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REVIEW

# Sociality of Marine Mammals and Their Vulnerability to the Spread of Infectious Diseases: A Systematic Review

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## ABSTRACT

**Introduction:** Social structure plays a crucial role in shaping the transmission dynamics of infectious diseases within animal populations, yet its influence remains understudied in marine mammals.

**Aims:** This review investigates links between marine mammal sociality and disease vulnerability, focusing on social network metrics and their influence on disease transmission. The study aimed to (1) identify patterns in disease transmission, (2) map gaps in current knowledge to inform strategic directions for future investigation and (3) discuss implications for conservation and disease management.

**Methods:** Through systematic database searching, 14 studies were identified that investigated social network metrics and their influence on disease transmission in marine mammal social networks.

**Results:** Results show that stronger associations and greater social connectivity increase disease prevalence, although this relationship varied across species. Central individuals acted as 'super-spreaders', facilitating disease spread to conspecifics and vaccination efforts targeting these individuals are a recurrent proposed mitigation strategy. At the population level, network fragmentation reduced disease burden, while highly connected subgroups facilitated pathogen transmission. Research is concentrated on few key species, revealing significant gaps in taxonomic and geographic representation. Additionally, studies were geographically biased toward North America and Australia, with limited collaboration across research clusters, highlighting the need for broader representation and interdisciplinary partnerships.

**Conclusion:** These findings underscore the need for interdisciplinary approaches integrating epidemiological modelling, social network analysis and conservation strategies to better predict and mitigate disease risks in marine mammal populations. Future research should expand species coverage and incorporate ecological and environmental variables to develop targeted disease management frameworks.

## 1 | Introduction

The increasing emergence and spread of infectious disease in wildlife is a significant concern to biodiversity and human health. Several terrestrial animal populations have faced the devastating effects of disease-driven declines, including amphibians (Akçakaya et al. 2023; Scheele et al. 2019), bats (*Myotis lucifugus*; Dzal et al. 2010) and the Tasmanian Devil (*Sarcophilus harrisii*; Jones et al. 2007). The increasing variety of emerging and re-emerging wildlife diseases and concerns about more frequent outbreaks, highlight the threat these diseases pose to species survival (Daszak et al. 2000; Holmes 1996). This alarming trend is mirrored in marine ecosystems, where infectious diseases pose similar risks to vulnerable marine mammal populations, exacerbated by environmental change (Greer et al. 2008; Harvell et al. 2002), pollution (Behringer et al. 2020; Vignal et al. 2021) and human activities (Bossart 2007).

Emerging and resurging diseases in the marine environment, including viral, bacterial, helminth, fungal and protozoal have led to mass mortality events in different areas around the world including South America, North America, Europe and Australia (Cunha et al. 2021; Kemper et al. 2016; Van Bressem et al. 2009). Additionally, these outbreaks are not only a conservation concern but also pose significant risks to human populations. Many pathogens affecting wildlife have zoonotic potential, meaning they can cross species barriers and infect humans (Daszak et al. 2000). The severe acute respiratory syndrome caused by the zoonotic SARS-CoV-2 virus and responsible for the COVID-19 pandemic offered us a vivid, lived demonstration of how patterns of social interactions and the underlying social structure of human populations can shape the transmission and persistence of diseases (Ahmad et al. 2020). This lesson emphasised the critical need to understand the relationship between social structure and infectious disease spread, not only in humans but across wildlife populations (Costa-Silva et al. 2025).

In recent years, there has been a growing recognition of the importance of studying the intersection between epidemiology and social structure due to the role that social connectivity plays in shaping how infectious diseases spread and persist in wildlife populations (Silk and Fefferman 2021; Silk et al. 2019). Social network analysis shows that not just group size, but specific patterns and qualities of interactions, such as the presence of key individuals or subgroups, can influence disease transmission (Bansal et al. 2007; Sah et al. 2017; Silk et al. 2017; Volz et al. 2011). This highlights the need for targeted and informed conservation strategies that account for both pathogen characteristics and the social structures of host populations, as these factors shape how disease spreads and can be managed within wildlife populations (Silk et al. 2019).

Mammals exhibit a diverse range of social systems, characterised by different drivers and patterns of social organisation, social structure, mating systems and care systems (Kappeler et al. 2019). While some species live solitary lives, others form complex social groups that influence survival and reproductive success (Connor et al. 2000). Sociality facilitates critical interactions among individuals that influence various aspects of their lives, including fitness (Alexander 1974), genetic structure (Sugg et al. 1996) and information and disease transmission (Altizer et al. 2003). While group living provides key benefits including improved foraging success and resource acquisition (Fortin and Fortin 2009), protection from predators and access to mates (Rubenstein 1978), it also presents significant costs. These include heightened intra-group competition for resources, as well as an increased risk of disease and parasite transmission (Landry and Li 2019).

One component of social systems, social organisation, describes how individuals are grouped, including factors of group size, age and sex composition and kinship. Another dimension is social structure, which captures the nature of social interactions, relationships and communication among individuals (Kappeler et al. 2019). Earlier classifications such as the relatively solitary, gregarious and socially hierarchical framework (Sah et al. 2017) combine aspects of both organisation and structure, offering useful but coarse descriptions of sociality. For example, relatively solitary species, such as the desert tortoise (*Gopherus agassizii*), interact infrequently outside of mating or territorial disputes (Sah 2017). Gregarious species, such as bison (*Bison bison*) and common bottlenose dolphins (*Tursiops truncatus*), form groups for various activities, but their group composition is unstable or shifts over time (Parra et al. 2011; Sah 2017; Wells et al. 1987). Socially hierarchical species are characterised by stable, long-term relationships and include species such as yellow baboons (*Papio cynocephalus*) and male elephant seals (*Mirounga angustirostris*) (Sah et al. 2017). Throughout evolution, species' life history, ecology and environmental pressures have intricately shaped the structure and dynamics of these diverse social systems (Kutsukake 2009). Variation in both social organisation and structure influences the topology of emergent social networks, which has direct implications for processes such as information flow and the extent and rate of disease spread (Altizer et al. 2003).

Understanding the relationship between sociality and disease transmission requires looking beyond simple assumptions, such as the idea that larger groups inevitably face a higher disease burden. While some studies support this notion, Côté and Poulin (1995) found a positive correlation between group size and parasitism rate and Daviews et al. (1991) observed a similar pattern with malaria infection in primates; others suggest a more nuanced relationship. For instance, Arnold and Lichtenstein (1993) found no clear association between group size and ectoparasite load in alpine marmots (*Marmota marmota*), suggesting that disease burden is influenced by additional factors. Nunn et al. (2015) found that while larger groups might initially facilitate disease transmission due to frequent and close contact, the presence of subgroups within the population can act as a barrier and slow disease spread. Other studies highlight that aspects of social structure such as subgroup cohesion, network diameter and individual centrality also influence disease risk (Ezenwa et al. 2016; Godfrey et al. 2009; Sah 2017; White et al. 2017). These findings underscore the complexity of disease transmission in social species.

