A systematic review of the diversity and virulence correlates of metastrongyle lungworms in marine mammals.

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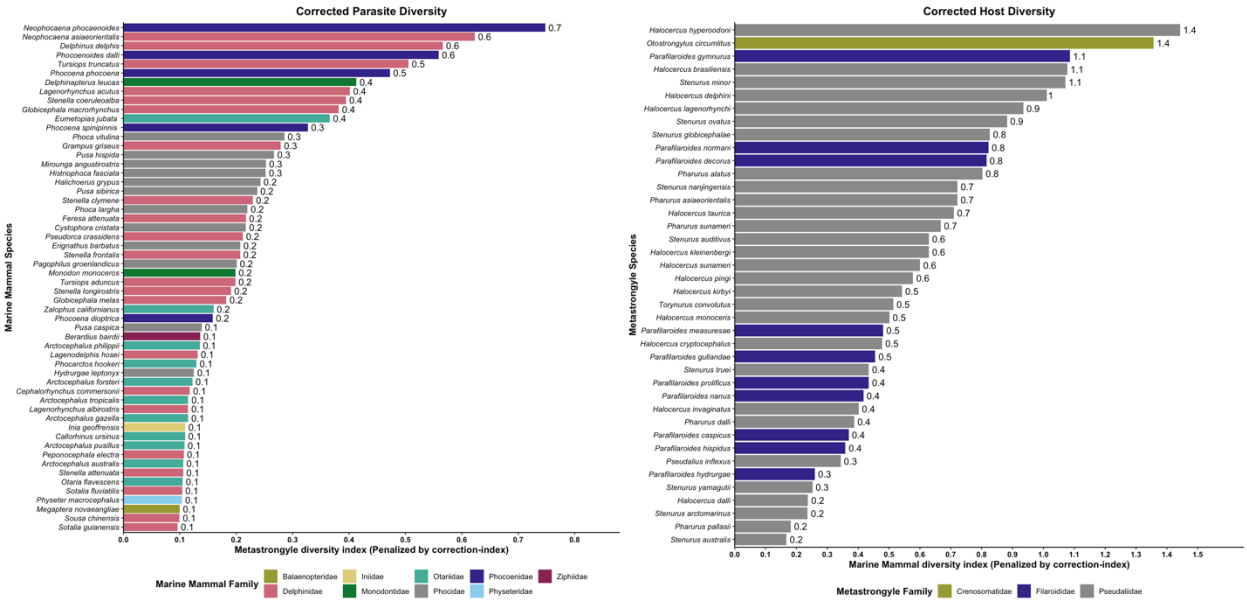
Graphical Abstract:



Abstract

Metastrongyle lungworms could be particularly detrimental for diving animals such as marine mammals, however little is known of the drivers of pathogenic host-parasite relationships in this group. This systematic review analyzed the diversity of metastrongyles in marine mammals and the host and parasite traits associated with virulence. There have been at least 40 species of metastrongyles described in 66 species of marine mammals. After penalization for study biases, *Halocercus hyperoodoni*, *Otostrongylus circumlitus*, *Parafilaroides gymnurus*, *Halocercus brasiliensis*, and *Stenurus minor* were the metastrongyles with the widest host range. Most studies (80.12%, n=133/166) reported that metastrongyles caused bronchopneumonia, while in the cardiovascular system metastrongyles caused vasculitis in nearly half of the studies (45.45%, n=5/11) that assessed these tissues. Metastrongyles were associated with otitis in 23.08% (n=6/26) of the studies. Metastrongyle infection was considered a potential contributory to mortality in 44.78% (n=90/201) of the studies while 10.45% (n=21/201) of these studies considered metastrongyles the main cause of death. Metastrongyle species with a wider host range were more likely to induce pathogenic effects. Metastrongyles can cause significant tissue damage and mortality in marine mammals although virulent host-parasite relationships are dominated by a few metastrongyle species with wider host ranges.

Keywords: marine mammals, metastrongyles, lungworms, parasites, pathogenicity, virulence.

