Impacts of human disturbance in marine mammals: Do behavioral changes translate to disease consequences?

Melissa Collier, Sania Ali, Janet Mann, Shweta Bansal

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Abstract

Humans have been altering wildlife habitats and wildlife behavior worldwide at an accelerated pace in recent decades. While it is well-understood how human-induced behavioral changes affect infectious disease risk in terrestrial wildlife, less is known in marine life. Here we examine this link in marine mammal populations by (1) conducting a systematic literature review to determine how human disturbances change marine mammal behavior in ways that can impact disease spread, and (2) examining how these behavioral changes might influence potential epidemics using a mathematical modeling framework. We find that human disturbances can influence marine mammal behavior in a way that increases their exposure and susceptibility to pathogens, as well as their infectivity, or ability to effectively shed pathogens and infect conspecifics. When these changes to exposure, susceptibility, and infectivity are applied in four different marine mammal case studies, epidemics are predicted to be larger and more likely to occur. Considering the rate at which human disturbance is increasing in the marine environment, and the large number of marine mammal species that are endangered or on the verge of extinction, we advocate for the careful consideration of the direct and indirect impact of human disturbance on marine mammal health.

1 Introduction

Humans have been altering wildlife habitats worldwide at an accelerated pace in recent decades. According to a 2019 assessment by a 94 nation intergovernmental body, 75% of the terrestrial environment has been altered by human disturbance and approximately 1 million plant and animal species are at risk of extinction due to human threats [1, 2]. Human disturbance also alters animal behavior- the adverse consequences of which have been well documented. For example, human activity decreases home range size for many terrestrial mammals [3], and exacerbates spatial and temporal avoidance of humans (e.g., caribous [4]; cheetahs [5];[6], coyotes and bobcats [7]; leopards [8]). Importantly, these behavioral changes are known to impact pathogen transmission among terrestrial wildlife [9, 10], but critical gaps remain, particularly for marine fauna. Most of the marine environment is currently being altered by human associated disturbances (approximately 66%) [1], and marine wildlife disease has markedly increased over the past 40 years [11]; recent reports suggest the true magnitude of marine disease is grossly underestimated [12]. Despite this, few studies have examined the link between human-induced behavioral changes in marine life, and their potential consequences for infectious disease. Here, we examine this link by focusing on marine mammals, given their visibility as flagship, sentinel, and umbrella species.

Marine mammals are ideal targets for this type of study. First, they are the most visible marine species given that they are large, surface to breathe, and pinnipeds breed and rest on land or ice. When marine mammals strand, they garner considerable amount of attention and concern from the public [11]; consequently the causes of these strandings (e.g. fishery entanglements, disease) are well documented [13]. Because of their visibility and charisma, marine mammal tourism is a multi-billion dollar industry, producing more revenue than aquaculture and fisheries combined [14], a strong indication of human interest in these megafauna. Second, while mass mortalities of marine mammals are clearly of concern to the public, their status as top predators and sentinel marine species attracts scientific scrutiny. Declines in top predator populations can alter population dynamics and abundance [11], cause extinction of endangered species, and alter the predator/prey ratios that can affect healthy ecosystems [15]. Additionally, marine mammals are sentinels for ocean health and can therefore aid in the protection of entire ecosystems, thus making them umbrella species[16, 17, 18]; protecting marine mammals and their habitats necessarily protects other species living within their habitats. Finally, with extensive research available on the how human disturbance impacts marine mammal behavior, we can model how behavior change can affect pathogen transmission.

Human disturbance is a known cause of marine mammal mortality by way of fishing gear entanglements [19], vessel strikes [20], loud sounds [21] , and ending up as bycatch in major fisheries [22]. But humans are also responsible for the increased risk of emerging infectious disease in the oceans. For example, we have introduced pathogens into marine habitats via storm water runoff and man-made fresh water intrusions [23, 24, 25, 26], and immune function in many species has been greatly deteriorated from exposure to toxic chemicals and warming global temperatures [27, 28, 29, 30]. Interestingly, the frequency of marine mammal mass mortality events has increased substantially in the past several decades [11, 12, 13]. In the United States, there have been 70 recorded events of marine mammal mass mortalities since 1969 [13]. While 47% of these mortalities are cause unknown, 12% have been identified as epizootics from infectious disease. Of these epizootics, 66% occurred after the year 2000; the two most recent epizootics are the 2013 cetacean morbillivirus outbreak on the Atlantic Coast that resulted in more than 1,650 bottlenose dolphin (*Tursiops truncatus*) deaths, and the ongoing 2018 phocine distemper virus outbreak in the Northeast United States that has already resulted in more than 3,100 harbor (*Phoca vitulina*) and grey (*Halichoerus grypus*) seal deaths [13].

Humans may also be influencing the spread of these pathogens within marine mammal species, which is vital to understanding population viability and vulnerability. Specifically, human disturbances can impact individual *host competence*, or the ability of one host to transmit parasites effectively to another host[31]. Host competence has both a behavioral component (e.g. host ability to transmit disease based on its social interactions), and an immunological component (e.g. host ability to both transmit and be infected by a pathogen based on their immune system's resistance and tolerance of parasites) [32]. Human disturbances influence both components of host competence in wildlife species [27, 9]. For example, increased ocean temperatures can suppress diverse immune responses in corals and sea crabs, thus increasing their likelihood of infection [27]. (Martin et al. 2010). Behaviorally, when relocated by humans, captive primates increase their time spent in groups, thus increasing their exposure to potentially infected individuals [33]. Changes in host competence can impact disease spread through a population, which can be examined using wildlife contact networks [34, 35, 36].

In contact networks, individuals are represented by nodes that are connected by edges, which indicate contact capable of disease transmission between two individuals. When contact network structure is altered by human disturbances, there can be significant consequences on pathogen transmission [6, 33, 37]. For example, altering network connectivity to account for changes in wildlife population densities due to urbanization, translocation, or sickness behaviors (e.g. lethargy, decreased mating activity) influences pathogen transmission in terrestrial wildlife species[9].

We examined the impacts of human disturbance in the marine environment on infectious disease risk in marine mammals. In particular, (a) we characterized how human activity alters the individual behavioral and immunological aspects of host competence of marine mammal species, and (b) considered the impact of altered host competence on disease transmission using an epizoological network modeling approach. Although humans clearly have a significant impact on marine wildlife species worldwide, the indirect effects of human disturbance on wildlife behaviour and physiology, which in turn enhance infectious disease risk are rarely considered. As such, we may be underestimating the true burden of anthropogenic pressure on wildlife species as a whole.

2 Impact of Human Disturbances on Marine Mammal Behavior

To examine the ways in which the behavioral and immunological aspects of host competence are impacted by human disturbances in marine mammals, we conducted a systematic literature review using the PRISMA framework [38]. A human disturbance was defined as any anthropogenic activity that acts directly on a marine mammal species, and assigned these to one of four categories: (1) coastal human activity (vessel traffic, construction, noise pollution, etc.), (2) human associated feeding (provisioned animals, foraging using trawl nets, etc.), (3) marine debris, and (4) human-made pollution (polychlorinated biphenyls, polycyclic aromatic hydrocarbons, etc). Indirect disturbances that resulted from intermediate species, such as prey depletion from over-fishing were not considered. Climate change and extreme climate events were excluded as a disturbance category because it exacerbates disease transmission directly by increasing pathogen fitness (e.g. increasing pathogen development rates, relaxing overwintering restrictions on pathogen life cycles)[30], making it difficult to parse out whether resulting disease consequences will be due to this, or increased host competence.