The social structures of marine mammals range over a spectrum from weak or infrequent associations to stable groups, fission-fusion dynamics and highly organised multilevel societies (Mann 2000; Rendell et al. 2019). This variation in social organisation gives rise to different social structures, which researchers portray as networks of social relationships. For example, baleen whales (Mysticeti) tend to be solitary or form short-term aggregations beyond the mother-calf pair, resulting in many weak social relationships. Consequently, baleen whale social networks tend to be dense and unstructured (Krause et al. 2015). In contrast, toothed whales (Odontoceti) display greater variability in social organisation, with differences observed across species, populations, habitats and sexes (Rendell et al. 2019; Weiss et al. 2021; Edwards et al. 2025). Larger odontocetes, such as orcas (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*), have highly structured and multileveled societies, including matrilineal groups and units (Whitehead 2003; Williams and Lusseau 2006). Conversely, smaller odontocetes, such as bottlenose dolphins (*Tursiops* spp.), are more prone to dynamic fission-fusion social behaviours, where the size and composition of groups change dynamically over time as individuals frequently split or merge (Aureli et al. 2008; Connor et al. 2000; Krause et al. 2015; Parra et al. 2011). Variation in social organisation and structure can also be observed among pinnipeds, with leopard seals (*Hydrurga leptonyx*) being relatively solitary (Hiruki et al. 1999), harbour seals (*Phoca vitulina*) forming loose aggregations on land but maintaining relatively weak social bonds (Andersen et al. 2011) and grey seals (*Halichoerus grypus*) being highly gregarious, particularly during the pupping season (Boness and James 1979). Given the diversity of social structures observed in marine mammals, the ways in which diseases spread within and between populations can vary significantly (Cantor et al. 2021; Sah et al. 2017; Silk et al. 2019).

Many pathogens, including those affecting marine mammals, spread through host populations via close contact among individuals including direct contact, airborne particles, bites, or sexual transmission (Table 1) (Antonovics et al. 2017). The frequency, intensity, or nature of such contacts may critically influence the extent and rate of disease spread (Altizer et al. 2003). In addition to transmission pathways, factors such as transmissibility, contagiousness, duration of infectiousness and recovery rate also play a crucial role in shaping disease impacts (Collier 2023). In marine systems, the survivability of pathogens in the aquatic environment becomes particularly important, as it can facilitate indirect transmission by allowing pathogens to persist in the environment and indirectly infect hosts (Cook et al. 1998; Cohen et al. 2018; Collier et al. 2025).

Reports of these pathogens span all major groups of marine mammals, highlighting that the threat of disease is not confined to a few species, but rather affects a broad taxonomic range. Cetaceans (odontocetes and mysticetes) are hosts to multiple viral, bacterial, fungal and protozoal agents, including papillomaviruses, poxviruses, morbilliviruses, influenza viruses, herpesviruses and caliciviruses (Caldwell et al. 1974; Domingo et al. 1990; Van Bressem et al. 1996, 1999, 2001, 2003, 2009, 2024; Foster et al. 2002; Dubey et al. 2003; Conrad et al. 2005; Maness et al. 2011; Fereidouni et al. 2016; Bossart and Duignan 2018; Runstadler and Puryear 2020). Pinnipeds are also widely affected, with documented cases of morbillivirus, influenza, herpesvirus, calicivirus, papillomavirus, poxvirus and brucellosis in various seal and sea lion species (Dierauf and Gulland 2001; Foster et al. 2002; Maness et al. 2011; Fereidouni et al. 2016; Bossart and Duignan 2018). Sirenians, such as manatees, have been reported with papillomavirus and morbillivirus (Duignan, House, Walsh, et al. 1995; Bossart et al. 2002; Sonne et al. 2018; Bossart and Duignan 2018), while marine fissipeds (e.g., sea otters, polar bears) have shown susceptibility to toxoplasmosis, brucellosis and morbilliviruses (Foster et al. 2002; Dubey et al. 2003; Van Bressem et al. 2009) (Table 1). The wide range of hosts, from fully aquatic cetaceans and sirenians to amphibious pinnipeds and fissipeds, highlights both the ecological extensiveness and cross-taxonomic relevance of these pathogens in the marine environment.

**TABLE 1** | Common pathogens found in marine mammals and their primary modes of transmission.

| | Mode of transmission | | | | |
|---|---|---|---|---|---|
| **Disease** | **Direct contact** | **Airborne/ Respiratory** | **Bites/ Wounds** | **Sexual transmission** | **Key references** |
| *Papillomavirus* | Yes | | Yes | Yes | Antonsson and Hansson (2002); Van Bressem et al. (2009, 1996) |
| *Poxvirus* | Yes | | Yes | | Van Bressem and Van Waerebeek (1996); Van Bressem et al. (2003) |
| *Morbillivirus* | Yes | Yes | | | Domingo et al. (1990); Van Bressem et al. (1999, 2001); Cunha et al. (2021) |
| *Influenza* | Yes | Yes | | | Fereidouni et al. (2016); Runstadler and Puryear (2020) |
| *Herpesvirus* | Yes | | | Yes | Bossart and Duignan (2018); Maness et al. (2011) |
| *Caliciviruses* | Yes | | | | Bossart and Duignan (2018); Dierauf and Gulland (2001) |
| *Lobomycosis* | Yes | | Yes | | Caldwell et al. (1974); Van Bressem et al. (2009); Van Bressem et al. (2024) |
| *Brucellosis* | Yes | | | Yes | Corbel (1997); Foster et al. (2002); Sonne et al. (2018) |
| *Toxoplasmosis* | Yes | | | | Van Bressem et al. (2009); Conrad et al. (2005); Dubey et al. (2003) |

Given the ethical and technical constraints of conducting direct disease experiments on wildlife, researchers have increasingly turned to social networks as a tool for unravelling the relationship between social structure and disease transmission. By mapping interactions between individuals, researchers can identify key transmission pathways, assess which individuals or groups are most at risk and predict the potential speed and extent of disease outbreaks (Danon et al. 2011; Sah et al. 2017). Social network analysis has been used to successfully predict transmission of a variety of diseases across terrestrial taxa, including HIV in humans (Liljeros et al. 2003), foot-and-mouth disease in livestock (Kao et al. 2006), bovine tuberculosis in African Buffalo (*Syncerus caffer*) (Cross et al. 2004), intestinal pathogens in honey (*Apis* spp.) and bumble (*Bombus* spp.) bees (Naug 2008; Otterstatter and Thomson 2007) and parasites in primates (MacIntosh et al. 2012). Its application to marine mammals, however, remains comparatively limited due to the logistical challenges of observing these animals and tracking transmission events in their natural environment.

This review synthesises existing research on socially transmitted diseases in marine mammals, examining the mechanisms of disease spread within social groups and evaluating the role of social patterns, such as group size, social networks and contact rates, on transmission dynamics. By synthesising current findings, this review identifies patterns in disease transmission, highlights gaps in current research and discusses the implications for conservation and disease management of marine mammal populations.

## 2 | Methods

### 2.1 | Search Strategy

We searched three databases Google Scholar (Google; scholar.google.com), Web of Science (WoS, Thompson Reuters; webofknowledge.com) and Scopus (Elsevier; elsevier.com) to identify relevant studies. PubMed was not included as it primarily indexes biomedical and clinical research, whereas our focus was on ecological and behavioural studies of marine mammals. We refined the search queries using Boolean operators (AND, OR), combining keywords targeting marine mammal species, disease and social structures in the search terms (Table 2).

