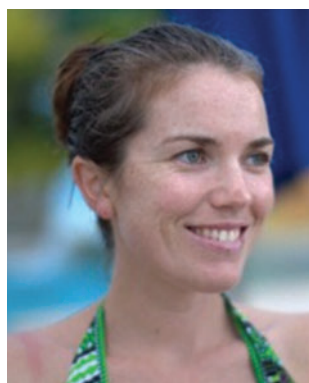


# The marine mammal microbiome: current knowledge and future directions



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Marine mammals are globally significant because of their sensitivity to environmental change and threatened status, often serving as 'ecosystem sentinels'<sup>1</sup>. Disease is a major cause of marine mammal population decline and the role of the microbiome in disease has generated considerable interest. Recent research in humans has greatly enhanced our understanding of how the host-associated microbial community, the microbiome, affects host health. In this review, we provide an overview of the extent of the marine mammal microbiome with a focus on whole community characterisation using genomic methods. This research highlights the overlap in microbial communities between geographically distinct species and populations of marine mammals, suggesting tight links between marine mammals and their microbial symbionts over millions of years of evolution. An understanding of these links in both healthy and compromised hosts is essential to identifying at-risk populations and making ecologically appropriate management decisions. We advocate further development of innovative sampling and analytic techniques that advance the field of microbial ecology of marine mammals.

Recent investigations have highlighted the capacity of the microbiome to act strongly and significantly in maintaining host health with a vital role in disease manifestation and immune system function<sup>2,3</sup>. Members of the microbial community can directly influence the progression of a disease via infection and also modulate the host's own immune system regulation and response<sup>4</sup>. Indeed the host's microbial partners are essential to immune system function. The microbiome has been observed to be species-specific in a variety of vertebrate hosts<sup>5–7</sup> and is influenced by host phylogeny, as a result of millions of years of co-evolution<sup>8</sup>. Marine mammals represent unique evolutionary lineages and investigations into their associated microbes will provide a deeper understanding of their ecology and evolution.

Marine mammals form a diverse group of 129 species in three orders, and of those, 28 are considered endangered or threatened<sup>9</sup>. Disease is one of the main causes of death in marine mammals and some populations have suffered mass mortalities caused by bacterial pathogens<sup>10</sup>. Bacteria exist as part of the normal, or even beneficial, flora associated with a host, fluctuating and changing with a host's physiology and metabolism<sup>11</sup>. In mammals, disease can occur under

a number of different circumstances, most commonly on occasions when the host's immune system is compromised. For marine mammals, susceptibility to pathogens may be particularly elevated due to anthropogenic stressors such as depleted food resources, habitat degradation and chemical or sound exposure<sup>12–15</sup>. Additionally, succession events occurring after an initial bacterial infection may lead to dysbiosis, and alterations in the host's microbiome may be a better predictor of disease progression than following the presence of individual pathogenic agents<sup>16</sup>. Hence, we need to establish baseline data on microorganisms commonly associated with marine mammals in order to detect anomalies. In the last decade genomic sequencing technologies have provided a previously unrecognised diversity of microorganisms in numerous diverse habitats. In this brief review we highlight the current knowledge of the microbial composition in associations with marine mammals with a focus on whole community characterisation.

## Skin microbiome

Skin, as the largest organ of mammals, serves as a thick physical barrier that provides defense against the surrounding marine environment. Marine mammal skin is prone to lesions and disorders, however the role of microorganisms in these conditions is still largely unresolved and knowledge is primarily founded on cultivation-based studies<sup>17</sup>. The recent application of cultivation-independent sequencing-survey approaches to humpback whale (*Megaptera novaeangliae*) skin has demonstrated that a unique ecosystem of microbes resides on the skin surface (Table 1), which differs from the community present in seawater<sup>18</sup>.

Among populations of humpback whales surveyed in diverse geographic regions, two genera of bacteria (Bacteroidetes genus *Tenacibaculum* and Gammaproteobacteria genus *Psychrobacter*) were found to be cosmopolitan and abundant associates on humpback whale skin<sup>26</sup>. Scanning electron microscopy of humpback whale skin revealed a rich layer of microbial cells on the skin surface<sup>26</sup>, but as humpback whales regularly undergo skin sloughing through both behavioural<sup>27</sup> and physiological activities<sup>28</sup> it is possible that the robust *Tenacibaculum* and *Psychrobacter* cells may have some means to maintain their residence on the whale skin and could provide benefits to their host. Sequencing survey-based data also demonstrate differences between the skin bacterial associates of healthy and health-compromised humpbacks<sup>18,26</sup>. Additional data on and study of the skin microbiome might potentially improve our ability to assess health status among free-ranging marine mammals, in particular cetaceans.