We began with several well known studies of human disturbances in the marine mammal literature, and conducted an electronic database search for additional studies published since 1995 in Web of Science and Google Scholar using the terms "human", "disturbance", "marine mammal", "behavior", "response", "pollution", "boat" and "fishery", yielding a total of 757 studies. These were screened to exclude papers if: (1) the study subject was not a marine mammal or was in captivity; (2) there were no behavioral changes as a result of a direct human disturbance; (3) results did not demonstrate a potential impact to marine mammal health; it was a review paper or not peer reviewed (grey literature and dissertations).

In total, there were 126 studies that demonstrated human induced impacts to individual marine mammal host competence. The scientific quality or soundness of these studies was not evaluated, but in aggregate they present a consistent picture (Table 1, Figure 1).

These impacts were then considered through the lens of networks. Disturbances that affected the behavioral aspect of host competence impact host contact network structure by altering the number of interactions (edges) of affected individuals (Figure 2A&B). Pathogens propagate through edges in contact networks, and changes to these edges affect opportunities for pathogen exposure. Disturbances that increased the immunological aspect of host competence impact a network by increasing the vulnerability of an individual (node) to pathogen spread (Figure 2C&D). In other words, a pathogen will be more likely to transmit along edges connected to nodes with high immunological competence. Changes to competence brought on by human disturbances are summarized by the perspective of the network change below. To add additional perspective, these changes are also summarized by the type of human disturbance in Table 1.

2.1 Behavioral Competence

Behavioral competence accounted for how social behavior affects transmissibility. Typically, any change in an individual's activity will affect social contact behaviors and/or gregariousness, which can increase or decrease their exposure to pathogens respectively [32]. Here we discuss how human disturbances alter behavioral competence by considering their impact on individual-level and group-level network connectivity. Specifically, disturbances influenced the individual exposure of hosts to transmission which will alter their degree (the number of unique associates where an individual can transmit disease within their population) (2A). Disturbances also influenced group exposure which affects network modularity (the tendency for a population to be tightly interacting within [sub]groups and sparsely interacting between groups) (2B). Finally, disturbances influenced the introduction of novel pathogens by increasing contact with humans (zooanthroponosis or reverse zoonosis)[39])

Individual Exposure. We found 18 studies on 11 marine mammal species that demonstrate increased risk of individual level exposure to pathogens within populations. For 15 of these studies, individual degree was increased as a result of coastal human activity which decreased the average distance between animals and increased their group sizes and aggregations.

Four studies showed increased degree between "human-associated foragers", or animals that obtain food via anthropogenic pathways. Human-associated foraging has been seen in at least 25 different marine mammal species [40] such as California sea lions (*Zalophus californianus*), common bottlenose dolphins (*Tursiops truncatus*), and botos (*Inia geoffrensis*) removing fish from gillnets; rough-toothed dolphins (*Steno bredanensis*), and killer whales (*Orcinus orca*) stealing hooked fish, sperm whales depleting long-lines [41], and bottlenose dolphins following trawl nets to forage for prey [40, 42, 43] or begging from human vessels for food handouts [44, 45, 46, 47, 48]. Human-associated foragers aggregated near human food sources, which increased their connections with other human-associated foragers, and their risk of exposure to pathogens. Similar results were seen in a separate review of 115 studies on terrestrial wildlife, where 95% of the studies demonstrated increased contact rates between human-provisioned hosts resulting in increased pathogen transmission risk [49].

In contrast, decreased individual exposure was seen in four studies on three cetacean species, involving individuals entangled in marine debris. In each of these studies, entangled individuals decreased their individual degree while entangled. For example, in New England, USA researchers observed a group of Atlantic white-sided dolphins (*Lagenorhynchus acutus*) abandoning an individual upon entanglement with fishing gear [50]. Similarly, a young adult bottlenose dolphin in Australia was uncharacteristically socially isolated when entangled in fishing gear, but resumed normal social contacts once freed from the line [51]. While encountering entangled individuals during behavioral research surveys is rare, similar results in group composition have been reported over time that show a decrease in contacts during periods of entanglement. While the risk of individual exposure to disease is reduced for entangled individuals, this may be outweighed by increases in immunological effects in such a setting.

Group Exposure. In 12 studies that examined group size and composition, 11 reported increases to group sizes and aggregations, a pattern which decreases the modularity of their contact networks, and increases the probability of pathogen exposure for unique subgroups of individuals. However, one study found that human activity actually fractured groups and increased network modularity, thus decreasing the probability of group level exposure to pathogens [52].

Increased modularity was documented in nine studies on two bottlenose dolphin species, engaged in human-associated foraging. Because not all individuals in a population participated in human-associated foraging, group-level connectivity was affected. Typically, human-associated foragers displayed behaviors that are highly specialized for small communities [42, 48, 43, 53, 54]. As a result, human-associated foragers were shown to have unique group sizes and habitat preferences [55], resulting in little interaction with "natural" foragers. This increased network modularity might decrease the risk of group exposure to pathogens.

There was both increased and decreased group-level pathogen exposure risk that resulted from human disturbance. However, in all nine studies where this risk was decreased, there were also increases to either individual-level exposure (high contact with other conspecifics or with humans) or to pathogen susceptibility (discussed below). Therefore, while a particular human disturbance decreased behavioral competence by lowering group exposure risk, the same disturbance also negatively influenced pathogen spread in other ways.

Pathogen Introduction. Marine mammals that participated in certain methods of human-associated foraging increased their contact with humans in seven studies on two bottlenose dolphin species. This increased their potential exposure to novel pathogens, raising concern for zoonotic (wildlife to human) and reverse zoonotic (human to wildlife) disease transmission potential. Disease transmission from marine mammals to humans has been reported in managed care populations for many bacterial, viral and fungal pathogens [56, 57]. Few studies examine the potential for reverse zoonotic transmission in marine mammals. However, a recent study found evidence for human pathogens present in bottlenose dolphins that have high human contact due to a provisioning program in Shark Bay, Australia [58], supporting the idea that the opportunity for pathogen transmission between certain provisioned and beggar animals and humans (such as by touching/breathing on animals) is much higher than with naturally foraging animals.

2.2 Immunological Competence

Immunological competence accounted for the portion of host competence that examines how individual's immune system responds to pathogens [32]. It should not be confused with the medical term "immunocompetence", or the body's ability to defend itself from pathogens [59]. Instead it should be thought of from the point of view of the pathogen, where a host with higher immunological competence provides a more competent environment for the pathogen to reproduce and spread. Disturbances influenced immunological competence by increasing an individual's *susceptibility*, or the probability that an individual will become infected with a pathogen upon exposure to it. Disturbances also influenced the immune system's tolerance of pathogens, or their ability to reproduce to the minimum threshold number required for transmission[60]. Therefore, disturbances potentially increased an individual's outward *infectivity*, or ability to spread infection.

In the context of networks, increased susceptibility and infectivity of an individual is reflected by increased edge vulnerability, where pathogens are more likely to transmit on these more vulnerable edges. In the context of networks, we argue that disturbances can influence the susceptibility and infectivity of an individual by increasing the vulnerability of their edges. By increasing the susceptibility of a node, the individual becomes more vulnerable to transmission *from* any infected contacts (Figure 2C). By increasing the infectivity of a node, the individual becomes more likely *to* transmit to their contacts upon infection (Figure 2D).

Susceptibility. Human disturbances impacted marine mammal behavior which can in turn contribute to energy loss. Energy loss has been linked to immunosuppression in vertebrate species [61] by impeding "allostasis", or the ability of an animal to maintain homeostasis during life history events (e.g. migration, mating, reproduction) [62]. Marine mammals experiencing an energetic loss could see a drop in their allostasis, resulting in pathological conditions from lack of immune function [63].