**TABLE 2** | Database search strings for literature retrieval of studies on sociality of marine mammals and infectious diseases.

| Database | Search String |
|---|---|
| Google Scholar | "marine mammal" AND intitle:(disease OR infection OR pathogen OR virus OR epidemiology) AND intitle:("social organisation" OR "social structure" OR "social network" OR "contact network") |
| Scopus | TITLE-ABS-KEY (marine AND mammal) AND TITLE (disease OR infection OR pathogen OR virus OR epidemiology) AND ALL (social OR organisation OR structure OR network OR contact) |
| Web of Science | TS = (marine AND mammal) AND TS = (disease OR infection OR pathogen OR virus OR epidemiology) AND ALL = (social OR organisation OR structure OR network OR contact) |

### 2.2 | Data Extraction and Management

This review follows the Preferred Reporting Items for Systematic reviews and Meta-Analysis (PRISMA) reporting guidelines designed to facilitate transparent and complete reporting of systematic reviews (Page et al. 2021). We used Covidence (Covidence systematic review software, Veritas Health Innovation, covidence.org) to screen studies, remove duplicates and facilitate data extraction and synthesis following a standardised data extraction protocol to ensure consistency and reproducibility. First, all search results were exported into Covidence, which automatically identified and removed duplicate records. The dataset was then manually verified to ensure no duplicate studies remained. Each study was subsequently screened by title and abstract to assess its relevance to the research question. We then applied the inclusion and exclusion criteria (outlined in Table 3), excluded studies that clearly did not qualify and retained those deemed potentially relevant or lacking sufficient information in their title or abstract for further review.

We assessed the remaining studies in full to confirm their eligibility, excluded those that did not meet the inclusion criteria and documented the reasons for exclusion. The most common reasons for exclusion were a lack of focus on the relationship between marine mammal sociality and infectious disease transmission; exclusive focus on stranded or captive animals; studies not involving marine mammals; or dissertations later published in peer-reviewed journals already included. For the included studies, key information was extracted using a standardised extraction form within Covidence (Table S1).

## 3 | Results

The literature search retrieved a total of 1920 publications (1383 from Google Scholar, 345 from WoS, 187 from Scopus, 5 from citation searching), covering topics related to disease dynamics and social behaviour in marine mammal populations. Sixty-three duplicates were identified and removed, reducing the dataset to 1857 studies for title and abstract screening. Following this screening, 1628 studies were found to be irrelevant, leaving 229 studies for full text review. Out of these studies, 215 were excluded for the following reasons: 161 did not explore the relationship between marine mammal sociality and infectious disease transmission, 44 focused only on diseases in stranded animals, four examined only captive populations, three did not involve marine mammals and three were original dissertations later published in peer-reviewed journals already included in the analysis. This left 14 studies eligible for data extraction (Table S2, Figure 1).

**TABLE 3** | Inclusion and exclusion criteria for study selection in systematic review of the relationship between marine mammal sociality and infectious disease transmission.

| | |
|---|---|
| **Inclusion criteria** | |
| Focus | Studies examining the relationship between marine mammal sociality and infectious disease transmission |
| Study design | Observational studies, experimental studies, modelling approaches and epidemiological research |
| Participants | All marine mammals |
| Publication type | Peer-reviewed journal articles, book chapters and dissertations |
| Language | English-language publications |
| Geographic Scope | No regional limitations |
| **Exclusion criteria** | |
| Non-research content | Opinion pieces, editorials, commentaries and letters to the editor |
| Case reports | Excluded unless providing novel insights into disease transmission dynamics and social structure |
| Captive populations | Excluded unless findings had direct relevance to wild populations |
| Stranded individuals | Excluded unless findings could be linked to social structure |
| Insufficient data | Studies lacking adequate methodological detail or data were excluded |
| Non-marine mammals | Research focusing exclusively on terrestrial species was excluded |

### 3.1 | Methodological Approaches, Temporal Scope and Study Species

The 14 studies used diverse methodological approaches, reflecting the complexity of studying both epidemiology and social structure. Most studies (12) relied on observational methods using photo-identification, which allowed researchers to document associations between individually identifiable marine mammals (Table 4). Additionally, five studies reviewed photographs to identify external lesions, providing a non-invasive method to detect disease. Three studies reviewed multiple previously collected datasets, including photo-identification records of marine mammals. Six studies incorporated epidemiological modelling techniques, including Susceptible–Infected (SI), Susceptible–Infected–Recovered (SIR) and Susceptible–Exposed–Infected–Recovered (SEIR) models, to simulate disease transmission within social networks (Table 4). These models are powerful mathematical frameworks used in epidemiology to understand and predict how infectious diseases spread through populations (Kermack et al. 1997; Keeling and Rohani 2008).

The temporal scope of data collection varied considerably. Some studies, such as Robinson et al. (2018), spanned a single year, while others, like Powell et al. (2020), used long-term datasets spanning 34 years. Four studies lasted five years, two lasted seven years and two lasted eight years.

Researchers studied seven marine mammal species across the 14 included studies (Figure 2). The common bottlenose dolphin, *Tursiops truncatus*, appeared most often in six studies (Magileviciute 2007; Sah et al. 2017; Félix et al. 2019; Galvez et al. 2022; Szott et al. 2022; Van Bressem et al. 2024). The Indo-Pacific bottlenose dolphin, *Tursiops aduncus* (Sah et al. 2017; Powell et al. 2020; Leu et al. 2020), featured in four studies, and killer whale, *Orcinus orca* (Guimarães et al. 2007; Sah et al. 2017; Weiss et al. 2020; Collier et al. 2022) in three studies. Two studies (DiVittore-Goodrum and Gibson 2023; Collier et al. 2025) examined Tamanend's bottlenose dolphin, *Tursiops erebennus*, while one study each focused on the California sea lion, *Zalophus californianus* (Collier et al. 2025), Australian humpback dolphin, *Sousa sahulensis* (Collier et al. 2025), and Hawaiian monk seal, *Neomonachus schauinslandi* (Collier et al. 2025).

These species spanned a range of conservation statuses across global and regional assessments. As IUCN classifications may not reflect local population-level threats, we summarised the species, global IUCN status, study site, country, regional assessment and corresponding citations in Table 5.

### 3.2 | Social Network Metrics Used in Studies

At the individual level, nine studies explored the relationship between social structure and disease transmission using association indexes. Six studies used the Half-Weight-Index (HWI) and four used the Simple-Ratio-Index (SRI), with one study opting to use both HWI and SRI (Table 6). These metrics are particularly relevant as they capture the strength and frequency of associations, directly influencing opportunities for pathogen transmission. Seven studies explored degree measures, including synchrony degree, while five studies assessed centrality metrics such as eigenvector and betweenness centrality, which identify individuals with more connections or influence on how disease spreads through a population (Table 6).

At the population level, researchers frequently analysed network fragmentation and clustering coefficients. Six studies explored how network fragmentation relates to disease transmission and four examined clustering coefficients (Table 6). These are particularly important metrics as they capture the overall connectivity of a population, influencing how quickly a pathogen could spread through an entire network.

