habitat conservation	4	Marine protected areas support populations of the urchin predator spiny lobsters, which lower urchin density and decreases bacterial disease transmission among urchins.	Improve marine ecosystem health.	**Lafferty,** 2004; Page et al., 2009; Raymundo et al., 2009; Shapiro et al., 2010; Lamb et al., 2015, 2016; Lamb, van de Water, Bourne, Altier, 2017; Groner et al., 2016; Roberts et al., 2017; Davies, 2020
Stage 2: Surveillance for outbreaks				
2a: Monitor outbreaks	4	Eyes of the Reef, a volunteer reporting network in Hawaii, reported black band disease in coral, spurring into action rapid testing and treatment for the disease.	Form marine disease monitoring and response networks, understand the links between climate change and disease.	Coral Reef Evaluation and Monitoring Project, California Department of Fish and Wildlife Shellfish Health Laboratory, West Coast Marine Mammal Stranding Network, Local Environmental Observer Network, Wildlife Health Information Sharing Partnership, Primary Responders in Marine Emergent Disease, **Aeby et al.**, 2015; Shields, 2017
2b: Forecast outbreaks	3	Machine learning models forecast outbreaks of multiple coral pathogens using sea surface temperature and host density.	Increase basic research on marine disease systems, understand the links between climate change and disease.	Lafferty & Kuris, 1993; Bruno et al., 2007; Miller et al., 2009; Maynard et al., 2011, 2015, 2016; Pollock et al., 2014; **Caldwell et al.**, 2016; Lamb et al., 2016, 2018; Cohen et al., 2018
Stage 3: Outbreak response				
3a: Diagnostics	4	Metagenomics identified the ciliated protozoan pathogen as the cause of leopard shark epizootics and mass die-offs along the California coastline.	Increase basic research on marine disease systems, form marine disease monitoring and	Pollock et al., 2011; Hewson et al., 2018, 2019; Lamb et al., 2018; **Retallack et al.,** 2019; Mordecai et al., 2019b; Gravem et al., 2020; Matsuyama et al., 2020

(Continues)

TABLE 1 (Continued)

Management strategy	Score	Example	Associated recommendation	Further references
			response networks, develop marine veterinary medicine programs in the USA.	
3b: Isolation strategies	1	Spread of viral hemorrhagic septicemia virus is mitigated through quarantine of aquaculture fishes.	Increase basic research on marine disease systems, form marine disease monitoring and response networks, develop marine veterinary medicine programs in the USA.	**Hastein et al.,** 1999; Ocean Wise Research, Vancouver Aquarium, reviewed in Shields, 2017
3c: Antimicrobials	2	Antibiotics are used to treat leptospirosis in sea lions.	Increase basic research on marine disease systems, develop marine veterinary medicine programs in the USA.	Friedman et al., 2007; **Prager et al.,** 2015; Neely et al., 2020
3d: Culling	2	Culling is used to prevent spread of viral hemorrhagic septicemia (VHS) in hatchery salmon to wild populations.	Increase basic research on marine disease systems.	**Amos et al.,** 1998; Elston & Ford, 2011; Ben-Horin et al., 2016; reviewed in Shields, 2017
3e: Epidemiological models	4	Oceanographic-epidemiological models determined sea surface temperatures influence high mortality rates and rapid spread of sea star wasting disease.	Increase basic research on marine disease systems, understand the links between climate change and disease, develop marine veterinary medicine programs in the USA.	Dulvy et al., 2004; Sokolow et al., 2009; Kough et al., 2014; Maynard et al., 2016; Ben-Horin et al., 2018; Lupo et al., 2019; Ben-Horin et al., 2020; **Aalto et al.,** 2020
Stage 4: Targeted Recovery				
4a: Translocations	3	No examples for managing disease directly, but is a common practice for restoring marine populations (Swan et al., 2016)	Increase basic research on marine disease systems, form marine disease monitoring and response networks.	Jameson et al., 1982; Lafferty & Tinker, 2014; Swan et al., 2016; Norris et al., 2017
4b: Captive breeding and reintroduction	3	Captive-bred Olympia oysters are used to restore oyster reefs in central California estuaries.	Increase basic research on marine disease systems, form marine disease monitoring and response networks.	Fraser, 2008; Burton et al., 2008; Robeck et al., 2009; Rogers-Bennett et al., 2016; **Foo & Byrne,** 2016; **Wasson et al.,** 2020
4c: Targeted habitat restoration	3		Improve marine ecosystem health.	

(Continues)

TABLE 1 (Continued)

Management strategy	Score	Example	Associated recommendation	Further references
		No examples for managing disease directly, but has been successful for some ecosystems.		Hashim et al., 2010; Orth et al., 2012; Lipcius & Burke, 2018; Eger et al., 2020
4d: Endangered species lists	4	Sunflower sea stars (*Pycnopodia helianthoides*) were placed on the IUCN critically endangered list to facilitate its recovery from sea star wasting disease, which was exacerbated by warm temperatures.	Understand the links between climate change and disease.	International Union for the Conservation of Nature (IUCN) Red List, Balsiger, 2009; **Gravem et al.,** 2020
Stage 5: Targeted Outbreak Prevention				
5a: Vaccines	2	Monk seals in Hawaii that would disproportionately contribute to virus spread are vaccinated against morbillivirus.	Increase basic research on marine disease systems, develop marine veterinary medicine programs in the USA.	Syed Musthaq & Kwang, 2014; Shields, 2017; **Robinson et al.,** 2018
5b: Natural therapeutics	3	Probiotics treat and prevent stony coral tissue loss disease in *Montastraea cavernosa* coral; ongoing work is evaluating delivery to and efficacy in wild corals.	Increase basic research on marine disease systems develop marine veterinary medicine programs in the USA.	Stokes & Burreson, 2001; Ninawe & Selvin, 2009; Gibson et al., 2011; Prasad et al., 2011; Atad et al., 2012; Friedman et al., 2014; Foo & Byrne, 2016; Peixoto et al., 2017; Wang et al., 2017; Figueroa et al., 2017; Rosado et al., 2019; Tarnecki et al., 2019; Karvonen et al., 2019; **Paul et al.,** 2019, 2020; Smithsonian Marine Station, 2020; Kuebutornye et al., 2020

Note: Example reference emboldened.