We found 79 studies on 29 marine mammal species where coastal human activity could contribute to energy loss in marine mammals. In 72 of these studies, marine mammals displayed short-term avoidance behaviors, where they increased the amount of time they spent traveling or diving away from the disturbance, and decreased the amount of time they spent resting, socializing, and foraging. In 11 of these studies, marine mammals reoriented or completely changed their swimming paths or patterns. Changes in movement or behavior in response to human presence and noise are known to elevate energy loss and consequently impact fitness [64]. For example, in minke whales (*Balaenoptera acutorostrata*) and killer whales subjected to increased boat traffic, both species spent more time traveling and less time foraging, resulting in an estimated 42% and 18% decrease in energy intake for the respective species [65, 66]. Similarly, boat interactions with bottlenose dolphins during foraging activities showed decreased net energy gains for both males and females [67], and when fleeing shipping noise, beaked whales (*Ziphius cavirostris*), saw a more than 30% increase in their metabolic rates [68].

Some marine mammal populations also demonstrated long-term avoidance behaviors, such as abandoning their habitats. Eleven studies reported long-term avoidance behaviors. For example, the abundance of Indo-Pacific bottlenose dolphins in Australia significantly decreased when the number of dolphin tour boats in their habitat reached two, suggesting that the cost of tolerating their presence has exceeded any benefits of remaining in the area [69]. Although long term avoidance will remove the individuals from the disturbance, this type of shift can still negatively affect the animals and impact their energy budgets by forcing them from their preferred habitats. For example, increased tourist activity has significantly affected the southern resident population of killer whales; while the animals could move to a different area (such as out to the Juan de Fuca Strait) to evade whale watching boats and heavy shipping traffic, this could also place them in habitat of low prey density, making it more difficult to forage in an area they are unfamiliar with [70, 71]. That population is now on the verge of extinction due to human impacts [72]

Entanglements in fishing gear also changed the energy budgets of marine mammals, as noted in 4 studies on 3 cetacean species. Individuals showed significant decreases to foraging and diving behaviors and increases in traveling while entangled in heavy and obstructive fishing gear. For example, an entangled Indo-Pacific bottlenose dolphin in Shark Bay, Australia demonstrated significant decreases in foraging and socializing behaviors and an increase in the amount of time spent fast traveling while entangled, compared to both before entanglement and after freeing itself [51]. Additionally, in northern right whales (*Eubalaena glacialis*) dive depth and duration is shown to be significantly shorter when entangled [73] as the cost of the whale towing heavy fishing gear was calculated as an increase in total power input from 1.6% to 120.9%, with locomotive power requirements increasing 60.0%–164.6% [74].

Malnutrition might also increase marine mammal susceptibility to pathogens, as it has been linked to immunosuppression and increased infection susceptibility in both humans and animal species [75]. The cellular immune system is depressed in malnourished individuals, which predisposes the host to increased morbidity and mortality as demonstrated in human systems [76, 77, 78, 79] and more recently in animal systems [80, 81, 82, 49]. Indeed, in humans, malnutrition is the primary cause of immunodeficiency worldwide and has been strongly related to both infant mortality and infectious disease prevalence [83], suggesting that malnutrition in wildlife could have similar consequences [84].

Human-associated foraging, such as food provisioning, contributed to malnutrition in marine mammals and decreased overall health in four studies in two bottlenose dolphin species. For example, human provisioning negatively affected both female reproductive success and calf survival at two sites in Western Australia [53, 85, 86]. Additionally, observers in the United States have witnessed wild beggar dolphins being fed beer, pretzels, liquor, candy bars, bread, bologna, and baited hooks from recreational boaters [87], ls, liquor, candy bars, bread, bologna, and baited hooks from recreational boaters (Orams 2002), as well as spoiled bycatch or baitfish, which was deadly for marine mammals [44]. Indeed, provisioned food was a source of immunosupressive contaminants in 80% of studies on food-provisioned terrestrial wildlife [49].

Human-made pollution can also increase marine mammal susceptibility to disease [27]. Marine mammals are consistently exposed to marine pollutants such as Polychlorinated biphenyls (PCBs), heavy metals, and polycyclic aromatic hydrocarbons (PAHs), resulting from mine drainage, offshore oil and gas exploration, industrial and domestic effluents, agricultural runoff, oil spills, and other human activity [88, 89]. These pollutants alter immune homeostasis, resulting in immunosuppression and inflammation linked to hypersensitivity and autoimmune disease[28, 29]. Immune impairment was seen in harbor seals exposed to cumulative environmental contaminants [90, 91] bottlenose dolphins compromised by the Deepwater Horizon oil spill [92, 93], and in vitro studies of PCBs in California sea lion [94], bottlenose dolphin [95] and killer whale lymph node cells [96]. Pollutants were also linked to reproductive failure in harbor porpoises in the UK [97]. A total of 14 studies in 16 species documented pollutants at high levels in marine mammals, raising concern for the greater potential of disease spread among populations of marine mammals living in polluted waters.

Infectivity. We defined infectivity as an infected individual's likelihood of passing along their infection to another individual upon interacting with them. Infectivity can increase in wildlife species with an increase in stress hormones. While it is well known that the elevation of stress hormones is linked to immunosuppression in many taxa (and therefore increased susceptibility) [98]), increased levels of stress hormones in an individual has also recently been associated with an increase in their suitability to pathogens [99, 100, 10]. For example, one study on West Nile Virus in songbirds showed that individuals with experimentally elevated stress hormones were significantly more viremic than control hosts, and only these individuals had viral loads at or above the infectious threshold [99].

Six studies on eight cetacean species reported increased stress in marine mammals associated with coastal human activity. For example, the complexity of dolphin's temporal dive patterns was shown to decrease upon an increase in vessel traffic [101]; the reduction of behavioral complexity is an indicator of stress in many species [102]. Additionally, the stress levels of highly endangered North Atlantic right whales in the Bay of Fundy Canada were found to decrease following the events of September 11th, 2001 in which shipping traffic and noise was significantly lower [103]. These increases in stress can increase both susceptibility and infectivity, meaning highly stressed individuals are more likely to both infect, and be infected by, their contacts.

3 The Effect of Human Disturbances on Disease Transmission Through a Population

Our literature review found that human disturbances in the marine environment can increase individual host competence in marine mammal communities by altering their behavior and directly impacting their health. These individual changes can also alter the contact network structure of a population by changing individual degree, group level modularity, and edge vulnerability. While highlighting the changes to individual host competence is a good first step, it is more beneficial for wildlife managers and researchers to understand how these impacts aggregate to influence population level transmission dynamics by examining the spread of disease on the resulting altered networks. In other words, how might the changes to network structure resulting from the individual host competence highlighted in our review, translate to epidemic consequences on marine mammal populations as a whole?

To investigate this, we made predictions about infection spread using an susceptible-infected-recovered (SIR) model [104], focusing on four marine mammal case studies for which empirical data are available on social networks in the published literature: 1,007 California sea lions

(*Zalophus californianus*) [105, 106], 50 Australian humpback dolphins (*Sousa sahulensis*) [107], 43 killer whales (*Orcinus orca*) [108], and 371 Indo-Pacific bottlenose dolphins from Shark Bay Australia (*Tursiops aduncus* [109]). We modeled changes to these empirical contact networks observed in our review to predict infection outcomes due to human disturbances.