### 3.3 | Geographical and Temporal Spread of Studies

Research effort on marine mammal sociality and infectious disease has been unevenly distributed across regions. In terms

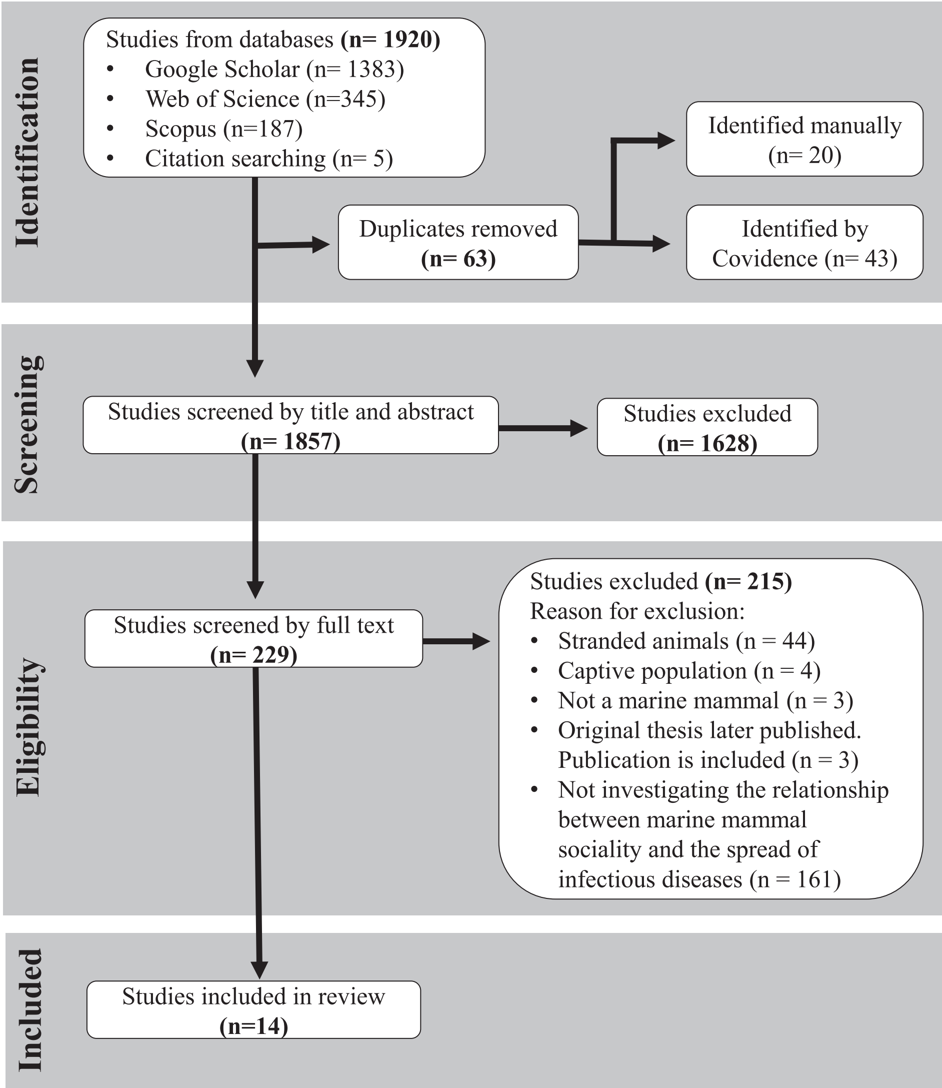


**FIGURE 1** | Preferred reporting items for systematic reviews and meta-analyses (PRISMA) flow diagram showing the literature search, screening process and inclusion/exclusion of studies in the systematic review on marine mammal sociality and disease vulnerability.

of geographical spread, we found that research was primarily concentrated in the Northern Hemisphere (14 studies), with fewer studies in the Southern Hemisphere (five studies) and some (three studies) used data from two or three countries. Only one study adopted a global perspective, incorporating data from multiple regions (Figure 3).

The temporal distribution of publications indicates an increasing research focus on the sociality of marine mammals and their vulnerability to infectious disease in recent years. The earliest studies appeared in 2007, followed by a 10-year gap in publications. From 2017 onwards, the number of studies increased, peaking in 2020 and 2022, before slightly declining again in 2023, 2024 and 2025.

## 4 | Discussion

Marine mammals are highly social animals, exhibiting a wide diversity of social organisations, ranging from solitary individuals to highly fluid fission-fusion dynamics and stable hierarchical group structures (Connor et al. 2000; Krause et al. 2015; Whitehead 2003; Williams and Lusseau 2006). These social systems shape the frequency, duration and nature of interactions among individuals, which in turn influence the pathways for disease transmission and determine the probability of an epidemic, the number of animals infected or the speed of disease spread both within and between groups (Altizer et al. 2003; Keeling 1999; Moore and Newman 2000). Understanding how diseases spread through such varied social networks is therefore crucial not only for assessing species-specific vulnerability to disease, but also for improving our capacity to predict, manage and mitigate future outbreaks. However, the extent to which social organisation and structure influence disease vulnerability can vary across species and populations, raising the question: what aspects of a marine mammal's social organisation and structure make them vulnerable to disease, and what social network metrics can help assess this vulnerability? This review highlights key patterns in the relationship between social network metrics and disease transmission dynamics, whilst also identifying knowledge gaps and recommendations for future research. Upon reviewing the literature, it became evident that

**TABLE 4** | Summary of data collection techniques, disease modelling approaches and study duration used in the 14 studies investigating the relationship between social structure of marine mammals and disease transmission.

| Research aspect | Approach | Number of studies | Respective reference |
|---|---|---|---|
| Data collection method | Photo ID (including from previous studies) | 12 | Collier et al. (2025); Collier et al. (2022); DiVittore-Goodrum and Gibson (2023); Félix et al. (2019); Galvez et al. (2022); Guimarães et al. (2007); Leu et al. (2020); Magileviciute (2007) unpublished master's thesis; Powell et al. (2020); Szott et al. (2022); Van Bressem et al. (2024); Weiss et al. (2020) |
| | Focal follow | 2 | Collier et al. (2025); Powell et al. (2020) |
| | Review | 3 | Sah et al. (2017); Van Bressem et al. (2024) |
| | Analysis of photos for lesions | 5 | DiVittore-Goodrum and Gibson (2023); Félix et al. (2019); Galvez et al. (2022); Magileviciute (2007); Powell et al. (2020) |
| Disease modelling | Susceptible-Infected/ Susceptible-Infected-Removed/ Susceptible-Exposed-Infected-Removed modelling | 6 | Collier et al. (2025, 2022); Guimarães et al. (2007); Robinson et al. (2018); Sah et al. (2017); Weiss et al. (2020) |
| Duration | NA | 2 | Collier et al. (2022); Sah et al. (2017) |
| | 1–4 years | 2 | DiVittore-Goodrum and Gibson (2023); Robinson et al. (2018) |
| | 5–9 years | 8 | Collier et al. (2025); Félix et al. (2019); Galvez et al. (2022); Leu et al. (2020); Magileviciute (2007); Szott et al. (2022); Van Bressem et al. (2024); Weiss et al. (2020) |
| | 10–14 years | 1 | Guimarães et al. (2007) |
| | 15+ years | 1 | Powell et al. (2020) |

while numerous studies have examined epidemiological factors or social structure in isolation, there is a notable gap in research directly linking these two aspects.

### 4.1 | Methodological Approaches, Temporal Distribution and Study Species

Researchers continue to evolve their approaches to studying marine mammal sociality and epidemiology, using diverse methods and models. The extensive use of photo-identification, often in combination with association indices, is not surprising given its proven effectiveness in identifying and tracking individuals of different species across space and time (Urian et al. 2015) and in quantifying social bonds. However, relatively few studies have integrated advanced epidemiological modelling techniques such as SI, SIR and SEIR models, which offer a quantitative approach to understanding disease transmission dynamics. Where these models have been applied, they have greatly enhanced our ability to simulate outbreaks and predict epidemic outcomes, suggesting a shift to a data-driven and predictive approach to research in this area.

The variation in temporal scope among studies highlights the challenges of designing research that effectively captures both immediate and long-term aspects of marine mammal sociality. Short-term studies can provide valuable insights into the immediate social and disease transmission dynamics of marine mammals, but may fail to capture longer-term trends or shifts in social structure (e.g., Robinson et al. 2018). In contrast, long-term studies offer a more comprehensive understanding of how social structure evolves over time, though such studies require substantial resources and funding to maintain (Powell et al. 2020). The predominance of studies spanning five to eight years suggests a balance between capturing meaningful social interactions and maintaining feasibility in data collection and analysis.