35 **1. Introduction**

36 Metastrongyloidea (Nematoda: Strongylida), also known as lungworms or metastrongyles, are
37 common parasites of the respiratory, cardiovascular, and rarely the auditory system of mammals
38 (Measures, 2001). The definitive hosts become infected through ingestion of larval stages within
39 invertebrate intermediate hosts or free on pasture, therefore, metastrongyle infection can be quite
40 common among free-foraging domestic and wild mammals (Measures, 2001; Regassa *et al.*, 2010;
41 Niebuhr *et al.*, 2021). Like other helminth infections, the pathogenic effects of
42 metastrongyloidiasis can be broad with impacts that range from subclinical infection to
43 bronchopneumonia and death (Measures, 2001; Forbes, 2021). The reasons for these variable
44 outcomes are not fully understood but site of infection (e.g. upper vs lower airways), burden and
45 host immune status have been indicated as drivers of pathogenic outcomes (Forbes, 2021).
46 However, it is unclear if certain host-parasite relationships are more detrimental for the host and
47 if these more virulent associations obey to ecological factors that could illuminate conserved
48 drivers of pathogenicity in these nematodes. Interestingly, the virulence of metastrongyles could
49 be higher for animal species that require optimal respiratory and auditory function for fitness, such
50 as marine mammals (Bergeron *et al.*, 1997b; Measures, 2001; Seibel *et al.*, 2010). Marine
51 mammals rely on cardiovascular and lung capacity for foraging dives and the otic apparatus of
52 cetaceans is critical for communication and echolocation in the water column (Bergeron *et al.*,
53 1997b; Measures, 2001; Seibel *et al.*, 2010). Therefore, metastrongyles parasitism of these host
54 compartments could be associated with disease, stranding and death (Bergeron *et al.*, 1997b;
55 Measures, 2001; Seibel *et al.*, 2010), making this animal group an interesting model to test
56 conserved correlates of virulence among metastrongyle species. Nevertheless, metastrongyles are
57 one of the most diagnosed parasites in marine mammals, and in many circumstances are considered

58 incidental findings of little to no pathologic significance (Geraci and St. Aubin, 1987). This
59 conflicting evidence could be related to negative metastrongyle effects limited to specific host-
60 parasite relationships, parasite traits, environmental conditions, or the research methods employed
61 to assess the health impacts. However, a systematic assessment of the factors that could modulate
62 the health impacts of metastrongyles has not been reported.

63 Three families of metastrongyles are prominently found in marine mammals, spanning
64 seven genera, with a considerable diversity of species within each genus. Despite this diversity,
65 metastrongyles share similar life histories and host exploitation strategies in marine mammals.
66 Most aquatic metastrongyle species require an obligate intermediate host, usually an invertebrate,
67 where several larval stages develop until reaching an infective stage (Dailey, 1970a, 2006a). These
68 infective larvae are consumed by the definitive host and then migrate from the gastrointestinal
69 system to the respiratory or cardiovascular system where sexual maturity and reproduction occurs,
70 releasing embryonated-larvated eggs or larvae (Taylor *et al.*, 2015). Additionally, in some species,
71 maternal lungworms infect neonates through the placenta and/or milk (Dailey *et al.*, 1991a). In
72 the airways and respiratory sinuses or cardiovascular system, metastrongyles feed on epithelial-
73 endothelial cells, host debris and occasionally blood (Dailey, 1970a; Fauquier *et al.*, 2010; Rhyan
74 *et al.*, 2018a). These processes of migration through tissues, feeding and releasing eggs and larvae
75 illicit variable immune responses in the host (Baylis and Daubney, 1925; Fauquier *et al.*, 2010;
76 Groch *et al.*, 2020a). This immune response is usually directed against parasite cuticle, larvae,
77 eggs or parasite remains and usually consist in the attraction of macrophages, eosinophils and
78 lymphocytes to the site of infection (Fauquier *et al.*, 2010; Zafra *et al.*, 2015a; Seguel *et al.*, 2020a;
79 Groch *et al.*, 2020a). The degree of this inflammatory response and its impact on health status can
80 be quite variable ranging from minimal to severe bronchopneumonia (Fauquier *et al.*, 2010;