Each case study contained contact network data for a small population. The nodes in the network represented individuals and edges represented social association through shared group membership or spatial proximity through shared space use; it was assumed that these contacts are sufficient for the transmission of infection[110, 109]. Edges were treated as binary as the impact of an interaction weight (e.g. contact duration, frequency of contact) on transmission is not known for most pathogens. Instead, edge weight-thresholding was used to remove edges with low interaction weight, [111, 112] to account for the stability of groups and individual interactions (Figure S1; a more detailed explanation can be found in the Supplement).

On each network, infection spread was simulated using stochastic epidemiological simulations based on a chain binomial, susceptible-infected-recovered (SIR) model [104]. The SIR model is a well-established method in mathematical epidemiology and proves to be a good model for fully immunizing infections. At each time step, susceptible nodes became infected with a probability proportional to a fixed transmission rate and the number of infectious individuals they have interactions within the network. Infected individuals were assumed to be infectious for 7.5 days on average, and lead to 1.1 new infections on average to reflect the characteristics of morbilliviruses in marine mammals, a pathogen known to cause mass epidemics in both pinniped and cetacean species[113, 114]. (More detailed methods can be found in the Supplement.) To minimize standard error, 500 disease simulations were performed on each network to determine the disease outcomes for each case study, with and without the modeled human disturbances.

3.1 Modeling Human Disturbances

We examined the impact of disease consequences when susceptibility, infectivity, and exposure was increased in four different scenarios:

1. Individual susceptibility to pathogens was increased, representing fitness costs of human avoidance, exposure to toxic chemicals, or malnutrition from human-associated foraging.
2. Individual susceptibility was increased in concert with infectivity, representing increased stress in marine mammals exposed to high human activity.
3. Individual exposure (degree) was increased representing an increase in contacts for marine mammals exposed to high human activity or engaged in human-associated foraging.
4. Individual exposure was increased in concert with susceptibility and infectivity, representing individuals increasing their degree in response to high human activity, while also accounting for high stress levels.

Group exposure was not included as a scenario, since the impact of network modularity on disease consequences in contact networks has already been examined [115]. Pathogen introduction was also not included as a scenario, as it is discussed in a separate analysis below.

To model each scenario, we considered a proportion of the population that may be exposed to human disturbances based on the typical group size for that species 15% of the individuals in each network (150 sea lions, 8 humpback dolphins, 7 killer whales and 55 bottlenose dolphins) were randomly selected to be affected by human disturbances.[116, 117, 118, 119]. Based on these numbers and the assumption that more than one group in each network is likely to be impacted by humans, we randomly select 15% of the nodes in each network (150 sea lions, 8 humpback dolphins, 7 killer whales and 55 bottlenose dolphins) to be affected by human disturbances. To determine by how much to increase susceptibility and infectivity in these human-affected individuals, we examined quantifiable changes in these characteristics due to pollution, stress, and malnutrition in wildlife literature [120, 80, 99] . Based on our findings we increased both the susceptibility and infectivity of human-affected nodes by 1.6. To standardize increasing exposure of individuals for reliable comparison, we increased the total number of edges between human-affected nodes by a factor of 1.6. (A more detailed explanation of group sizes and parameter selections can be found in the Supplement).

3.2 Disease Outcomes under Disturbance

For each network we measured the epidemic size at the population level. Epidemic size is defined as the proportion of individuals in each network that were infected, averaged over all 500 simulations. We also calculated epidemic size at the individual level, where we kept track of the proportion of both human-affected and unaffected individuals that were infected over the 500 simulations. Finally, we carried out a tolerance analysis to understand how variation in our parameters and increased pathogen introduction would affect the results in all four scenarios. Results are only shown for the bottlenose dolphin and sea lion case studies; the humpback dolphin and killer whale networks showed similar results and are included in the tolerance analysis and further discussed in the Supplement.

Population Level Outcomes. In general, changes to host competence in all four scenarios had similar effects on the epidemic size for all four marine mammal networks (Figure 3a, 3b & S3). Increasing susceptibility alone did not increase epidemic sizes in any of the networks, and increasing individual exposure alone only increased epidemic size in the sea lion and bottlenose dolphin networks. However, increasing susceptibility and infectivity together, as well as increasing all three did show an increase in epidemic size for all four networks, with the latter scenario being by far the worst in all four networks. This scenario also showed that the peak of the epidemic occurred earlier in all four networks (Figure 3c, 3d & S3).

Affected Individual Outcomes. A larger proportion of the human-affected group was infected in each of the simulations than in the unaffected group (Figure 4 & S4). In the sea lion network, the epidemic size of the human-affected group was higher in every scenario, (results that were also seen in the killer whale network). However, in the bottlenose dolphin network, this was only true in the third and fourth scenarios where individual exposure was included.

Tolerance Analysis. As human disturbances increase, how does wildlife tolerance impact disease dynamics? Tolerance is defined in one of two ways: a) the minimum change required to behavioral or immunological competence for epidemic size to be significantly higher; and b) the minimum proportion of the population that needs to be affected for epidemic size to be significantly higher. This tolerance is considered under all four scenarios discussed above ((1) increased susceptibility, (2) increased susceptibility and infectivity, (3) increased individual exposure, and (4) all three processes increased). Significant changes to epidemic size were measured via a One-way ANOVA, and pairwise t-tests with a Tukey HSD familywise error-rate correction to identify which specific scenarios have significant differences compared to the baseline (i.e. no human disturbance).

The results of these analyses are in Figures 5a and 5b. In the first scenario (increased susceptibility), 15% of the individuals in each network needed to be between 1.7 to 4 times more susceptible to pathogens in order to see an increase in epidemic size. Alternatively, if the increase to susceptibility is maintained at 1.6, the number of individuals that would need to be disturbed in each network to see increased epidemic sizes ranged from 17% to more than 40%. This suggests that there must be major changes to marine mammal susceptibility in order to influence epidemics, if this is the only change to their individual host competence.

In the second scenario, susceptibility and infectivity need only be increased by 1.7 or less on 15% of all four networks to increase epidemic size. In fact, in the sea lion network, these factors need only be increased by 1.1 to see a worse epidemic. When maintaining the increase at 1.6, only 5% of individuals in the bottlenose dolphin and sea lion network needed to be affected to increase epidemic size, and between 10-20% individuals in the humpback dolphin and killer whale network. This suggests that small increases in infectivity and susceptibility together will have a huge influence on epidemic outcomes across marine mammal species.

In the third scenario, increasing exposure on 15% of the network never increased epidemic size for the humpback dolphin and killer whale network due to the small size of these networks; once the maximum number of connections to add between affected individuals was added, then connectivity could no longer increase. Only when more individuals in these networks were disturbed (between 20-28% of the network) will increased individual exposure have an effect on epidemic size. However, in the larger bottlenose dolphin and sea lion networks, there was an increase to epidemic size when 15% of the networks are 1.3 and 1.8 times more connected to each other respectively. This shows that increasing the individual exposure of networks will increase epidemic size, but only after a certain threshold of individuals are disturbed. This was likely due to our constraint of increasing exposure only between other human-affected individuals. Since contacts were only increased between other affected individuals, epidemics are likely contained within the affected individuals.

In the final scenario, susceptibility, infectivity and connectivity need only be increased by 1.1 or 1.2 on 15% of each network to show an increase in epidemic size. Additionally, when parameters were maintained at an increase of 1.6, only a very small number of each population needed to be affected (between 2-10%) to see a worse epidemic. Predictably, these results showed that when all aspects of competence were increased in a small number of individuals, or by a small amount, epidemic outcomes will be alarmingly worse.