Researchers have understandably overrepresented *T. truncatus* due to its cosmopolitan distribution, accessibility in nearshore waters and proximity to major urban areas (Perrin et al. 2008). Its wide distribution and presence across different environments have made it a key focus for multidecadal, long-term monitoring projects, such as those in Sarasota (Wells and McHugh 2025) and the St. Johns River in Florida, North America (Szott et al. 2022) and Veracruz State in Mexico (Galvez et al. 2022). In comparison, *T. aduncus* has a more geographically limited range in the Indo-Pacific region (Braulik et al. 2019) and has been the focus of fewer studies on social structure and disease vulnerability. Long-term

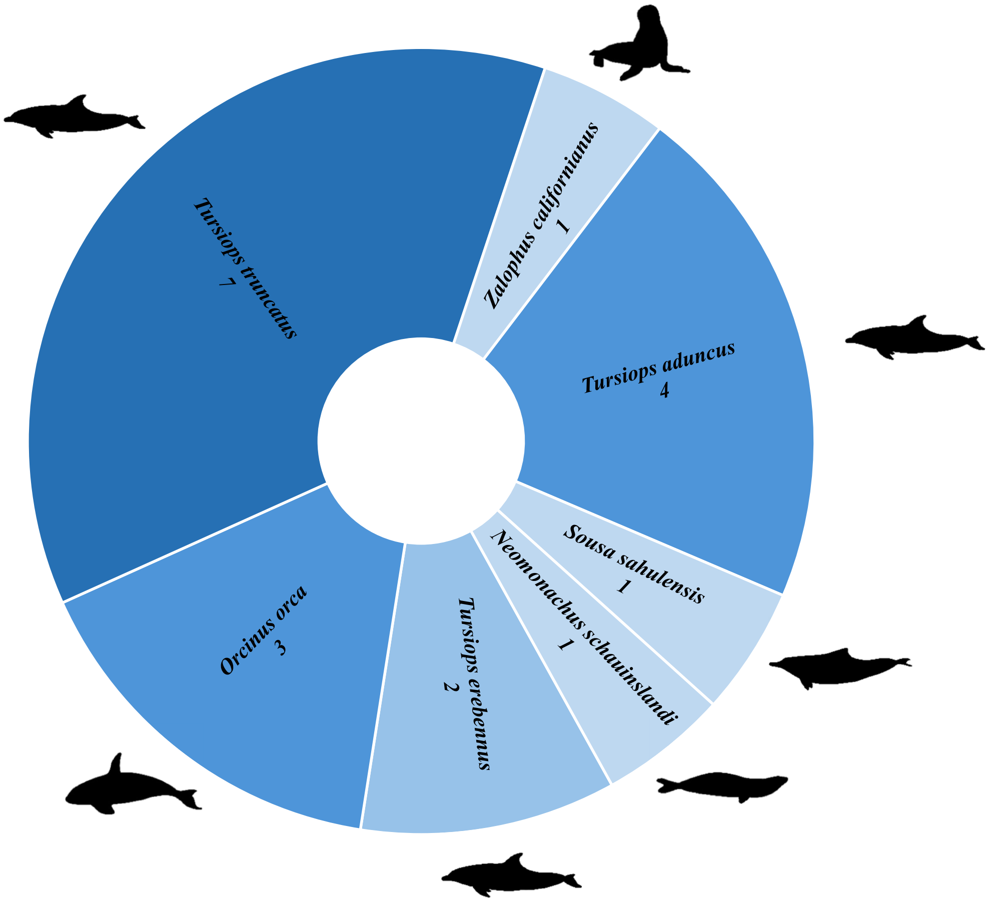


**FIGURE 2** | The distribution of species represented in studies included in the systematic literature review on marine mammal social structure and disease transmission. The figure shows the number of studies per species included in the review. Two studies included more than one species (Sah et al. 2017; Collier et al. 2022).

research projects, such as the Shark Bay Dolphin Project, continue to provide critical insights into its complex behaviour, with recommendations for further research into the species' susceptibility to disease (Powell et al. 2018). Similarly, *O. orca* has been the subject of three studies looking at marine mammal social structure and disease vulnerability, with their unique social behaviours, including matrilineal groupings (Whitehead 2003; Williams and Lusseau 2006), attracting researchers, particularly along the west coast of the North American and Canadian border.

While studies of these species provide valuable knowledge, they also raise concerns about taxonomic and ecological biases in disease ecology research. Including lesser studied species such as *T. erebennus*, *Z. californianus*, *S. sahulensis* and *N. schauinslandi* offers important, though limited, perspectives into the diversity of marine mammal social systems and their influence on disease transmission. However, an additional gap is the lack of research on interspecies disease transmission, the transfer of pathogens between different marine mammal species. Many species occur in sympatry, regularly coming in close contact and occasionally forming mixed species groups (Stensland et al. 2003; Sridhar et al. 2009; Goodale et al. 2017; Syme et al. 2021, 2023a, 2023b), creating opportunities for disease to spread both between and within species (Caley and Hone 2004). Despite its recognised importance in terrestrial systems, this remains an underexplored area in marine mammal disease ecology. Moreover, the overall sample size of this review, with only 14 studies meeting the inclusion criteria, further constrains the generalisability of these findings. Most studies focused on a narrow set of accessible species and regions, raising the question of whether our current understanding of disease-sociality relationships applies across the broader diversity of marine mammals. To address these limitations, future research must expand both taxonomic and geographic scope, particularly by including species of high conservation concern, to test whether the patterns observed in well-studied populations hold more broadly.

### 4.2 | Social Network Metrics Used in Studies

At the individual level, most studies found that individual animals with high association indices showed higher disease prevalence. Higher levels of social connectivity appear linked to increased disease occurrence in *Tursiops truncatus*. Infected *T. truncatus* individuals tend to have stronger coefficients of association than non-infected counterparts (Galvez et al. 2022) and the prevalence of lobomycosis-like disease (LLD) was markedly higher in communities where a high-rank male was affected (Félix et al. 2019; Van Bressem et al. 2024). Higher association

**TABLE 5** | Species, global IUCN status, study site, country, regional assessment and corresponding citations represented in the systematic review.

| Species | IUCN status (global) | Study site | Country | Regional assessment | Reference(s) |
|---|---|---|---|---|---|
| *Neomonachus schauinslandi* | Endangered (Baker et al. 2025) | Hawaii | North America | Endangered[b] (Robinson et al. 2018) | Robinson et al. (2018) |
| *Orcinus orca* | Data deficient Reeves et al. (2017) | Vancouver Island | Canada/North America | Endangered[a] NMFS (2005) | Guimarães et al. (2007); Weiss et al. (2020); Collier et al. (2025) |
| *Sousa sahulensis* | Vulnerable Parra et al. (2017) | Exmouth | Australia | Vulnerable[a] Queensland Government (2020) | Collier et al. (2022) |
| *Tursiops aduncus* | Near threatened Braulik et al. (2019) | Shark Bay | Australia | No regional assessment available | Powell et al. (2020); Leu et al. (2020); Collier et al. (2022, 2025) |
| *Tursiops erebennus* | Not evaluated | Potomac-Chesapeake Bay | North America | No regional assessment available | Collier et al. (2025) |
| | | St. Johns River | North America | No regional assessment available | DiVittore-Goodrum and Gibson (2023) |
| *Tursiops truncatus* | Least concern Wells et al. (2019) | Gulf of Guayaquil | Ecuador | Imminent risk of extinction[b] Félix and Burneo (2020) | Félix et al. (2019); Van Bressem et al. (2024) |
| | | Veracruz | Mexico | No regional assessment available | Galvez et al. (2022) |
| | | Cardigan Bay | United Kingdom | Least Concern[a] Genov (2023) | Magileviciute (2007) |
| | | Florida | North America | No regional assessment available | Sah et al. (2017) |
| | | Doubtful Sound | New Zealand | Critically endangered[a] Currey et al. (2011) | Sah et al. (2017) |
| | | St. Johns River | North America | Re-classified as *Tursiops erebennus* in 2023 No regional assessment available | Szott et al. (2022) |
| *Zalophus californianus* | Least concern Aurioles-Gamboa and Hernández-Camacho (2015) | Columbia River | North America | No regional assessment available | Collier et al. (2022) |

*Note:* Regional assessments include both ([a]) formal legislative listings (e.g., under the EPCB Act 1999, ESA 1973, IUCN Red List or state legislation) and ([b]) non-legislative recommendations from local scientific studies. Global (IUCN) and regional assessments are indicated where available.