## Gut microbiome

The gastrointestinal tract is home to an abundant community of microorganisms. The gut microbiome plays a significant role in food breakdown and digestion, the production of essential vitamins and minerals and regulation of the immune system<sup>3</sup>. In young mammals,

Table 1. Relative abundance of bacterial phyla compared between known studies of marine mammal species and anatomical sites in healthy individuals

Order	Sub-Order	Cetacea		Carnivora						Sirenia			
		Mysticeti	Odontoceti	Phocidae			Pinnipedia						
Common name		Humpback whale	Bottlenose dolphin	Leopard seal	Southern elephant seal	Hooded seal	Harbour seal	Grey seal	Australian fur seal	Australian sea lion	Dugong	Manatee	
Species		<i>Megaptera novaeangliae</i>	<i>T. truncatus</i> <i>T. truncatus</i> , <i>T. aduncus</i> , <i>T. hybrid</i> <sup>A</sup>	<i>Hydrurga leptonyx</i>	<i>Mirounga leonina</i>	<i>Cystophora cristata</i>	<i>Phoca vitulina</i>	<i>Halichoerus grypus</i>	<i>Archaeophagus pusillus darwini</i>	<i>Neophoca cinerea</i>	<i>Dugong dugong</i>	<i>Trichechus manatus latirostris</i>	
Age group		Adult	Adult and Sub-adult	Adult	Adult and sub-adult	Pup			9 m pup	6 m pup	2 m pup	Adult	Sub-adult
Sample		Skin	Blow	Faeces	Faeces	Faeces	Colon	Colon	Faeces	Faeces	Faeces	Faeces	Faeces
Bacterial phyla (% of community)	Firmicutes	1	1	44	43	18	22	76	83	87	83	83	79
	Bacteroidetes	40	1	8	21	14	68	24	10	6	4	15	79
	Proteobacteria	60	50	31	15	5	9	0	2	<1	4	<1	<1
	Fusobacteria	<1	1	13	20	62	1	<1	<1	<1	<1	0	<1
Number of individuals		51	24	12	18	6	9	1	4	4	4	1	11
Methodology		P	P	P	P	P	CL	CL	P	P	P	CL	P
Reference		19	19	7	7	7	21	21	22	22	24	25	25

Data summarised for the dominant bacterial phyla across species and anatomical sites. Table data are as follows: not recorded (NR); month (m); clone libraries (CL); pyrosequencing (P); metagenomic sequencing (M).  
<sup>A</sup>Hybrid bottlenose dolphin refers to individuals sired by *T. truncatus* to *T. aduncus* females born in captivity.

the gut microbiome is required for full development of the immune system and maturation of the gut<sup>29,30</sup>. Studies of the complete gut microbiome of marine mammals include leopard seals (*Hydrurga leptonyx*), southern elephant seals (*Mirounga leonine*), grey seals (*Halichoerus grypus*), hooded seals (*Cystophora cristata*), harbor seals (*Phoca vitulina*), Australian fur seals (*Arctocephalus pusillus doriferus*), Australian sea lions (*Neophoca cinerea*), Florida manatees (*Trichechus manatus latirostris*) and dugongs (*Dugong dugong*). Across all these species the gut microbiome is composed largely of Firmicutes, Bacteroidetes and Proteobacteria (Table 1). Diet and age have been identified as factors that shape the composition of the gut microbiome<sup>7,25</sup>.

Amongst the seals, the gut microbiome of pinnipeds has a greater abundance of the phylum Firmicutes compared with phocids (Table 1). A 'core' group of microorganisms including the genera *Ilyobacter*, *Psychrobacter*, *Fusobacterium*, *Bacteroides*, *Subdoligranulum*, *Sporobacter*, *Sutterella*, *Weissella*, *Anaerococcus* and *Campylobacter* have been observed within phocid seals<sup>7,21,22</sup> whilst their herbivorous relatives, within the order Sirenia, shared members from the order Clostridiales, including the genera *Clostridium* and *Ruminococcus*<sup>24,25,31</sup>. The presence of shared bacterial operational taxonomic units (OTUs) in multiple hosts from different studies highlights the strong phylogenetic influence on microbial assembly.

## Respiratory microbiome

Respiratory illnesses such as pneumonia are a major cause of mortality in both wild and captive marine mammals<sup>32</sup>. The cetacean upper respiratory tract terminates in a blowhole, positioned at the top of the head. This feature is a unique adaptation to life in the marine environment, and allows airways to be effectively sealed off from seawater. Upon surfacing, cetaceans forcefully exhale and in the process eject a substance termed blow (also called condensed respiratory vapor or exhaled breath condensate). This material has been shown to harbour potential pathogens in whales<sup>33</sup> and has also been used to characterise the normal respiratory-associated microbiome residing in the upper respiratory tract of bottlenose dolphins<sup>19,20</sup> (see collection methods in Figure 1). Members of the bacterial genera *Plesiomonas*, *Aeromonas*, *Escherichia*, *Clostridium* and *Pseudomonas*, *Burkholderia*, *Mycobacterium*, *Haemophilus*, *Streptococcus* and *Staphylococcus* (including multiple resistant *Staphylococcus aureus*) have been detected in both sick/dead<sup>34</sup> and healthy, free-ranging cetaceans<sup>20,33,35</sup>.