Granada et al., 2016; Lamb, van de Water, Bourne, Altier, 2017; Stabili et al., 2010). Natural characteristics of aquatic biomes and the filter-feeding species that inhabit them have been used as a source of biological filtration in freshwater and marine systems, presenting unique opportunities for marine wildlife disease management (Yang et al., 2008; reviewed in Burge et al., 2016; Raymundo et al., 2020; Wu et al., 2016). Mangroves, seagrass beds, and salt marshes act as passive filters by trapping microbes, changing water chemistry, and removing nutrients. Mangroves and seagrass beds have been shown to filter pathogenic bacteria in wastewater runoff (Lamb, van de Water, Bourne, Altier, 2017; Yang et al., 2008; Table 1, Figure 3c). As a management strategy, utilization, restoration, and conservation of passive filtering ecosystems has high potential to reduce disease risk, especially when the pathogen source is "upstream" of the affected host population (please refer to "*Reduce spillback*").

Filter-feeding taxa, such as bivalves, sponges, and polychaetes, actively filter pathogens in the water column, accumulating them in their tissues or sediment via pseudofeces (Burge, Closek, et al., 2016). Filter feeders serve as a viable option for inactivating or eliminating harmful microbes from the environment. However, if pathogens are not inactivated, filter feeders can serve as reservoirs for pathogens, accumulating them from the water column and serving as a source of infection for the primary host. Active filter feeders have been used to treat aquaculture effluents (Stabili et al., 2010; Vaughn & Hoellein, 2018), and modeling results have demonstrated their effectiveness at mitigating marine disease transmission in open systems (Ben-Horin et al., 2018). Furthermore, relatively easy-to-access filter feeders have the potential to be used as sentinel species in surveillance efforts when target hosts are challenging to sample (please refer to "*Monitoring outbreaks*"). Although efficacy of filter-feeding depends on a myraid of factors such as the density and distribution of the animals and hydrodynamics of the system, natural ecosystem filters could be applied in cases when diseases are

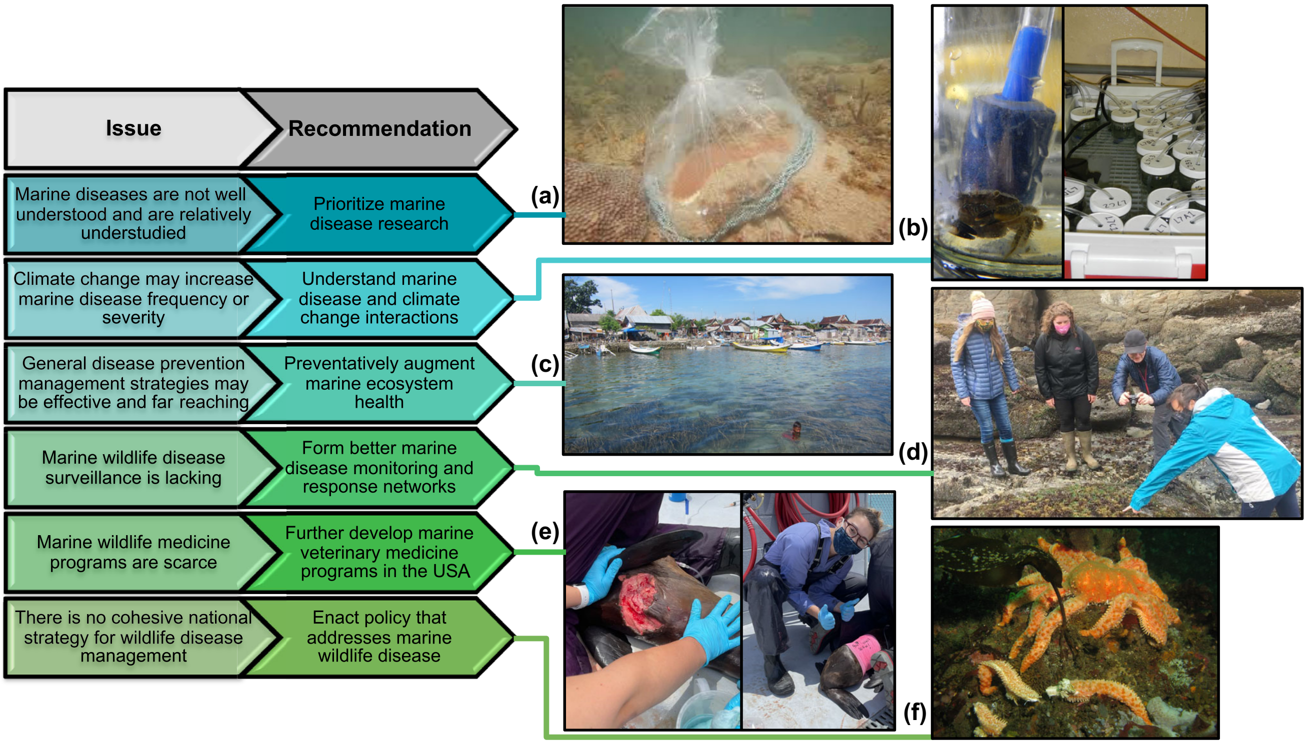

FIGURE 3 Issues in marine disease management and accompanying recommendations. (a) The CHAMP Laboratory (Coral Health and Marine Probiotics) of University of North Carolina Wilmington applies probiotics to corals off the coast of Florida, USA to treat stony coral tissue loss disease. Photograph by Hunter Noren. (b) Mesocosm infection experiments of the mud crab, *Eurypanopeus depressus* by parasitic barnacle *Loxothylacus panopaei* enable incorporating mechanistic environmental response in epidemiological models (Gehman et al., 2018). Photograph by Alyssa Gehman. (c) Restoration and conservation of sea grass bed habitats, which can act as natural ecosystem filters (Lamb, van de Water, Bourne, Altier, Hein, et al., 2017). (d) Members of the PRIMED Network training volunteers to identify and report marine diseases using iNaturalist. Photograph by Sarah Gravem. (e) A veterinary medicine student at Oregon State University treating a wound on an injured sea lion. Photograph Robyn Cates. (f) The Endangered Species Act is being used to help species recover from sea star wasting disease, yet there is no explicit policy managing wildlife disease. Photograph by Janna Nichols in Washington, USA

waterborne, when wastewater runoff increases exposure and susceptibility to pathogens, or when filter feeders could be used to reduce transmission from aquaculture to wildlife.