**TABLE 6** | Summary of social network metrics used in studies investigating the relationship between social structure of marine mammals and disease transmission.

| Network measure | Description | Relevance to disease spread | Number of studies | Respective reference |
|---|---|---|---|---|
| Affinity | The average strength of an individual's associates | Individuals with stronger average associations may experience higher contact rates with close associates, potentially increasing repeated exposure to pathogens | 1 | Szott et al. (2022) |
| Association index | A measure of the proportion of times two individuals were observed together relative to all observations involving either individual (e.g., simple-ratio and half-weight indices) and typically used to depict a link between nodes within an animal social network | Higher association indices reflect stronger or more frequent co-occurrence in groups, increasing the likelihood of repeated pathogen exposure | 9 | Magileviciute (2007), Guimarães et al. (2007), Félix et al. (2019), Weiss et al. (2020), Leu et al. (2020), Galvez et al. (2022), Szott et al. (2022), DiVittore-Goodrum and Gibson (2023), Van Bressem et al. (2024) |
| Assortativity | The tendency of an individual to connect with other nodes that are similar (or dissimilar) in some attribute (e.g., sex, degree) | When individuals preferentially associate with others sharing similar traits (e.g., sex, degree), pathogens may spread more readily within certain subgroups, potentially amplifying within-group outbreaks | 1 | Magileviciute (2007) |
| Centrality | The tendency of individuals to occupy central positions within a social network based on the number, quality and direction of their social connections. Can be quantified through various metrics including degree centrality, closeness centrality, betweenness centrality and eigenvector centrality | Highly central individuals have greater influence over pathogen flow and can act as potential "super-spreaders"; pathogens are more likely to pass through these positions and be widely redistributed | 5 | DiVittore-Goodrum and Gibson (2023); Magileviciute (2007); Sah et al. (2017); Szott et al. (2022); Weiss et al. (2020) |
| Clustering coefficient | Tendency of nodes to form tightly connected groups or triangles | High clustering increases local transmission opportunities within tightly connected groups, potentially sustaining infections even if the wider network is fragmented | 4 | Guimarães et al. (2007); Magileviciute (2007); Sah et al. (2017); Szott et al. (2022) |
| Degree | The number of direct connections a node has | Individuals with more associates have greater opportunities for pathogen contact, increasing infection risk and spread potential | 7 | Collier et al. (2025, 2022); Guimarães et al. (2007); Leu et al. (2020); Magileviciute (2007); Powell et al. (2020); Robinson et al. (2018) |

(Continues)

**TABLE 6** | (Continued)

| Network measure | Description | Relevance to disease spread | Number of studies | Respective reference |
|---|---|---|---|---|
| Degree distribution | The statistical spread of degrees across all nodes in the network | A highly skewed distribution (few individuals with very high degree) indicates the presence of potential "super-spreaders" whose infection could drive large outbreaks | 1 | Collier et al. (2025) |
| Degree heterogeneity | The variation in the number of individual contacts across a population | Greater variation creates conditions for uneven disease spread, where highly connected individuals disproportionately contribute to transmission | 1 | Sah et al. (2017) |
| Degree homophily | The tendency of individuals with similar number of connections to associate | When highly connected individuals preferentially associate with other highly connected individuals, infection can circulate rapidly within this well-connected "hub" causing epidemics | 1 | Sah et al. (2017) |
| Demographic assortativity | The preference of nodes to associate based on shared demographic attributes | Preferential association based on demographic traits can channel disease spread along demographic lines (e.g., age, sex), potentially affecting vulnerability of specific groups | 1 | Collier et al. (2025) |
| Density | The proportion of possible connections that actually exist in a network | Denser networks increase the overall number of potential transmission routes, enabling faster and broader disease spread | 1 | Magileviciute (2007) |
| Modularity | The degree to which a network is divided into distinct, densely connected groups | High modularity may contain outbreaks within modules, slowing or limiting spread between groups | 4 | Collier et al. (2022); Magileviciute (2007); Sah et al. (2017); Weiss et al. (2020) |
| Network diameter | The longest of the shortest path between any pair of nodes in the largest connected component of the network | Longer diameters may slow pathogen spread across the entire network, while shorter diameters enable pathogens to reach all individuals in fewer steps | 1 | Sah et al. (2017) |
| Network fragmentation | The extent to which individuals are divided into disconnected subgroups | Fragmented networks may limit large-scale outbreaks by reducing connectivity between subgroups | 1 | Sah et al. (2017) |
| Path length | The number of steps between two nodes, averaged across all node pairs in a network | Shorter average paths between individuals can facilitate rapid transmission across the network | 2 | Guimarães et al. (2007); Magileviciute (2007) |
| Reach | The number of nodes a selected individual can access within a given number of steps | Individuals with greater reach can indirectly contact more of the population, increasing potential transmission range | 1 | Szott et al. (2022) |

(Continues)

**TABLE 6** | (Continued)

| Network measure | Description | Relevance to disease spread | Number of studies | Respective reference |
|---|---|---|---|---|
| Residency | The tendency of an individual to stay within a specific location over a period of time | Individuals remaining in one location may experience repeated contact with the same associates, affecting local pathogen persistence; lower residency may facilitate spread between locations | 1 | DiVittore-Goodrum and Gibson (2023) |
| Subgroup cohesion | A measure of the strength of connections within a specific subset of a network | Highly cohesive subgroups may facilitate sustained transmission within the group | 1 | Sah et al. (2017) |
| Subgroup size | The number of nodes belonging to a specific subgroup within the network | Larger subgroups provide more opportunities for within-group pathogen transmission, potentially sustaining longer outbreaks | 1 | Sah et al. (2017) |
| Transitivity | Fraction of all possible triangles present in the interaction network | Higher transitivity indicates that an individual's associates are also connected to each other, creating multiple redundant transmission routes that can sustain or facilitate local outbreaks | 1 | Sah et al. (2017) |

indices typically indicate more frequent social interactions, resulting in greater contact rates and more opportunities for disease spread. Additionally, individuals with high association indices may experience greater competition for resources such as food or resting areas, which may not only increase the likelihood of pathogen transmission but also result in higher stress levels and compromised immune function (Dierauf and Gulland 2001). Whilst most of the reviewed studies suggested similar findings, DiVittore-Goodrum and Gibson (2023) found that there was no association between lesion presence and association indices, suggesting that the strength of an individual's associations alone does not contribute to the presence of lesions in the community of *T. erebennus* studied. It is important to note that skin lesions are not a definitive indicator of infectious disease. Some infections may not produce external lesions, some visible lesions may result from non-infectious conditions, and many lesions are driven by environmental, chemical, or physical stressors rather than direct pathogen transmission (Wilson et al. 1999; Van Bressem et al. 2007, 2009; Mouton and Botha 2012; DiVittore-Goodrum and Gibson 2023; Guinn et al. 2024). This highlights that the absence of a relationship between association indices and lesions does not necessarily imply a lack of socially mediated disease spread. The discrepancy between these studies suggests that the relationship between association index and a population's vulnerability to disease varies across populations and may be influenced by additional ecological, environmental and social factors.