In order to consider the impact of pathogen introduction from human contact on disease consequences in marine mammal networks, we conducted a third tolerance analysis where tolerance was defined as the minimum number of human-affected individuals initially exposed to pathogens where the probability of an epidemic was 50% or more. The probability of an epidemic was the proportion of simulations where epidemics occurred. Figure 5c summarizes the results of this analysis in each of the four disturbance scenarios. Overall, we found that for all four networks, only 6 or fewer individuals needed to be initially exposed for there to be a high epidemic probability.

4 Discussion

Our review chapter examined how human activity can influence pathogen transmission potential in marine mammals. Despite the increase in anthropogenic pressure on our oceans, very little work has been done to examine how human impacts are potentially contributing to the rise in disease in marine life. We showed that human disturbances likely contribute to behavioral and immunological changes in marine mammals, which in turn increases individual susceptibility and infectivity, and alters exposure. In effect, these scenarios predicted worse epidemics across four different marine mammal contact networks, highlighting the concern that indirect effects of human disturbance on marine wildlife may well exacerbate an already alarming trend.

Increased susceptibility, infectivity and individual exposure on less than half of a population resulted in significantly larger epidemic sizes in four different marine mammal networks. In other words, disturbances need not affect an entire population for an epidemic to propagate. A small subset can have a substantial impact. Additionally, individuals affected by human disturbances typically drive epidemics, as increasing susceptibility and individual exposure affected these individuals significantly more than undisturbed individuals. When human disturbances increased infectivity, however, total epidemic sizes increased dramatically in both affected and unaffected individuals, and only a small percentage of individuals needed to be affected by disturbance to result in an increase in epidemic size. This highlights and additional importance of reducing human-induced stress on marine mammals.

The effects of increased [sub]group exposure on the disease consequences of wildlife populations has already been demonstrated. Typically, networks with low modularity, (seen in marine mammal species exposed to high levels of human activity) have higher rates of group exposure, thus increasing the potential for an epidemic to spread across a population[115]. In contrast, networks with high network modularity have low group exposure rates, and will therefore result in lower disease burdens as they are able to 'trap' infections within communities, which delays the spread of disease outbreaks [115]. Human-associated foraging was shown to increase network modularity across marine mammal species, suggesting a potential decrease in disease consequences within a particular population, although this may be outweighed by other factors. For example, even though modularity is increased during human-associated foraging scenarios, their susceptibility may increase from declining health, and their exposure is increased from increased humans contact and contact with other human-related foragers.

It took an alarmingly small number of pathogen introductions (such as through increased human contact) for the probability of an epidemic to reach 50% or more. As discussed previously, there has been little to no documentation of reverse zoonosis in marine mammals, although researchers are noticing surprisingly high rates in livestock and terrestrial species. For example, one study demonstrated how human-to-swine transmission of influenza is far more frequent than swine-to-human transmission, transforming the decades-old stereotype that pigs are the sources of viruses, instead of the recipients [**?**]. Another review describes 56 documented human-to-animal disease transmissions among wildlife, livestock, and companion animals [39].

These findings of reverse zoonosis in animal species, the increased frequency of human contact with marine mammals described in this chapter, and the small number of pathogen introductions required to increase epidemic probability, raise concern for the potential of increased epidemic probability from pathogens of human origins.

4.1 Study Limitations

The indirect anthropogenic effects such as prey depletion on the behavior and health in marine species were not considered in this review. For example, the southern resident killer whales of the northeastern Pacific's primary prey is the highly endangered Chinook salmon. Studies have shown the impact of the salmon fishery on declining killer whale health, and the need for a reduction in annual fishery returns in order to improve killer whale fitness [121]. Furthermore, southern salmon stocks are found to have significantly higher levels of pollutants and lower lipid content, increasing the amount of salmon southern killer whale must eat to maintain energetic demands, while also exposing them to higher levels of toxins [122]. Future research should focus on these indirect effects, in order to gather a more inclusive picture of the full impact of human disturbances on marine life and disease.

The effects of climate change on potential disease consequences in marine mammals was also not considered here. Climate change has already been linked to phenological shifts in marine mammals and warming waters provide ideal habitats for many pathogen species [123, 30]. Additional stressors of climate change include increased exposure to persistent organic pollutants (POPs) among marine mammals, direct loss of the sea ice habitat, effects on body condition due to trophic shifts, and increased human habitation in the Arctic [123]. Forecasts on the vulnerability of marine mammals to the effects of climate change are available [124], but changes in disease dynamics are unknown. To establish clear links between climate change and disease spread, data from long-term studies are needed.

Methodological considerations are also vital. Social associations defined the edges of the contact networks, which do not always involve any sort of physical contact. Two of the most well known marine mammal diseases, cetacean morbillivirus and lobomycosis, are thought to be transmitted by close breathing interactions and skin to skin contact respectively [125, 26]. Therefore, using interaction types that are more specific to the route of transmission for common marine mammal pathogens are likely to produce more accurate epidemic size and probability results in a simulation. At present, there is only one study [109] that compares different modes of contact in a marine mammal, with disease risk. In another study, pox-like virus was linked to association with afflicted individuals in the year before becoming symptomatic [126]. Data collection should be more specific to relevant disease transmitting interactions between animals, in order to generate further data unique to particular pathogens of interest.

Finally, edge weight, or the strength of interactions between individuals, was not included in this analysis. The impact of interaction strength on transmission is unknown for most systems, though it is reasonable to expect that the risk of transmission may increase as individuals increase their interaction frequency or duration [127]. Data that provides insight into how transmission risk is impacted by increases in association strength is needed in order to reliably incorporate these measures into network analysis.

4.2 The Importance of Using Social Networks when Modeling Disease Spread

Contact networks provide a versatile and intuitive tool to examine how behavioral changes induced by environmental perturbations can shift disease dynamics [9]. Contact networks are one of the only tools that allow for researchers to incorporate the heterogeneity of individual contacts, and the potential changes to them. Examples of the impact of environmental perturbations on disease spread that have been successfully modeled using contact networks include (as discussed in [9]): simulations of potential pathogen spread through translocated tortoise [128] and guppy [129] populations, simulated pathogen spread in targeted removals of individuals African buffalo populations when their networks have been impacted by drought[130], and simulated pathogen spread through a mouse network when infected individuals exhibit sickness behaviors [131]. Here, networks were perturbed to reflect behavioral and immunological changes caused by human disturbances in the marine environment, to model the effect of these perturbations on pathogen spread in different marine species.

The perturbations needed to increase epidemic sizes in each of our scenarios, varied greatly amongst the different networks (Figure 5). These results demonstrate the importance of using social networks in wildlife disease analysis. Wildlife networks, especially marine mammal social networks will vary greatly by species. Many species such as killer whales (*Orca orcinus*), and sperm whales (*Physeter macrocephalus*) live in stable, matrilineal groups [132]. Other species such as bottlenose dolphins (*Tursiops spp.*) live in highly dynamic fission-fusion societies in which the number of contacts within a group is unstable and can vary greatly [133, 134]. Some species such as grey whales (*Eschrichtius robustus*) and humpback whales (*Megaptera novaeangliae*) are generally solitary, but will still join large groups when breeding, hunting, or migrating [132]. Pinniped species such as California sea lions and elephant seals will form massive social groups that haul out on land during the breeding season [135]. The sociality of a species has been shown to affect a population's network structure and in turn, the disease consequences for that population [35]. Our results support these findings, and show that making the same perturbation to different networks can result in different disease outcomes.