Strategy 1d: Biodiversity and habitat conservation

Score: 4. Biodiversity conservation aims to preserve the variety of species necessary to maintain naturally functioning ecosystems, and habitat conservation accomplish these goals by protecting the habitats in which those species live. Biodiversity and habitat conservation may protect wildlife from anthropogenic disturbances that increases physical damage and therefore disease susceptibility and pathogen exposure, such as trawling (Lamb, van de Water, Bourne, Altier, 2017; Shapiro et al., 2010). They may also enable host populations to recover from disease more quickly by alleviating human-associated mortality by, for example, reducing lethal take (Groner et al., 2016). Furthermore, conserved habitats can provide a source population for nearby areas affected by disease (Carr et al., 2003). In some cases, mitigating biodiversity loss can additionally decrease disease transmission through several processes such as promoting the health and diversity of "*Natural ecosystem filters*", increasing predation on vectors and hosts, by diluting transmission by increasing the relative abundance of **non-competent hosts**, or an interaction among these processes (Ostfeld & Holt, 2004; Rohr et al., 2020). For example, protected areas in California support larger populations of spiny lobsters, which increases predation on urchins. Ultimately, reduced urchin population size decreases density-dependent transmission of bacterial pathogens among urchins (Table 1, Lafferty, 2004). Furthermore, conservation of predators (sea otters) promotes natural ecosystem filter resilience (eelgrass), which could increase filtering of pathogenic bacteria (Foster et al., 2021; Lamb, van de Water, Bourne, Altier, Hein, et al., 2017). In contrast, reducing lethal take and conserving habitats may cause overcrowding of a taxon, ultimately increasing disease transmission (Davies et al., 2015; Lebarbenchon et al., 2007; McCallum et al., 2005; Wood et al., 2010; Wootton et al., 2012). As such, there is a need for additional research into the relationship between biodiversity and disease transmission in marine biomes and how conservation may aid in species recovery after a disease outbreak (but please refer to reviews by Davies, 2020; Raymundo et al., 2020).

Advantageously, biodiversity and habitat conservation via **marine protected areas** (MPAs) and marine spatial planning are already vital components of marine conservation efforts (Grorud-Colvert et al., 2021). Elucidating the relationships between biodiversity, habitat conservation, and disease will facilitate the incorporation of disease management into these ongoing intiatives. If integrative management (such as through targeted culling; Davies, 2020) or different levels of protection within and around the MPA (Grorud-Colvert et al., 2021) alleviates the effects of overcrowding on pathogen transmission, the potential benefits of biodiversity and habitat conservation combined with the existing well developed infrastructure for MPAs and marine spatial planning make this a top management strategy.

Stage 2: Outbreak surveillance

Strategy 2a: Monitor outbreaks

Score: 4. Infectious disease surveillance in wild populations includes the ongoing systematic collection, analysis, and interpretation of data to detect and monitor the status of diseases (WHO, 2006). In all systems, active surveillance programs (i.e., planned, systematic surveillance for a particular pathogen or group of pathogens; Sleeman et al., 2012) are limited by high costs and complex logistics. This is especially true in marine systems, where it is typically more expensive and more challenging to sample organisms directly than on land. Because pathogens in the ocean are relatively undescribed compared with those on land, surveillance is also limited by the availability of specific diagnostic tools (please refer to "*Diagnostics*" in the following section). However, there are several successful examples of active marine surveillance programs including corals (Coral Reef Evaluation and Monitoring Project, (CREMP]) and abalone (California Department of Fish and Wildlife Shellfish Health Laboratory). Potential strategies for overcoming difficulties sampling focal species include sampling sentinel species (Halliday et al., 2007), such as filter feeders (please refer to "*Natural ecosystem filters*"), and environmental DNA (Michaels et al., 2016; Sato et al., 2019). When pathogens have not been fully described, active surveillance could be accomplished via microscopy (Bateman et al., 2020b; Burge, Friedman, et al., 2016) and through non-specific or broadly specific molecular pathogen detection tools (e.g., biochemistry of innate immune markers Glidden et al., 2018), high-throughput amplicon sequencing (Huang et al., 2019), and metagenomics or meta-transcriptomics (Geoghegan et al., 2021; Retallack et al., 2019).

Effective passive surveillance programs (i.e., non-systematic and often opportunistic surveillance; Sleeman et al., 2012) are contingent upon a network of observers (e.g., Rocky Mountain wildlife; Duncan et al., 2008). Although they are likely to be more challenging to implement in less accessible marine environments, there are some excellent examples of these programs for marine taxa or habitats with demonstrated impacts on marine disease management (e.g., West Coast Marine Mammal Stranding Network, Local Environmental Observer (LEO) Network, Wildlife Health Information Sharing Partnership (WHISPers), Eye of the Reef, Reef Watch, PRIMED, MARINe; Table 1, Figure 3d). For instance, a volunteer within the Eye of the Reef community reporting network reported the first occurrence of black band disease in Hawaiian coral, facilitating rapid diagnostics and treatment (Aeby et al., 2015; Table 1). Increasing connectivity among people or entities that study marine wildlife health, creating or augmenting reporting systems and databases to include marine organisms, and engaging public participation in surveillance would substantially increase the effectiveness of passive surveillance in marine systems. Generally, passive and active disease surveillance are key components of identifying and responding to many or all marine disease outbreaks. Advances in sequencing and sampling technology continue to improve their utility in all systems.

Strategy 2b: Forecast outbreaks

Score: 3. Disease forecasting relies on model-based early warning systems that typically use environmental and epidemiological data to predict if, when, and where outbreaks may occur (Maynard et al., 2016). Forecasting has been particularly successful for human diseases when pathogen, vector, or reservoir host biology is linked to environmental conditions (Chaves & Pascual, 2007; Muñoz et al., 2020; Raymundo et al., 2020). Due in part to the sensitivity of ectothermic marine organisms to temperature, existing forecasting strategies for terrestrial systems have been successfully applied to marine systems (e.g., using temperature to predict coral disease and lobster epizootic shell disease outbreaks (Caldwell et al., 2016; Maynard et al., 2015, 2016; Raymundo et al., 2020; Table 1). Unfortunately, except for sea surface temperature, current applications in marine systems are limited by environmental monitoring capacity underwater. However, this is rapidly improving for environmental pollutants (sediment from dredging: Pollock et al., 2014; plastic waste: Lamb et al., 2018).