Similarly, the reviewed studies suggest that degree (i.e., the number of direct connections a node has) is also a useful social network metric to assess the likelihood of both contracting and spreading infectious diseases. Greater social connectedness appears to increase disease vulnerability in both *Zalophus californianus* and *Tursiops aduncus*. Simulation models show that in these species, increasing an individual's degree led to larger epidemics (Collier et al. 2022). Similarly, male *T. aduncus* in Shark Bay with higher degrees faced elevated disease risk, while females and calves, who had fewer interactions with conspecifics, had a reduced pathogen transmission risk (Leu et al. 2020). However, it is important to note that immune function can vary between sexes, with females often exhibiting lower contaminant loads due to depuration through reproductive processes, which may, in turn, impact their immune resilience (Wells et al. 2005). An alternative variation of degree that also seems to be a good indicator of prevalence to disease spread is synchrony degree (i.e., individuals breathing synchronously). Collier et al. (2025) found that juveniles who had the highest synchrony degree were most at risk of infection. However, a study on bottlenose dolphins in Shark Bay by Powell et al. (2020) reported conflicting results, finding no association between an individual's average degree in the first year of life and disease status. However, individuals that developed Tattoo Skin Disease in their second year of life had significantly more symptomatic associates in their first year than those who remained disease-free.

Sah et al. (2017) also explored how disease relates to degree heterogeneity, the average and variation in the number of individual contacts across a population, and degree homophily, the tendency of individuals with similar number of connections to associate. They found that high variation in individual degree in social networks was predictive of small and short epidemic outbreaks, except for highly contagious diseases (Sah et al. 2017).

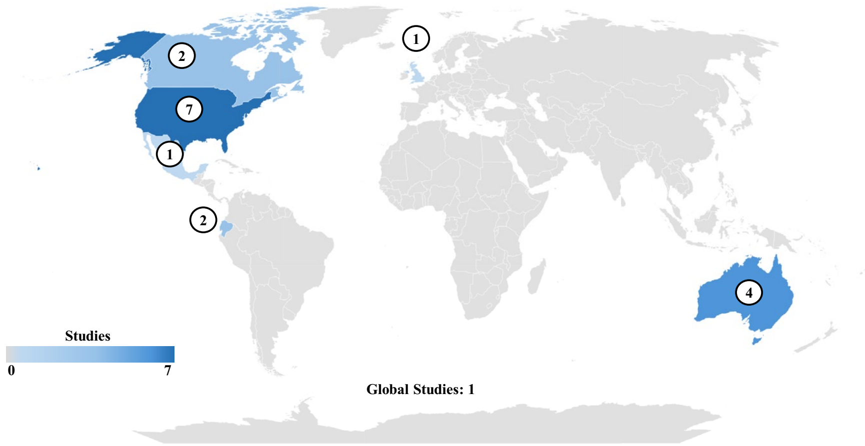


**FIGURE 3** | Geographical distribution of the data collected in the 14 studies included in the systematic review on marine mammal social structure and disease transmission. Numbers inside the circles and colour intensity indicate the number of studies undertaken in each continent. One study used globally distributed.

This demonstrates that a population's vulnerability to disease is influenced not only by an individual's degree, but also by the overall structure of the population, including factors such as degree heterogeneity and degree homophily.

Centrality refers to the tendency of individuals to occupy central positions within a social network based on the quantity, quality and distribution of social associations. Centrality can be quantified through various metrics including degree centrality, closeness centrality, betweenness centrality and eigenvector centrality (Freeman 1978; Opsahl et al. 2010). Researchers generally assume that infectious diseases spread more rapidly through highly centralised societies, where a few key individuals, or 'super spreaders', play a pivotal role in facilitating the spread of pathogens (Freeman 1978; Romano et al. 2016; Sah et al. 2017). However, the removal of these key individuals, through fatality or immunity, may fragment the network and disrupt the spread of disease, potentially reducing the overall vulnerability of a population to disease (Weiss et al. 2020). In *T. truncatus*, more central individuals and those who were connected to highly central individuals were more likely to be observed with lesions (Magileviciute 2007). Modelling work in *N. schauinslandi* indicated that selectively vaccinating these highly central individuals could substantially reduce epidemic size and duration (Robinson et al. 2018). However, because identifying and targeting such individuals is not always practically feasible, they concluded that broad vaccination, regardless of individuals' centrality, may be the more feasible strategy. Guimarães et al. (2007) also suggested that in populations of *O. orca*, highly central individuals, such as mature females, play an important role in the transmission of disease. Additionally, Szott et al. (2022) reported a highly central individual who interacted with a number of dolphins that later stranded after contracting cetacean morbillivirus, suggesting that this individual may have acted as a 'super-spreader' and transmitted the pathogen to those who later died and stranded. However, DiVittore-Goodrum and Gibson (2023) found no association between an individual's centrality and the presence or extent of lesion coverage in *T. erebennus*. Instead, they reported a significant correlation between residency and lesion presence, suggesting that where an individual spends its time, and the environmental conditions of that habitat, may play an important role in determining lesion occurrence. This highlights the complex relationship between network centrality, environmental conditions and disease susceptibility, while also indicating that, in some contexts, targeted control measures (e.g., vaccination of highly central individuals; targeted removal or euthanasia of highly infected individuals) could help mitigate disease outbreaks (Robinson et al. 2018).

Whilst individual level metrics such as association index, degree and centrality provide insights into how specific individuals may contribute to disease transmission, broader network-level properties can also influence the vulnerability of a population to disease. At a population level, network measures such as fragmentation and clustering coefficient influence the spread of pathogens through a population, affecting the size and duration of an epidemic. Measures of network fragmentation, including modularity, path length and diameter, indicate the extent to which individuals are divided into subgroups (Newman 2006). Highly fragmented networks may prevent the spread of disease through a population by breaking it into several tightly connected components. However, this subdivision may lower the threshold of an infection spreading within a subgroup, leading to more localised outbreaks (Sah 2017). Modelling work in *O. orca* suggests that increased modularity can lower the overall burden of morbillivirus (Weiss et al. 2020). Observations of *T. truncatus* subgroups exhibiting distinct, localised infection types (e.g., one subgroup with predominantly black fringe spots, another subgroup with predominately cloudy lesions) support the idea that modularity may limit pathogen spread (Magileviciute 2007). However, for highly contagious pathogens, increased network fragmentation may have the opposite effect, promoting larger and more prolonged epidemics by facilitating transmission between disconnected subgroups (Sah et al. 2017). These findings highlight how highly fragmented social networks can both limit and enhance the spread of disease, depending on the pathogen's transmissibility.

Another key population-level measure that was frequently mentioned in the included literature is clustering coefficient, a measure of how well connected the neighbours of an individual are. A high clustering coefficient likely facilitates rapid disease spread through closely connected subgroups (Croft et al. 2005; Newman 2003). In *O. orca* populations, modelling suggests that networks with high clustering coefficients are more vulnerable to disease epidemics (Guimarães et al. 2007). Further, the presence of tightly connected "cliques" (high clustering) in a population has been linked to prolonged but localised outbreaks of low transmissible pathogens, yet to elevated epidemic risk when pathogens are moderately or highly transmissible and can more easily spread between groups (Sah et al. 2017). These studies underscore the complex relationship between network structure and disease dynamics and in particular the importance of considering disease factors such as transmissibility when doing epidemiological modelling.