4.3 The Effects of Covariation on Infection Transmission

The results in this review also support the idea of a positive covariation between behavioral and immunological competence, that increases infection transmission [136]. Increasing either behavioral competence (exposure) or immunological competence (susceptibility or infectivity) separately resulted in increases to epidemic sizes and probabilities. However, an increase in both aspects of competence at the same time (as in the increase susceptibility, infectivity and connectivity scenario) will cause an extreme increase in epidemic size, resulting in a positive covariation that further boosts the transmission of disease and have potentially detrimental effects on wildlife populations[136]. Possible scenarios for such positive covariation in marine mammals include increased connectivity and increased immunological competence resulting from (1) elevated vessel traffic, combined with energy loss, and/or a polluted habitat (2) shipping noise and density inducing stress, (3) direct or indirect human contact (provisioning and human-associated foraging) that compromises marine mammal health.

4.4 Considering Marine Mammal Cycles

When considering disease transmission through social systems, these consequences might be further impacted by natural marine mammal cycles. Marine mammal circadian (cycles within a 24 hour period) and circannual (cycles within a one year period) rhythms can work in concert with human cycles to impact the spread of disease in a population. Biological rhythms play an important role in factors such as immunity, parasite activity, and disease incidence[137]. For example, infections occurring during a socially busy time of day will lead to new infections being generated at the same time on following days, suggesting a synchronization of host and pathogen circadian rhythms [138]. If the aligning of circadian rhythms does indeed maximize transmission periods to the most social times of the day, any type of human disturbance that might increase the number of social contacts or decrease host immunity during these highly social times, could increase transmission risk even further. Marine mammal and human circannual rhythms might also affect disease transmission; transmission risk could be much higher during the warm and typically breeding season when tourism and boating activity is high, and contact rates are also high. Seasonal changes in immunity (such as decreased immunity during migration and breeding seasons) could also align with human rhythms to either increase of decrease infection risk [137]. Future work in this area can identify the circadian and circannual rhythms that unique to the wildlife species of interest that co-align with human rhythms and examine how such synchronization might affect infectious disease risk.

5 Conclusion

As human activity increasingly encroaches on wildlife, emphasis on potential disease outcomes is vitally important, especially for endangered and threatened species. Our research can inform management strategies aimed at mitigating future epidemics, which is especially important for species that may already be at high risk of infection. In marine populations for example, special focus on reducing runoff and marine debris, or establishing wildlife sanctuary areas free from motorboat traffic could lessen the impact of human activity on disease transmission amongst marine mammal populations. We suggest that wildlife managers take into consideration the effects of human activity on disease transmission when assessing the potential anthropogenic impacts of increasing activity in a particular wildlife habitat.

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8 Data Availability

The network data for the sea lion, humpback dolphin, and killer whale contact networks can be found at https://github.com/bansallab/asnr/tree/master/Networks/Mammalia. The datum for the bottlenose dolphin network is available at https://datadryad.org/stash/dataset/doi:10.5061/dryad.bnzs7h46r.

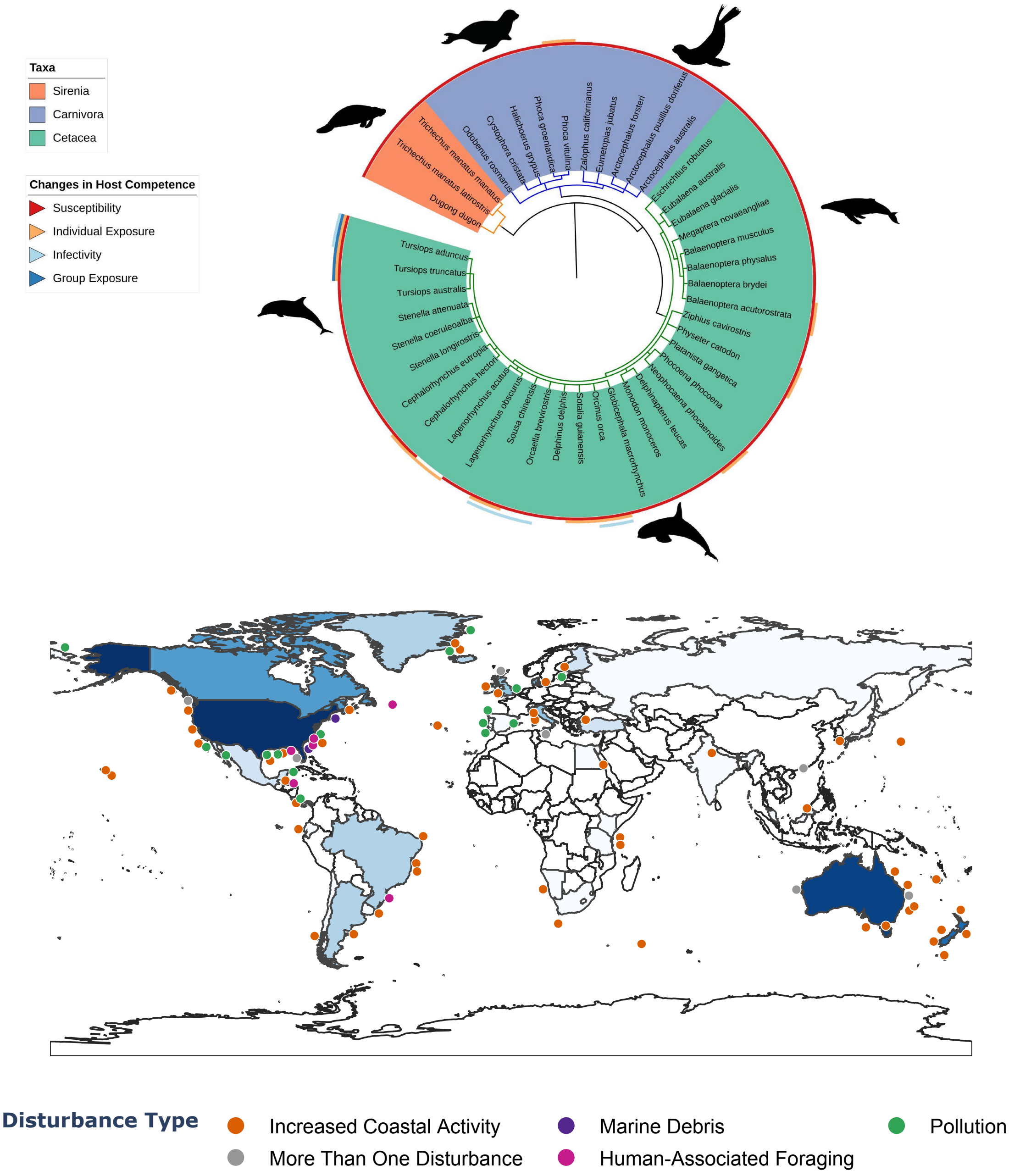


Figure (1) The phylogenetic and geographic distribution of animal species and locations represented in our systematic review. Top panel: The inner ring of the tree is color coded according to the taxonomic order of the species. The colors on each of the outer rings indicate the changes to host competence (both increased and decreased) that were observed for each species included in the review. The tree was constructed in the Interactive Tree Of Life from the NCBI taxonomy database. Bottom panel: The shading of the map indicates the number of studies from each country, where darker countries have more studies. Each point on the map denotes a specific study location and the type of human disturbance observed. Grey points denote locations with more than one disturbance type.