Furthermore, machine learning and statistical (e.g., autoregressive) models are commonly used for short-term forecasting (e.g., Caldwell et al., 2016; Chaves & Pascual, 2007). However, mechanistic models (please refer to "*Epidemiological models*") using environmental responses to estimate parameters (e.g., thermal response curves) are the most robust for long-term forecasts as they provide deeper insight into how and why an organism responds to its environment (Maynard et al., 2016; Mordecai, Caldwell, et al., 2019). As such, determining causal relationships between environmental variability, pathogen biology, and host physiology will continue to improve disease forecasts (Gehman et al., 2018; Maynard et al., 2016; Figure 3b). With more research and development of environmental monitoring systems, forecasting outbreaks is of great utility to marine systems, especially as the climate changes. However, disease emergencies will always be somewhat unpredictable, especially when new diseases emerge or are poorly understood.

Stage 3: Outbreak response

Strategy 3a: Diagnostics

Score: 4. Disease diagnostics characterize and identify the causative agent of disease in a host, and these diagnostics are critical for identifying the most effective management strategies given the pathogen biology. Many classic (gross observations, cell culture, microscopy, histopathology) and modern diagnostic tools (quantitative PCR, amplicon sequencing, metagenomics, analytical biochemistry) that are utilized in terrestrial settings are directly applicable to marine systems (reviewed in Bateman et al., 2020; Burge, Friedman, et al., 2016). However, there is a shortage of knowledge of marine disease agents (Behringer et al., 2020b; Harvell et al., 2004; but please refer to Bateman et al., 2020), requiring diagnostics that do not require *a priori knowledge of pathogen identity*. Such methods include microscopy (Bateman et al., 2020b; Burge, Friedman, et al., 2016), high-throughput amplicon sequencing (Huang et al., 2019), metagenomics or metatranscriptomics (Geoghegan et al., 2021; Retallack et al., 2019), and single-cell genomics (Martinez-Hernandez et al., 2017). For example, metagenomics was used to identify the previously cryptic infectious agent of leopard shark epizootics and die-offs (Retallack et al., 2019; Table 1). In organisms that lack adaptive immune systems, diagnostics are limited to tools that directly identify the pathogen (e.g., histology, PCR) rather than identify antibodies. Importantly, when using genetic tools, confirmation of an infectious agent often requires further pathology and experimental work to confirm that it is indeed disease causing (Bateman et al., 2020b; Burge, Friedman, et al., 2016).

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When pathogens are not quickly identified, many of the management strategies we cover elsewhere are hamstrung. For example, the cause of sea star wasting syndrome is still unclear (Hewson et al., 2018, 2019), and many proposed recovery efforts hinge on diagnosing the disease agent (Hamilton et al., 2021). Overall, diagnostics should be an integral part of any outbreak response, although sometimes development and use are hindered by a limited ability to sample in marine settings, lack of baseline knowledge of marine parasitomes and pathology, and limited ability of tools that leverage immunological memory (i.e., antibody response).

Strategy 3b: Isolation strategies

Score: 2. Isolation strategies include quarantine and geographic restriction. Although contentious, geographic restriction using fencing is widely used in terrestrial systems for ungulates and other large species to prevent disease spread (Mysterud & Rolandsen, 2019). However, geographic restriction is typically impossible in marine systems due to pathogen transmission and the logistic challenges of building infrastructure to limit host movement through water.

There are two primary quarantine strategies: isolating infected individuals until they are not infectious or isolating healthy animals until there is little risk of infection. Both can be used quickly and without extensive knowledge of a disease process. Quarantine has had some success but is generally restricted to wildlife that can be easily contained (e.g., frogs during chytridiomycosis outbreaks; Woodhams et al., 2011; isolation of fishes carrying viral hemorrhagic septicemia; Hastein et al., 1999). For marine species, in particular, self-contained seawater facilities are needed. While these facilities exist (e.g., United States Geological Survey field stations), they are primarily used for economically valuable species (e.g., fishes, corals). To make quarantine a viable option for marine wildlife disease outbreaks, infrastructure and expanded partnerships with existing institutions are necessary (e.g., zoos and aquariums: Ocean Wise Research, Vancouver Aquarium). Overall, quarantine only has utility for a marine taxon that can be maintained in these facilities but could be very useful in those instances.

Strategy 3c: Antimicrobials

Score: 2. Antimicrobial treatments are used extensively in human medicine, veterinary medicine, and aquaculture to combat disease (Foy & Trepanier, 2010; Rohayem et al., 2010; Schwarz et al., 2001; Vignesh et al., 2011; Woods & Knauer, 2010). Like terrestrial wildlife disease, the use of antimicrobials in marine disease may be challenging in many wild systems because of the logistics associated with drug distribution and delivery over large areas or many individuals. But localized distribution in small, accessible marine populations can be effective. For example, antibiotic pastes have successfully treated stony coral tissue loss disease in wild corals (Neely et al., 2020), and antibiotics can treat leptospirosis in captive California sea lions (Prager et al., 2015; Table 1, Figure 3e). Furthermore, antimicrobials in aquaculture may reduce the spillback of disease to wild populations (Vignesh et al., 2011). However, antibiotics applied repeatedly or over a wide area can promote antibiotic resistance, which is a concern for wild animal health (Cabello et al., 2013; Vignesh et al., 2011). Antibiotic-resistant bacteria have already been found in marine mammals and sea turtles (Foti et al., 2009; Schaefer et al., 2009; Wallace et al., 2013). As such, antimicrobials are being increasingly replaced by preventive measures, such as probiotics (please refer to "*Natural therapeutics*"). Overall, antibiotics can be beneficial in controlled circumstances of smaller populations, but their utility for managing large-scale disease threats is limited.

Strategy 3d: Culling

Score: 2. Targeted culling is the selective killing or removal of wildlife and applies to both outbreak response and prevention. Culling of infected hosts and/or reservoir hosts can prevent pathogen spread between populations and has historically been used in terrestrial systems to slow disease transmission (Daszak et al., 2000). In marine systems, culling has been used to prevent the spread of viral hemorrhagic septicemia (VHS) in hatchery salmon to wild populations (Amos et al., 1998; Table 1) and proposed to reduce spread of withering syndrome in aquacultured red abalone (Ben-Horin et al., 2016). Additional research has shown that fishing can lower parasite prevalence by "fishing out" large fish that carry the highest parasite burdens and reduce overcrowding (Wood et al., 2010).