81 Seguel *et al.*, 2020a; Groch *et al.*, 2020a), being the drivers of the variable responses poorly
82 understood.

83 There is conflicting evidence regarding the connection between metastrongyle infections
84 and cetacean strandings (Arbelo *et al.*, 2013). Currently, there is no consensus on whether
85 inflammation in the otic apparatus, elicited by a presence of metastrongyle parasites, can impair
86 hearing or echolocation to a significant enough degree to be considered a contributory factor in
87 cetacean strandings (Geraci and St. Aubin, 1987; Wohlsein *et al.*, 2019a). Similarly, the presence
88 and feeding behavior of the nematodes in bronchi and lung parenchyma facilitates secondary
89 bacterial infections with conflicting documented outcomes, ranging from little importance for lung
90 physiology to fatal bronchopneumonia, especially when parasites are found in the lower
91 respiratory system (Siebert *et al.*, 2001; Lehnert *et al.*, 2010; Ulrich *et al.*, 2015, 2016; Reckendorf
92 *et al.*, 2021). This conflicting evidence could be related to several host and parasite traits, although
93 across biological systems, parasite biomass, usually assessed in terms of burden, is a common
94 driver of negative health outcomes (Pedersen and Fenton, 2015; Seguel and Gottdenker, 2017).
95 Similarly, parasite and host sizes play an important role in assessing total parasite biomass and can
96 sometimes serve as useful proxies of biomass to identify particularly detrimental host-parasite
97 relationships across studies (Seguel and Gottdenker, 2017). Another potential factor impacting
98 health outcomes across host-parasite systems is the capacity of certain helminths to parasitize
99 multiple host species. Parasites with a wider host range can potentially become more virulent
100 because decreases in host fitness due to infection can be compensated by infecting other
101 susceptible species (Poulin, 2011; Schmid-Hempel, 2021). However, the role of these host and
102 parasite traits on the health impact of metastrongyles is not well defined.

103 The objectives of this systematic review were to i) summarize existing literature concerning
104 relationships between marine mammals and metastrongyle parasites, ii) assess the relative host
105 and parasite diversity of infections iii) outline the pathology and health consequences that result
106 from metastrongyle infections in marine mammals, with assessment of the potential drivers of
107 these effects.
108

109 **2. Materials and Methods**

110 *2.1 Searching methods and inclusion criteria*

111 A systematic literature review on metastrongyle parasites in marine mammals was
112 conducted on July 6, 2021. The search was conducted using Google Scholar and PubMed,
113 following the best practices outlined by Haddaway and Watson (2016) to conduct an aggregative
114 systematic review in the field of parasitology (Haddaway and Watson, 2016) and the
115 recommendations outlined in the "Preferred Reporting Items for Systematic Reviews and Meta-
116 Analyses" (Page *et al.*, 2021).

117 The search terms used for the literature search on PubMed were as follows: "((Marine) OR
118 (Cetacean) OR (Delphinidae) OR (Phocidae) OR (Phocoenidae) OR (Otariidae) OR
119 (Monodontidae) OR (Mustelidae) OR (Trichechidae) OR (Odobenidae) OR (Ursidae) OR
120 (Odobenidae) OR (Balaenidae) OR (Neobalaenidae) OR (Eschrichtiidae) OR (Balaenopteridae)
121 OR (Physeteridae) OR (Kogiidae) OR (Ziphiidae) OR (Platanistidae) OR (Iniidae) OR (Lipotidae)
122 OR (Pontoporiidae) OR (Dugongidae) OR (Seal) OR (Porpoise) OR (Otter) OR (Dolphin) OR
123 (Sea lion) OR (Whale) OR (Walrus) OR (Manatee)) AND ((Metastrongyle) OR (Metastrongylus)
124 OR (Metastrongyloidea) OR (Metastrongylidae) OR (Parafilaroides) OR (Stenurus) OR

125 (Halocercus) OR (Pseudaliidae) OR (Filaroididae) OR (Crenosomatidae) OR (Otostrongylus) OR
126 (Skrjabingylus))".