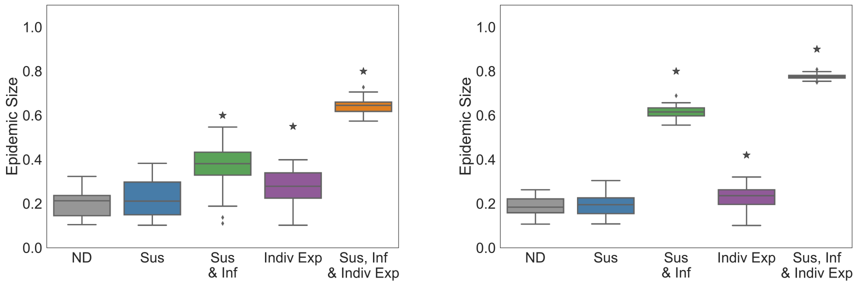
(A) Individual Exposure

(B) Group Exposure

(C) Susceptibility

(D) Infectivity

Figure (2) A schematic representation of four changes to network structure. Nodes (circles) represent individuals, and edges (lines) represent interactions capable of disease transmission between individuals. The color of the node denotes group membership, and nodes outlined in orange represent human-affected individuals. (A) shows an increase to individual exposure, in which the degree (number of interactions) of human-affected individuals is increased (new red edges). (B) shows a change to group exposure, in which the modularity of the network is increased. Here, edges are increased within the group affected by human disturbance and decreased between the two groups. (C) shows increased susceptibility, where human-affected nodes will be more likely to be infected by their contacts, represented by the direction of the red arrows. (D) demonstrates increased infectivity of human-affected nodes, where these nodes will be more likely to infect their contacts upon infection.



(a) Bottlenose Dolphin (b) Sea Lion

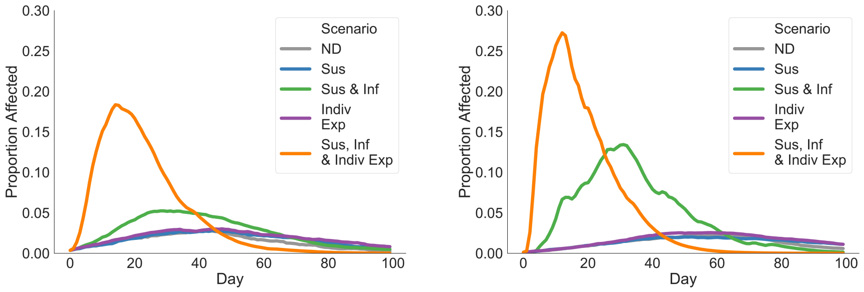
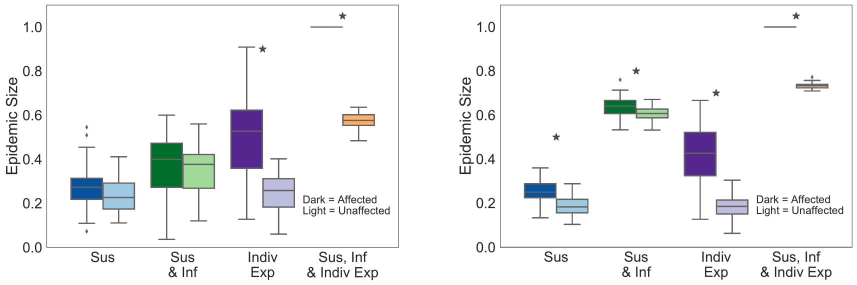
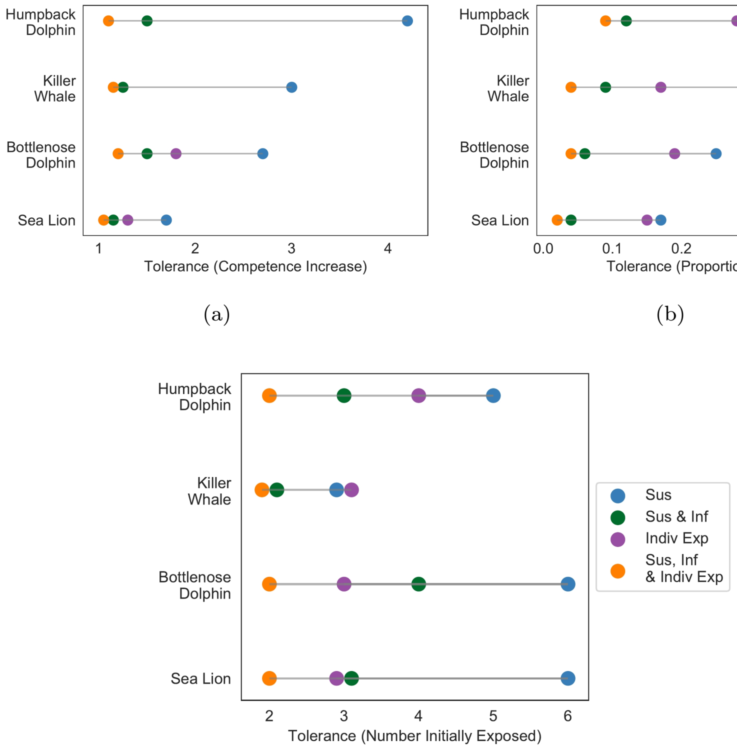


Figure (3) For each network, we compared the epidemic consequences among a no disturbance (ND, grey) scenario and four human disturbance scenarios: increased susceptibility ("Sus", blue), increased susceptibility and infectivity ("Sus & Inf", green), increased individual exposures ("Indiv Exp", purple), and increased susceptibility, infectivity and individual exposure ("Sus, Inf, & Indiv Exp", orange). The top panels show the average epidemic sizes for each scenario in the (A) bottlenose dolphin and (B) sea lion populations. Stars indicate epidemic sizes that are higher than the baseline epidemic size in the no disturbance scenario. The bottom panels show the growth and decline of the epidemic through time, measured as the proportion of the population affected per day, for each scenario in the (A) bottlenose dolphin and (B) sea lion populations.



(a) Bottlenose Dolphin (b) Sea Lion

Figure (4) We examined the difference in epidemic size among disturbed and undisturbed individuals. Within each the four scenarios (ND = no disturbance; Sus = increased susceptibility; Sus & Inf = increased susceptibility and infectivity; Indiv Exp = increased individual exposure; and Sus, Inf, & Indiv Exp = increased susceptibility, infectivity; and individual exposure) we compared the average epidemic size of the individuals affected by a human disturbances (darker colors) to the average epidemic size of individuals that were not affected by disturbance (lighter colors) over 500 simulations for the (a) bottlenose dolphin and (b) sea lion networks. The results of the independent samples t-tests are denoted by asterisks which indicate a difference between the two epidemic sizes in each of the four scenarios.



(a)

(b)

(c)

Figure (5) We performed a tolerance analysis that examined the minimum increase in competence required to cause increases in epidemic size or probability for every scenario in each of the four marine mammal networks. Panel (a) shows the lowest increase in immunological competence (susceptibility and infectivity) and behavioral competence (individual exposure) that is needed in each of our scenarios to increase the average epidemic size when 15% of the network is affected by human disturbance. Panel (b) shows the smallest proportion of each network that would have to be affected by human disturbance to increase the average epidemic size when affected individuals have their behavioral or immunological competence increased by 1.6. Panel (c) shows the smallest number of affected individuals that must be initially exposed and infected with a pathogen to increase the probability of an epidemic to 50%, when competence is increased by 1.6 and 15% of the network is affected by human disturbance.