However, culling should be exercised with caution because it can often have unintended consequences for disease transmission. For instance, culling of badgers to reduce bovine tuberculosis transmission alters badger behavior to ultimately increase transmission (Bielby et al., 2014). Furthermore, culling may place selective pressures on pathogens, increasing their virulence and hampering eradication efforts (Bolzoni & de Leo, 2013). As such, successful implementation requires a mechanistic understanding of how host population and community ecology influence disease transmission and the ability to eliminate diseased individuals and/or populations. Culling has been overshadowed by other more effective management strategies in terrestrial systems (Sokolow et al., 2019) and is less likely to be valuable in most marine systems, except perhaps when reducing spillback between aquacultured and wild populations or reducing overcrowding in high risk and accessible areas (please refer to "*Reduce spillover*").

Strategy 3e: Epidemiological models

Score: 4. Epidemiological models broadly refer to a wide range of mathematical tools used to track the temporal and spatial distribution of infected hosts and disease-induced mortality. They are extensively used in terrestrial disease systems to understand disease dynamics, evaluate efficacy of intervention strategies, and predict outcomes of population-wide transmission (e.g., Beeton & McCallum, 2011; Craig et al., 2014; Silk et al., 2019; Viana et al., 2015). Epidemiological models have been relatively underutilized in relation to terrestrial pathogens due to an incomplete understanding of pathogen transmission and host susceptibility (Powell & Hofmann, 2015; Shore & Caldwell, 2019). However, incorporating within-host processes (Bidegain et al., 2017), among host heterogeneity (intra- and interspecific; Bidegain et al., 2016, 2017), environmental conditions (Aalto et al., 2020; Lu et al., 2020; Maynard et al., 2016; Zvuloni et al., 2015), metapopulation dynamics (Sokolow et al., 2009), and oceanographic models (e.g., Aalto et al., 2020; Ben-Horin et al., 2020; Ferreira et al., 2014; Kough et al., 2014; Pande et al., 2015) has rapidly advanced the utility of marine disease models. For instance, a coupled oceanographic–epidemiologic model, which mapped pathogen spread via ocean currents, was used to determine the effect of temperature on sea star wasting disease spread and mortality (Aalto et al., 2020; Table 1). Additionally, modeling variation within and among hosts enabled the evaluation of the efficacy at which natural ecosystem filters reduce spillback disease risk for wildlife (Ben-Horin et al., 2018). Overall, epidemiological models are a powerful tool for understanding disease processes, pre-emptively evaluating management strategies, and forecasting disease dynamics. Their application to marine disease management has great potential as new data streams and computational methods emerge.

Stage 4: Targeted recovery

Strategy 4a: Translocations

Score: 3. Translocation involves taking individuals from larger or healthier populations and moving them to smaller populations that have been severely reduced by disease. Translocation as a general conservation management tool is used regularly in terrestrial systems (e.g., the Australian Western Shield Program, Mawson, 2004), and only since the late 1990s has also been increasingly used in marine systems (Swan et al., 2016). Although we found very few examples of translocations being utilized as a strategy for marine disease management, it is likely that translocations can be used successfully to manage disease in marine systems, similar to successes for other conservation goals. However, it is important that there is a sufficient understanding of epidemiology and natural history to ensure that translocated animals will stay in the area, remain healthy, and increase the breeding pool. Challenges can arise when organisms are highly mobile or live in groups with complex social structures (e.g., failed sea otter translocations in Oregon, Jameson et al., 1982; but note efforts by Elakha Alliance [elakhaalliance.org] and Lafferty & Tinker, 2014). Furthermore, careful maintenance of genetic diversity to minimize bottleneck effects in small populations is key (Willoughby et al., 2015). Additional considerations after an outbreak include avoiding disease reintroduction in the target area and avoiding moving healthy organisms to areas where disease is present (Stabili et al., 2010). Overall, translocations can be a useful but currently underutilized tool for marine wildlife managers to bolster vulnerable populations when amenable conditions are met and can be especially effective when combined with other direct management strategies such as *Captive breeding*, *Diagnostics*, and *Habitat restoration*.

Strategy 4b: Captive breeding and reintroduction

Score: 3. Captive breeding and reintroduction involve maintaining adult breeding populations in captivity to produce healthy offspring that can be successfully reintroduced to the wild. This method can help to recover populations that have been severely reduced by disease or are experiencing low genetic diversity after disease (e.g., black-footed ferret; Thorne & Williams, 1988). Captive breeding has been successful for many species in zoos, aquariums, and research and private facilities (Association of Zoos and Aquariums (AZA) Reintroduction Programs; Fraser, 2008; Wasson et al., 2020). As with quarantine, implementing this strategy for marine wildlife is contingent on increased the availability of breeding and housing facilities. Additionally, captive breeding must be carefully designed to align with conservation goals, maintain genetic diversity, and avoid disease introduction (Albert et al., 2015; Grogan et al., 2017; Wacker et al., 2019; Williams & Hoffman, 2009). In cases in which the population decline is so severe that few remain in the wild, captive breeding may be the only way to maintain the population (Rogers-Bennett et al., 2016; Snyder et al., 1996; The IUCN Policy Statement on Captive Breeding, 1987).

There are successful examples of reintroducing captive-bred animals in terrestrial and freshwater systems (e.g., California condor, Ohio river basin freshwater mussels, Oregon frog, AZA Reintroduction Programs). In marine systems, Olympia oysters have successfully been bred in captivity and reintroduced to California estuaries, as have white abalone (Wasson et al., 2020; Table 1; Kerlin, 2019; Rogers-Bennett et al., 2016). However, there are limited successful examples in other marine systems, and reintroduction has failed for some species of salmonids (Fraser, 2008). Reintroducing captive-bred animals to the wild has many of the same limitations and considerations mentioned for *Translocations* (i.e., high risk of failure, need to maintain genetic diversity, avoiding disease introduction, financial cost). However, the abundant reproductive capacity of many species and partnerships with commercial aquaculture facilities may support successful implementation. Ultimately, captive breeding and reintroduction is a key tool for marine wildlife managers, but more investment in infrastructure and research is needed before this is a scalable option for most marine species.