Blow samples from both free-ranging *Tursiops truncatus* and captive *T. aduncus* and *T. truncatus* were dominated by three novel dolphin associated clades (termed DAC 1, 2 and 3) within the Cardiobacteraceae lineage of the Gammaproteobacteria<sup>19,20</sup>. The Cardiobacteraceae are facultative anaerobic, Gram-negative rod-shaped cells, members of which form part of the commensal

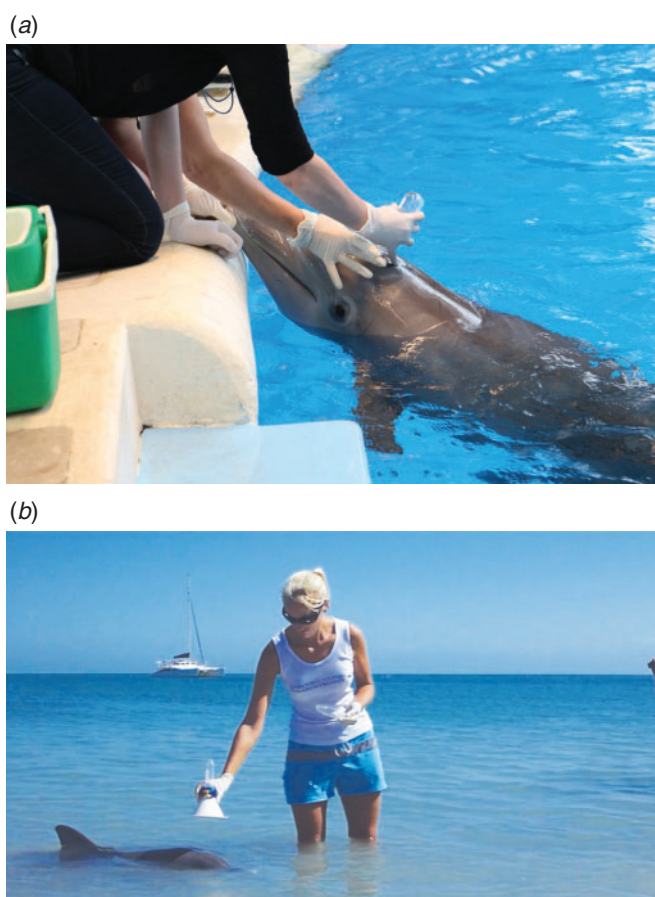


Figure 1. Exhaled 'blow' samples provide access to respiratory microbiome, host DNA, hormones and associated metabolites. Bottlenose dolphins can be trained to exhale on demand allowing collections to be made routinely as shown here by Jillian Wisse from the National Aquarium in Baltimore, Maryland, USA in captive dolphins (a) and Dr Ewa Krzyszczyk, collecting samples from wild bottlenose dolphins that visit a beach in Shark Bay, WA, Australia (b). Photo credit monkeymiadolphins.org.

microbiome of humans, and whose growth is enhanced by the presence of carbon dioxide<sup>36</sup>, which occurs in high abundances at the termination of the respiratory tract. Representatives from each of DAC 1, 2, and 3 have been present in every bottlenose dolphin surveyed thus far, although the majority of sequences are associated with DAC 3, indicating this is likely a ubiquitous and critical component of the dolphin respiratory system. Other 'core' taxa associated with the dolphin respiratory microbial community appear to include the *Arcobacter*, Hydrogenimonaceae, *Halotalea*, *Aquimarina*, *Helococcus*, *Mycetocola*, *Methylococcus* and *Marinimicrobium*<sup>19</sup>. Temporal analysis of captive dolphins suggests community composition in healthy animals is quite stable and that individual dolphins harbour consistently unique microbial communities<sup>19</sup>.