Beyond marine mammals, research across taxa shows that network topology, including centrality, fragmentation and clustering, plays a fundamental role not only in the spread of pathogens but also in socially learned information. Comparative and theoretical studies in birds, primates and insects have demonstrated parallels between the spread of infectious diseases and cultural traits such as innovations, behaviour and vocalisations (Slater 1986; Horner et al. 2006; Leadbeater and Chittka 2007; Voelkl and Noë 2008; Mann et al. 2012; Cantor and Whitehead 2013; Cantor et al. 2021), with highly central individuals often accelerating the diffusion of innovations, and modularity and clustering promoting the development of distinct cultures or behavioural variants among groups. These insights reinforce that the network metrics highlighted here are part of a broader framework considering the feedback between individual and population processes (Cantor et al. 2021) governing multiple forms of transmission in social systems and highlight the practical implications for not only epidemiological modelling, but for understanding the evolution and persistence of animal cultures (Whiten 2021).

### 4.3 | Geographical and Temporal Spread of Studies

Compared to the extensive research effort on infectious diseases in terrestrial mammals, the number of studies examining these processes in marine mammals is relatively limited. Most research focuses on North America and Australia, with limited or no representation in the Global South, such as for regions such as Asia and Africa, where research has been comparatively chronically underfunded. This bias in research distribution highlights the challenges, costs and logistical barriers to sustain the long-term studies required to assess the social systems and health status of marine mammals. Critically, it may also result in an incomplete understanding of disease transmission dynamics in marine mammals globally, as different ecological conditions could influence social structure and, in turn, disease dynamics in underrepresented regions. Addressing this gap by promoting studies in and collaborations with institutions from diverse geographical regions is crucial for the development of a comprehensive global perspective on disease transmission and dynamics.

Publication trends show that researchers increasingly recognise the role of social structure in marine mammal disease ecology, particularly in the last decade. The observed peak in publications around 2020 and 2022 may reflect an increased interest following notable disease outbreaks in marine mammal populations, such as the phocine distemper (Osterhaus and Vedder 1988; De Koeijer et al. 1998) and morbillivirus (Van Bressem et al. 1991; Duignan et al. 1996) epidemics of 1988 and 1990 and/or advancements in social network and epidemiological modelling methods. However, the recent decline in publications may suggest the need for continued funding and interdisciplinary collaboration to maintain momentum in this emerging field.

## 5 | Implications for Conservation and Management

Understanding how social structure influences disease transmission has important implications for the conservation and management of marine mammal populations. This review highlights that individuals with high connectivity or centrality in social networks can act as 'super-spreaders', while population-level structures like modularity and fragmentation can either buffer or exacerbate disease spread depending on pathogen traits. These findings suggest that disease mitigation strategies should be tailored to the social organisation and contact patterns of target species and populations. For example, several studies modelled social structure to identify highly connected individuals and explored targeted vaccination strategies focused on these 'super-spreaders'. Their findings suggest that prioritising such individuals for vaccination can substantially reduce both outbreak size and duration (Robinson et al. 2018; Weiss et al. 2020).

However, while targeted vaccination strategies may be feasible in some populations, they may be logistically challenging or ethically complex in others. In these cases, alternative management approaches, such as enhanced disease surveillance, minimising human-induced stressors or prioritising the health and quality of the surrounding habitat, may be critical in managing and reducing disease risk (Soares et al. 2022). One promising strategy is the regular health monitoring of key individuals within a population, which may serve as an early warning system for emerging outbreaks and enable timely and effective intervention.

The effectiveness of these approaches will largely depend on the social structure of the target population, as we have argued. In theory, populations in which individuals are structured into modular or fragmented social networks may respond best to strategies that preserve the integrity of these social clusters, whereas well-mixed populations may require early-warning systems and interventions to effectively control disease spread. Expanding research on the social systems and health of underrepresented species and regions is essential for refining these approaches and avoiding one-size-fits-all solutions that may be ineffective or even counterproductive in poorly understood systems.

While the reviewed studies encompassed species spanning the full range of the IUCN Red List categories, threatened taxa remain underrepresented. Currently, over a quarter of marine mammal species are classified in a threatened category (The IUCN Red List of Threatened Species 2025), with disease one of the leading causes of mortality in marine vertebrates (Bogomolni et al. 2008). Given the increasing threats to marine mammals from environmental change (Greer et al. 2008; Harvell et al. 2002), pollution (Behringer et al. 2020; Vignal et al. 2021) and human activities (Bossart 2007), expanding research to include a broader range of marine mammal species, particularly those at greater risk, is essential for developing effective, species-specific conservation strategies.

Whilst social structure is a key driver in disease transmission dynamics, it does not act in isolation. Other epidemiological and ecological variables, such as mode of transmission, infectious period, transmissibility, immunity and host genetic diversity, act synergistically to shape disease dynamics. For example, inbreeding can reduce genetic variability and compromise immune competence, potentially increasing population susceptibility to infectious disease outbreaks (Valsecchi et al. 2004). In addition, many species engage in interspecific interactions and can form mixed-species groups (Stensland et al. 2003; Sridhar et al. 2009; Goodale et al. 2017; Syme et al. 2021), creating potential pathways for interspecific infection. Future research must recognise and incorporate these factors to develop a more nuanced understanding of disease risk in marine mammal populations.

Interdisciplinary collaboration across ecology, epidemiology and conservation biology will be critical to designing robust, evidence-based management strategies tailored to each population's unique social and ecological context. By integrating social dynamics into conservation planning, health monitoring frameworks and management strategies, we can enhance the effectiveness and efficiency of interventions to support the long-term health and resilience of marine mammal populations.

## 6 | Conclusions

This systematic review demonstrates that multiple aspects of sociality, including association strength, centrality, degree, network fragmentation and clustering, can influence disease transmission. Highly connected and central individuals, or 'super-spreaders', have been identified as key drivers of disease transmission, whilst highly fragmented networks can both limit and enhance the spread of disease, depending on the pathogen's transmissibility. Despite these insights, it is evident that previous research has been mainly focused on *T. truncatus*, with limited studies on lesser-known or more threatened species, emphasising the need for broader taxonomic representation in future research.

Given the increased frequency and severity of emerging and re-emerging infectious diseases in the marine environment, along with the range of social structures seen across marine mammal populations, a more comprehensive and species-specific approach is required for disease monitoring and management. The integration of comprehensive social and health data with novel epidemiological modelling should be applied to underrepresented species to explore disease mitigation strategies. Future research should incorporate a broader range of social, ecological and epidemiological factors, ensuring that disease management efforts are informed by a holistic understanding of marine mammal social networks, pathogen transmission and disease outcomes.

### Author Contributions

**Caitlin R. Nicholls:** conceptualization, investigation, writing – original draft, methodology, validation, visualization, writing – review and editing, formal analysis, data curation. **Mauricio Cantor:** conceptualization, writing – review and editing, supervision, validation. **Luciana Möller:** conceptualization, supervision, writing – review and editing. **Guido J. Parra:** conceptualization, supervision, validation, writing – review and editing, resources.

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

All data supporting the findings of this study are provided in the Supporting Information.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Data extraction form used in covidence. **Table S2:** Comprehensive list of articles included, detailing the species studied, region of data collection, length of study and methods used for each study.