Strategy 4c: Targeted habitat restoration

Score: 3. Targeted habitat restoration, which involves renewing or restoring degraded ecosystems, has been generally used to aid recovery of species experiencing severe population declines, including Pacific salmonids in the Columbia River Basin (Barnas et al., 2015) and birds in the woodlands of Victoria, Australia (Vesk et al., 2015). Targeted restoration benefits from strategically identifying optimal locations (Geist & Hawkins, 2016) with access to a source population. Habitat restoration may protect a site from new outbreaks (Sokolow et al., 2019) but does not typically protect a species from disease re-emergence if the pathogen has not been extirpated from the area. The ubiquity of larval stages in the marine environment may be either a challenge or an advantage for a successful habitat restoration project: recruitment of larvae is often sporadic and unpredictable, but high population connectivity means that larvae may easily settle in newly restored habitats. One way to circumvent this uncertainty is to pair habitat restoration with *Translocations* or *Captive breeding and reintroduction*. Because of the relative inaccessibility of marine compared with terrestrial environments, marine habitat restoration can be logistically intensive and expensive, especially on a large scale (e.g., kelp forest restoration; Eger et al., 2020). However, many economically and ecologically important marine habitats have been successfully restored, including those founded by *Natural ecosystem filters*: mangroves, seagrass meadows, and oyster reefs (Hashim et al., 2010; Lipcius & Burke, 2018; Orth et al., 2012). As such, additional research and adequate resources are needed to ensure viability of marine habitat restoration for aiding species recovery following a disease outbreak.

Strategy 4e: Endangered species lists

Score: 4. Listing species as threatened or endangered offers direct protection for that species and facilitates restoration efforts by providing funding and resources for terrestrial and marine taxa. A major driver outcome of listing is to increase visibility of a declining species. For example, the International Union for the Conservation of Nature (IUCN) Red List can raise public awareness, help generate funding, and facilitate management actions. For example, the sunflower sea star, *Pycnopodia helianthoides*, is now listed as critically endangered due to continental-wide sea star wasting disease-induced mortality (Gravem et al., 2020; Table 1, Figure 3f). Less than a year since the listing, the plight of sunflower sea stars has been reported by national news outlets (e.g., Greenfieldboyce, 2021) and efforts are underway to breed populations in captivity (Ma & Taguchi, 2021). Furthermore, when tied to legislation (e.g., the United States Endangered Species Act), a listing can criminalize harvest or other detrimental activities by humans (please refer to "*Reduce harvest*"). However, listing does not directly alleviate disease outcomes. It can also be politically fraught, and protections are ultimately dependent on enforcement. In some cases, listing can limit basic research and hinder recovery (Miller et al., 1994). Overall, endangered species listing is a helpful strategy in situations in which individual species are already recovering from disease and would further benefit from funding, attention, and policy action (e.g., black abalone; Balsiger, 2009).

Stage 5: Targeted outbreak prevention

Strategy 5a: Vaccines

Score: 2. Vaccination exposes organisms to a deactivated, live attenuated, or recombinant antigen that elicits an antibody response in the host's adaptive immune system and defends against subsequent infection (Sallusto et al., 2010). Vaccines are used in terrestrial wildlife (reviewed in Langwig et al., 2015), aquaculture of many fishes (reviewed in Sommerset et al., 2005), and marine mammals (Robinson et al., 2018). Three prerequisites must be met before vaccination is feasible. First, taxa must generally have an adaptive immune response. This is lacking in most invertebrates, which comprise a considerable proportion of marine taxa (Roch, 1999). Some research suggests that priming of the innate immune system may work as a partially effective, moderately specific vaccine. However, this has only been demonstrated for white spot syndrome virus in shrimp (Syed Musthaq & Kwang, 2014). Second, vaccines are often delivered via injections and bait, sometimes requiring multiple doses

(Sharma & Hinds, 2012). For marine wildlife, lack of access to individuals and dispersal of bait reduces the feasibility of these methods. Third, vaccines are expensive to develop, and, except for charismatic megafauna, funding to develop vaccines for wildlife is limited. Currently, vaccines are primarily useful in marine systems for vertebrates that have small, easy-to-access populations (e.g., Hawaiian monk seals; Robinson et al., 2018; Table 1).

Strategy 5b: Natural therapeutics

Score: 3. In wild systems, hosts are typically simultaneously infected with multiple commensal, symbiotic, and parasitic organisms that comprise the **microbiome** and **parasitome** (Bateman et al., 2020b; Vega Thurber et al., 2020). The composition and stability of these 'omes are inherent to disease resistance and tolerance across all taxa (Carthey et al., 2020; Hoarau et al., 2020; Hoyt et al., 2019; Kueneman et al., 2016; Pollock et al., 2019; Vega Thurber et al., 2020). These 'omes can be manipulated to prevent or treat disease via three tools: **phage therapy**, **probiotics**, and **co-infection** (Inal, 2003; Newaj-Fyzul et al., 2014; Rynkiewicz et al., 2015; Vaumourin et al., 2015). These tools inoculate hosts with microorganisms (bacteriophages, beneficial bacteria, parasites) that limit pathogen replication or reduce disease symptoms. Phage therapy and probiotics are developing treatments in humans, domestic animals, and wildlife (reviewed in Doss et al., 2017; McKenzie et al., 2018). In marine systems, phage co-infection has been documented to reduce withering foot syndrome in black abalone and has been successfully used to experimentally treat several bacterial diseases in aquaculture (Doss et al., 2017; Wang et al., 2017). Probiotics are widely used to improve health and prevent disease in aqua-cultured organisms (reviewed by Martínez Cruz et al., 2012), and probiotic treatment is in development to treat and prevent infection in wild coral (Paul et al., 2019, 2020; Peixoto et al., 2017; Figure 3a). Co-infection is not commonly used as a therapy. However, co-infection with flukes has been shown to reduce bacterial virulence in aquaculture salmonids (Karvonen et al., 2019).