## Sampling techniques

Sampling of material for microbiological analysis from marine mammals is logistically challenging (reviewed by Hunt *et al.*<sup>37</sup>), hence the majority of information on microbial disease comes from captive or stranded animals that are not necessarily representative of



the greater wild population. However, current sampling methods (see examples in Figures 1 and 2) still provide considerable insight into the microbiome of marine mammals. Capture by sedation or restraint has been employed on smaller species such as seals and dolphins<sup>7,38,39</sup> and has recently been used for some larger whales<sup>40</sup>. However, there are few opportunities to sample using these methods. It is increasingly common to use biopsy darts for collection of skin and blubber samples for genetic and, now, microbiological studies<sup>18,41</sup>. Permissions for biopsy sampling can be challenging for some species of marine mammals, and repeated samplings are often not possible for the same individuals. In order to increase existing data on the marine mammal microbiome, logistically feasible, non- or minimally-invasive sampling protocols that are easily reproducible and provide biological material suitable for a range of studies are necessary. For example, respiratory blow can be used to examine host DNA<sup>42</sup> and hormone levels<sup>43,44</sup> as well as respiratory associated microorganisms<sup>19,33,37</sup>, while non-invasively collected fecal samples can be used to study host DNA<sup>45</sup>, prey items<sup>46</sup> and the gut microbiome<sup>22,23</sup>.

## Future research

It appears likely that there are deep branching clades of bacteria that are uniquely associated with marine mammals and have been conserved throughout the evolution of their hosts. Many bacterial sequences obtained from marine mammal studies have close relatives that originate from other marine mammal species. This has significant implications for the transmission of disease amongst these hosts. As they are usually highly social animals, there are numerous opportunities for the transfer of microorganisms between individuals<sup>47</sup>. Diseases in marine mammals have also been shown to have their roots in other mammals, including dogs<sup>48,49</sup> and humans<sup>50</sup>. In many cases where disease has caused significant

mortality in wild marine mammals, it has been linked to viruses, including morbillivirus, phocine distemper and influenza virus<sup>51–55</sup>. Despite these links being made there is really very little known regarding the ecological role of viruses in marine mammal hosts.

Further investigations into the factors responsible for shaping the marine mammal microbiome need to be made. Designing studies that control for host variation will allow us to make headway in our understanding of disease manifestation. Studies that focus on the functionality of the microbiome will reveal the interactions between host and the microbial community<sup>23,56</sup>. In human subjects, similar target investigations have allowed for the development of novel metabolites to treat and prevent disease<sup>57</sup>. Unlike humans, however, to access adequate biological material, strides need to be taken to develop innovative and non-invasive techniques for the collection of relevant samples from wild populations.

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Figure 2. Collection of samples from wild marine mammals is logistically challenging. The collection of quality biological material with minimal impact on the animal requires the development of innovative sampling methods. This photo shows petri dishes attached to a modified pole for the collection of exhaled 'blow' samples from a southern humpback whale off the coast of northeast Australia. Photo credit Tracey Rogers.

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## Biographies

**Tiffanie Nelson** is a researcher from Australia currently undertaking a postdoctoral fellowship at Montana State University, Bozeman, USA. Tiff is a microbial ecologist, who focuses on the microbiome

of marine mammals as well as humans and environmental samples. Her interests are in health and disease associated with the microbiome. Tiff's current project is investigating the vaginal tract microbiome of women in relation to bacterial vaginosis using both culture-dependant and -independent methods.

**Amy Apprill** is a researcher at the Woods Hole Oceanographic Institution in Massachusetts, USA. Amy is a marine microbiologist researching questions that focus on the contribution of microorganisms to the health and ecology of marine animals. Amy is also interested in how animal-associated microbes reflect the alterations occurring in their surrounding marine environment. Her current research uses a combination of field measurements and observations and laboratory experiments and relies on diverse methodology (cultivation, genomic, metagenomic and bioinformatic) to examine the microbiomes of reef-building corals and marine mammals.

**Janet Mann** is professor of biology and psychology and vice provost for research at Georgetown University, Washington DC, USA. Janet has expertise in the field of animal behavior with extensive research focusing on marine mammals. Her work has focused on social networks, female reproduction, calf development, life history, conservation, tool-use, social learning and culture among bottlenose dolphins in Shark Bay, Australia. Her long-term study 'The Shark Bay Dolphin Research Project', tracks over 1600

dolphins throughout their lives and includes an international team on three continents where each group studies different aspects of delphinid biology.

**Tracey Rogers** is associate professor at the University of New South Wales. Tracey works across a diverse range of research fields with many years of experience working in Antarctica with marine mammals. The common theme in Tracey's research is in attempting to understand how mammals respond to change. Tracey uses multidisciplinary approaches to understand the ecology of mammals. Most of her work uses models and techniques with captive populations for applications in field settings. Other techniques include stable isotope analysis, satellite telemetry and acoustics.

**Mark Brown** is a senior research fellow at the University of New South Wales, Sydney, Australia. He has extensive expertise in research that focuses on microbes (Bacteria, Archaea and microbial Eukaryotes), primarily from marine environments. Mark's main interest is in investigating how microbes interact with each other and their environment to form communities that sustain critical ecosystem processes. His current research couples innovative *in situ* sampling methods, genetic tools, bioinformatics and ecological theory to elucidate and predict the form, function and impact of microbes in rapidly changing ecosystems.



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