	Behavior or Physiological Change	Network Change	Impact on Competence	Species Affected	Geographic Location	References
Coastal Human Activity	Decreased inter-animal distances	Higher degree (Increased Individual Exposure)	Increased behavioral competence	*Tursiops truncatus, Cephalorhynchus hectori, Sotalia guianensis*	Florida (USA), New Zealand, Chile, Brazil	[139, 140, 141, 142]
	Increased breathing synchrony	Higher degree (Increased Individual Exposure)	Increased behavioral competence	*Tursiops truncatus, Tursiops aduncus*	Northern Scotland, Mississippi (USA), Brazil	[142, 143]
	Increased group sizes, aggregations and cohesion	Higher degree and lower modularity (Increased Individual and Group Exposure)	Increased behavioral competence	*Tursiops truncatus, Tursiops aduncus, Sousa chinensis, Neophocaena phocaenoides, Orcinus orca*	South Carolina (USA), Northern Scotland, New South Wales, Australia, Japan, Crozet Islands, Iceland, New Zealand, Mississippi (USA, Canada)	[140, 143, 144, 145, 146, 147, 148, 149, 150, 151, 152]
	Fractured groups	Higher network modularity (Decreased Group Exposure)	Decreased behavioral competence	*Tursiops aduncus*	Australia	[52]
	Increased traveling and diving behaviors, decreased foraging and resting behaviors	Higher edge vulnerability (Increased Susceptibility)	Increased immunological competence	*Tursiops truncatus, Tursiops aduncus, Tursiops australis, Neophocaena phocaenoides, Sotalia guianensis, Phocoena phocoena, Trichechus manatus latirostris, Stenella longirostris, Eschrichtius robustus, Arctocephalus pusillus doriferus, Phoca vitulina, Sousa chinensis, Balaenoptera acutorostrata, Orcinus orca, Phoca hispida Arctocephalus australis, Dugong dugon, Lagenorhynchus obscurus, Megaptera novaeangliae, Cephalorhynchns hectori, Delphinus delphis; Halichoerus gryus, Eumetopias jubatus; Orcaella brevirostris, Arctocephalus pusillus, Platanista gangetica gangetica, Arctocephalus forsteri, Eubalaena australis, Balaenoptera physalus, Stenella attenuata, Ziphius cavirostris, Eumetopias jubatus, Ziphius cavirostris, Balaenoptera musculus*	New Zealand, Belize, Turkey, Australia, Italy, Scotland, Japan, Brazil, Wales, Florida (USA), Egypt, Oregan (USA), Namibia, Alaska (USA), Denmark, Hong Kong, Iceland, Canada, Kenya, Greenland, Uruguay, Mississippi (USA), Washington (USA), Malaysia, India, Hawaii (USA), Portugal, Costa Rica, Ecuador, Ligurian Sea, Argentina, Netherlands, Panama, Italy, Texas (USA), Tanzania, California (USA)	[52, 66, 67, 101, 133, 145, 147, 150, 153, 154, 155, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166, 167, 168, 169, 65, 170, 171, 172, 173, 174, 175, 23, 176, 177, 178, 179, 180, 181, 182, 183, 184, 185, 186, 187, 188, 189, 190, 191, 192, 193, 194, 195, 196, 197, 198, 199, 200, 201, 202, 203, 204, 205, 206, 207, 208, 209, 210, 211, 212, 213, 214, 215, 216, 217]
	Decreased time spent in habitat	Higher edge vulnerability (Increased Susceptibility)	Increased immunological competence	*Tursiops truncatus, Tursiops aduncus, Phocoena phocoena, Balaenoptera acutorostrata, Arctocephalus pusillus doriferus, Delphinus delphis, Sousa chinensis, Orcinus orca, Platanista gangetica gangetica, Stenella longirostris*	Belize, Australia, Turkey, Wales, Ireland, South Africa, Hong Kong, New Zealand, India, Hawaii (USA)	[69, 153, 158, 160, 165, 173, 176, 191, 194, 218, 219]
	Reorientation or changes to swimming patterns	Higher edge vulnerability (Increased Susceptibility)	Increased immunological competence	*Tursiops truncatus, Tursiops aduncus, Ornicus orca, Sousa chinensis, Arctocephalus pusillus, Megaptera novaeangliae, Eubalaena australis, Stenella longirostris, Arctocephalus pusillus doriferus*	Florida (USA), Canada, Hong Kong, Australia, New Caledonia, Argentina, Ecuador, Hawaii (USA), Argentina, Texas (USA), Tanzania	[64, 188, 189, 198, 205, 214, 215, 220, 221, 222, 223]
	Increased stress hormones	Higher edge vulnerability (Increased Susceptibility and Infectivity	Increased immunological competence	*Tursiops anduncus, Eubalaena glacialis, Balaenoptera physalus, Megaptera novaeangliae, (Balaenoptera musculus, Sousa chinensis, Orcaella brevirostris*	Australia, Canada, Northern Pacific Ocean, Northern Atlantic Ocean, Malaysia,	[69, 103, 187, 224]
	Increased stress behaviors	Higher edge vulnerability (Increased Susceptibility and Infectivity)	Increased immunological competence	*Turiops sp.*	Australia	[101, 225]
Human associated Foraging	Increased contact or larger group sizes associated with animals engaged in human associated foraging	Higher degree (Increased Individual Exposure)	Increased behavioral competence	*Tursiops truncatus, Sousa chinensis, Physeter catodon*	Georgia (USA), Hong Kong, Florida (USA), Canada	[54, 173, 226, 227]
	Decreased contact with natural foragers	Higher network modularity (Decreased Group Exposure)	Decreased behavioral competence	*Tursiops truncatus, Tursiops aduncus*	Australia, Georgia (USA), North Carolina (USA), Florida (USA), Brazil, Italy	[42, 43, 48, 54, 55, 226, 228, 229, 230]
	Accepting contaminated handouts or not meeting nutritional demands	Higher edge vulnerability (Increased Susceptibility)	Increased immunological competence	*Tursiops truncatus,Tursiops aduncus*	Australia, Georgia (USA), Florida (USA), Belize	[48, 53, 226, 231]
	Close contact with humans	Higher "human" degree (Increased Initial Exposure)	Increased behavioral competence	*Tursiops truncatus,Tursiops aduncus*	Australia, Georgia (USA), Florida (USA), Brazil, Belize	[48, 53, 226, 229, 230, 231, 232]
Marine Debris	Increased fast swimming and increased drag from fishing gear	Higher edge vulnerability (Increased Susceptibility)	Increased immunological competence	*Tursiops anduncus, Eubalaena glacialis*	Australia, Florida (USA)	[51, 73, 233]
	Decreased number of associates when entangled	Lower degree (Decreased Individual Exposure)	Decreased behavioral competence	*Tursiops truncatus, Tursiops aduncus, Lagenorhynchus acutus*	Florida (USA), Australia, New England (USA)	[51, 50, 233, 234]
Pollution	High levels of PCBs, heavy metals and PAHs in body	Higher edge vulnerability (Increased Susceptibility)	Increased immunological competence	*Tursiops truncatus, Zalophus californianus, Ursus maritimus, Phoca vitulina, Phocoena phocoena, Trichechus manatus manatus, Physeter catodon, Globicephala macrorhynchus, Megaptera novaeangliae, Balaenoptera physalus, Balaenoptera musculus, Balaenoptera brydei, Balaenoptera acutorostrata, Odobenus rosmarus, Orcinus orca, Stenella coeruleoalba*	California (USA), United Kingdom, British Isles, Australia, Gulf of Mexico, Sea of Cortez, Mexico, Spain, Greenland, Portugal	[36, 89, 92, 96, 97, 235, 236, 237, 238, 239, 240, 241, 242, 243, 93]

Table (1) Behavioral and physical changes in marine mammals cited in the literature and their potential impact on host competence and network structure. Colors denote the particular human disturbance that causes the corresponding change.

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