Importantly, disease may arise from complex shifts in microbiome composition instead of infection by a single agent (Mera & Bourne, 2018; Vega Thurber et al., 2020). Furthermore, co-infection is the norm in marine wildlife systems (Bateman et al., 2020b). In both terrestrial and marine wildlife, co-infection hinders disease management by reducing the sensitivity and specificity of diagnostic tools and influencing mortality and transmission rates (e.g., (Beechler et al., 2015; Ezenwa & Jolles, 2015; Figueroa et al., 2017; Gibson et al., 2011; Stokes & Burreson, 2001; Ushijima et al., 2020). As such, effective marine disease management requires a better understanding of how infectious organisms and microbes interact to propagate and cause disease.

In practice, phage therapy, probiotics, or co-infection necessitate specific knowledge of the infectious agent and the natural therapeutic that benefits the host and the ability to produce the therapeutic (e.g., culturing a co-infecting parasite). Conversely, developing some natural therapeutics, mainly probiotics, may be less costly and time consuming than developing vaccines or synthetic antimicrobials and can be the most viable treatment option for organisms lacking adaptive immune systems. Furthermore, although effective delivery of natural therapeutics is still in early research stages, administration of natural therapeutics may be more effective than vaccines and antimicrobials because they can spread to neighboring hosts, increasing protection across a population (Paul et al., 2019). For example, the Coral Health and Probiotics Laboratory at the Smithsonian Marine Station has found a bacterium that stops stony coral disease progression and possibly prevents infection (Paul et al., 2019, 2020; Table 1). This bacterium may spread among corals and has recently been applied to wild corals off the coast of Florida (Paul et al., 2019; Smithsonian Marine Station, 2020; Table 1, Figure 3a).

Overall, our understanding of healthy baseline microbiomes and parasitomes is still in development, with the notable exception of a few intensively studied marine disease systems, namely corals, abalone (Wang et al., 2017), and fishes in aquaculture (reviewed in Richards, 2014). Natural therapeutics offer a promising management strategy for some marine systems but more research on this topic is necessary before natural therapeutics can be widely used in marine wildlife.

RECOMMENDATIONS

The nuance and complexity of the strategies we discuss here broadly emphasizes the challenges marine disease researchers and managers face. In the following section, we outline preliminary recommendations to guide scientists, managers, and funding bodies to prepare for the expected future increases in the frequency and severity of marine disease outbreaks (Figure 3).

Recommendation 1: Increase basic research capacity for marine disease systems

Terrestrial disease systems have historically received larger amounts of research attention and funding than marine disease systems, largely due to their use in elucidating general disease dynamics applicable to human disease, livestock, and agriculture. (Behringer et al., 2020a; Harvell et al., 2004). There is a growing appreciation for the importance of marine wildlife for supporting human livelihoods and ecosystem services (FAO, 2020), but there remains a relative dearth of knowledge of marine disease ecology, with the possible exceptions of corals, eelgrasses and some aquacultured species. To wit, multiple initiatives have been undertaken in the last decade to increase this knowledge base, including an NSF-supported Research Coordination Network (RCN) on the Ecology and Evolution of Infectious Disease in Marine Systems, a resulting special issue in the Philosophical Transactions of the Royal Society B: Biological Sciences on Marine Disease (Issue 371, 2015), the recent inclusion of marine systems in Ecology and Evolution of Infectious Diseases NSF grants (EEID), and the recent publication of a marine disease ecology textbook (Behringer et al., 2020a). These initiatives are an excellent start, and we recommend increased attention and resources be directed to marine disease research to better monitor, manage, and ideally prevent or mitigate marine disease emergencies. For example, we first need to better define variation in baseline distributions of pathogens across host species, environmental gradients, and time. An improved mechanistic understanding of interactions between hosts, pathogens, and the environment that form the disease triad (Figure 1) will facilitate a comprehensive, and hopefully predictive, understanding of major marine disease systems. Improved funding for basic marine disease ecology, advancement of molecular tools, and development of disease models (e.g., Aalto et al., 2020) should enable scientists to construct this baseline and understand disease dynamics more accurately. An increased basic understanding of marine disease systems will also bolster our ability to employ multiple management strategies described here, including *Forecasting outbreaks*, *Diagnostics*, *Antimicrobials*, *Epidemiological models*, and *Natural therapeutics* (Table 1, Figure 3a). Hand in hand with this increase in basic marine disease research is support of the facilities in which this research can be undertaken (e.g., the USGS National Wildlife Health Centers Honolulu Field Station or the Northwest Fisheries Science Center). Support and expansion of these facilities will also increase our collective ability to test or employ various management strategies, including *Forecasting outbreaks*, *Diagnostics*, *Isolation strategies*, *Antimicrobials*, *Culling*, *Epidemiological models*, *Translocations*, *Captive breeding*, *Vaccines*, and *Natural therapeutics* (Table 1, Figure 3a,b).

Recommendation 2: Understand the links between climate change and disease

Climate change is one of the greatest threats to both human and wildlife health and it is expected to cause a marked increase in wildlife disease emergencies (Burge et al., 2014). Slowing climate change is a crucial component of improving marine wildlife health. While addressing climate change itself is well beyond the scope of management strategies, ameliorating the impacts of it is one of the most important long-term goals for improving marine wildlife health. Over the short term, we recommend prioritizing research that improves the understanding of the effects of climate on host–pathogen relationships in marine ecosystems. For example, explicitly incorporating climate change-related stressors in *Epidemiological models* of disease transmission or in models that *Forecast outbreaks* is of high importance (Table 1, Figure 3b). Furthermore, considering the combined effects of warming and disease is critical for understanding the threats to populations or extinction risk of species, and may warrant consideration when assessing species for *Endangered species lists*. Finally, we suggest incorporating long-term ecological studies on consequences of climate change on marine disease systems, at community and ecosystem scales, into programs that *Monitor outbreaks*.

Recommendation 3: Improve marine ecosystem health

Current funding for marine disease management at state and federal levels is typically dominated by mammals, birds, or those that have other economic value (e.g., fisheries). While this is logical, these "valuable" organisms do not exist in a vacuum, and they fundamentally depend on broader ecosystem health for survival. Furthermore, our own health as humans is tied to ecosystem health. Therefore, we recommend an increase in holistic approaches to disease management that are focused on entire ecosystems rather than isolated target species. This is exemplified by the OneHealth Initiative for the Centers for Disease Control, with "the goal of achieving optimal health outcomes recognizing the interconnection between people, animals, plants, and their shared environment" (CDC, 2018). We emphasize that marine ecosystem health is similarly important to humans as terrestrial ecosystem health, especially as a huge proportion of our global population relies on marine systems as their primary food source (FAO, 2020). One increasingly popular and effective approach for increasing marine ecosystem health is to designate MPAs (please refer to "*Biodiversity and habitat conservation*"). Additional management strategies that also increase ecosystem health include *Targeted habitat restoration*, *Increasing biosecurity*, *Reducing spillback*, and *Natural ecosystem filters* (Figure 3c).

Recommendation 4: Form marine disease monitoring and response networks

To enable timely detection and response to marine disease emergencies, infrastructure must be in place before an emergency begins (please refer to "*Monitor outbreaks*"). The excellent models of the West Coast Marine Mammal Stranding Network and the LEO Network, should be expanded to encompass more taxa over larger areas. For example, the recently formed PRIMED Network (Primary Responders in Marine Emergent Disease, https://www.primednetwork.org/; Figure 3d) covers a wide range of wildlife taxa with the goal of increased disease surveillance and responsiveness to marine disease emergencies on the North American West Coast. We believe these types of networks are crucial for effectively detecting and responding to marine disease outbreaks. However, long-term funding pathways for this and additional networks are not clear. We recommend that state and federal agencies further incorporate marine wildlife disease monitoring and response initiatives into their priorities. Federal-level agency programs, such as the USGS National Wildlife Health Center or National Oceanic and Atmosphere Administration (NOAA) Fisheries, are well situated to sustain monitoring and response programs for a wider range of marine wildlife and to create the infrastructure necessary to employ marine disease management tools such as *Diagnostics*, *Isolation strategies*, *Captive breeding*, and *Translocations*. Diagnostic approaches and surveillance strategies have already been developed for many marine diseases that affect aquacultured or fished species and a similar approach could be undertaken for more marine wildlife disease systems.

Recommendation 5: Develop marine veterinary medicine programs in the US

Another pathway to increased research on marine disease systems and toward forming monitoring and response networks is through an increase in marine wildlife veterinary experts. However, there are currently no American Veterinary Medical Association-accredited Doctor of Veterinary Medicine (DVM) programs with a focus on aquatic and/or marine wildlife medicine. Programs that do incorporate marine wildlife are skewed toward marine mammals. Marine-focused internships and residency programs for veterinarians are few in number (but please refer to programs associated with the International Association of Aquatic Animal Medicine and World Aquatic Veterinary Medical Association), and few funded positions for wildlife veterinarians exist. Legislation addressing these deficits has not received support (please refer to the rejected Wildlife VET Act 2019 by Representative Alcee Hastings of Florida [Hastings et al., 2019]). Policy actions supporting experts are key to wildlife disease management and response, and it is critical that they explicitly include resources and support for marine wildlife veterinarians. This support will improve the capacity for nearly all management strategies described in the *Outbreak response* strategies and *Targeted outbreak prevention* strategies (Figure 3e).

Recommendation 6: Enact policy that addresses marine wildlife disease

As touched on above, a major pathway to increased research on marine disease systems and toward forming monitoring and response networks is through legislation. However, to the best of our knowledge, there is currently no enacted legislation in the USA or globally that addresses wildlife disease emergencies. Wildlife population health is an underlying concern of multiple state and federal agencies, and the time-sensitive nature of disease emergencies has inspired multiple federal-level legislative proposals, but none has been successful. Examples include the Marine Disease Emergency Act of 2015 introduced in response to SSWS by Representative Dennis Heck of Washington (Heck et al., 2015), the Wildlife Disease Emergency Act of 2018 introduced by Representative Carol Shea-Porter (Shea-Porter et al., 2018), and the Global Wildlife Health and Pandemic Prevention Act of 2020 introduced by Senator Christopher Coons of Delaware (Coons & Graham, 2020). This type of legislation would increase our capacity to identify and declare wildlife disease emergencies and to coordinate rapid responses, with benefits to the economy and human health. We recommend that continued efforts be undertaken to achieve the goals outlined in these pieces of legislation. That said, marine wildlife disease occurs worldwide, and both hosts and pathogens disregard political boundaries. So, it is important that countries coordinate their monitoring and response programs whenever possible. At the international level, we recommend a greater focus on incorporating marine wildlife disease management into existing international agreements such as the United Nations' Sustainable Development Goals or organizations such as the World Organization for Animal Health.

CONCLUSION

Active management of high value or charismatic megafauna, particularly terrestrial wildlife species, has been practiced for more than a century (Bolen & Robinson, 2003;

Leopold, 1987). In marine systems, the will to embrace these management practices is more modest and is typically focused on managing commercial and recreational fisheries. For other wildlife, we have been more inclined to adopt geographically specific, ecosystem-level management such as the creation of MPAs (Grorud-Colvert et al., 2021; Lubchenco & Grorud-Colvert, 2015). Recently, active management and rehabilitation efforts have been slowly "moving seaward" into estuarine ecosystems, mangroves, and coral reefs (Barbier et al., 2011). But the considerable efforts that managers regularly undertake for terrestrial wildlife, such as rehabilitating wolves in Yellowstone National Park or condors in California, are rarely considered for threatened marine species (exception: sea otter reintroduction, Jameson et al., 1982; and southern resident orcas, Clevenger, 2020). In the event of a marine wildlife species decline, the types of strategies outlined in this manuscript may become crucial in marine systems. Adopting active management may be especially pressing as we are witnessing the collapse of entire coral reefs ecosystems (Hughes et al., 2018) and the outbreaks of marine epizootics on a global scale (Groner et al., 2016; Hamilton et al., 2021).

Proactive rather than reactive approaches to marine disease management are needed to avoid catastrophic population loss. This approach will require a collaborative effort across academic institutions, federal agencies, and nonprofits. It will require people with expertise across disciplines spanning marine sciences, disease ecology, and veterinary medicine. We encourage broad collaboration, and for marine managers to follow the lead of their terrestrial counterparts to proactively manage marine systems.

AUTHOR CONTRIBUTIONS

Sarah A. Gravem conceptualized the manuscript. Caroline K. Glidden, Laurel C. Field, Sarah A. Gravem led writing. All authors helped write the manuscript and approved the final version.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study.

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