127 The search terms used for the literature search on Google Scholar were reduced due to
128 limitations in the advanced search software, notably a 256-character limit on searches. The search
129 terms used for Google Scholar were as follows: "((Metastrongyle) OR (Metastrongylus) OR
130 (Metastrongyloidea) OR (Metastrongylidae) OR (Parafilaroides) OR (Stenurus) OR (Halocercus)
131 OR (Pseudaliidae) OR (Filaroididae) OR (Crenosomatidae) OR (Otostrongylus) OR
132 (Skrjabingylus)) AND ((Marine) OR (Cetacean))".

133 The search on PubMed yielded 120 results and the search on Google Scholar yielded 2110
134 results, excluding citations. As Google Scholar can only display 1000 results per search, only the
135 1000 articles deemed most relevant by the software were manually reviewed for inclusion in the
136 study, in addition to the 120 articles found via PubMed. To ensure all recently published literature
137 was consulted, a secondary search on google scholar was conducted with the same search terms,
138 filtering to only include articles published from 2017 and onward. This secondary search yielded
139 380 results, excluding citations, which were also manually reviewed for inclusion in the study. All
140 conference archives (e.g. IAAAM), theses not published in peer-reviewed journals, and posters
141 were excluded from this study. The full texts for the articles isolated through literature search
142 results were obtained and manually reviewed by the two authors, being included in the study if
143 they met the following inclusion criteria: i) The host species was any wild marine mammal, with
144 captive wild animals only included if the transmission of parasites was stated to have occurred
145 naturally, prior to their capture. ii) The parasite species belonged to a genus within the
146 metastrongyle superfamily, including studies that described the presence of parasitic eggs and
147 larvae provided they could be positively identified to at least the genus level (studies that described

148 parasites as “lungworms” or “nematodes” without specificity regarding genera were excluded). iii)
149 The article serves as the primary source describing a relationship between a marine mammal host
150 and metastrongyle parasite. Duplicate articles, existing in both the Google Scholar and PubMed
151 searches were manually removed. All non-primary sources which were found through the initial
152 search terms were screened, and citations were followed, leading to the inclusion of 15 additional
153 articles which met the inclusion criteria. Later, the World Register of Marine Species (WoRMS,
154 *https://www.marinespecies.org*), The Society for Marine Mammalogy
155 (*https://marinemammalscience.org*), and the Natural History Museum Host-Parasite database
156 (*https://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-*
157 *parasites/)* were consulted to ensure all known unique relationships were reported in this study
158 (WoRMS Editorial Board, 2022). A total of 35 articles could not be acquired in their full text form
159 for inclusion in data analysis, but the relationships they report are known through prior citations
160 in peer-reviewed journals or available abstracts. The articles which met the inclusion criteria were
161 further evaluated by the two authors, with significant attributes documented on a master
162 spreadsheet. Many included articles, including the articles not available in full-text form, report
163 multiple different host-parasite relationships, thus independent rows were created on the master
164 spreadsheet for each described host-parasite relationship (n=481), allowing for relationship-
165 specific attributes to be evaluated. The accepted common names and scientific names provided for
166 host species in this study are taken from the Society for Marine Mammalogy Committee on
167 Taxonomy (WoRMS Editorial Board, 2022).

168 A total of 207 full text publications met the inclusion criteria for this study, with 114
169 appearing only on Google Scholar, 6 appearing only on PubMed, 72 appearing on both Google
170 Scholar and PubMed, and 15 coming from other sources. Data was collected on all included full-

171 text publications, including whether they assessed pathogenic effect. An article was deemed to
172 assess pathogenic effect if it described some biological impact associated with a presence of
173 metastrongyle parasites in the host, or if it explicitly stated no pathogenic effect was associated
174 with the parasitism. Further data was collected on whether full-text publications which met the
175 inclusion criteria mentioned strandings or mortality. For the collection of this data, an article was
176 deemed to mention strandings if it contained the following terms (not including in the citations):
177 "stranded" or "stranding" or "strandings". For an article to have been deemed to mention mortality,
178 it must have contained the following terms (not including in the citations): "mortality" or
179 "mortalities". The inclusion terms for determining which articles mention stranding or mortality
180 were isolated through word searching in adobe acrobat, with technologically non-conforming
181 articles screened manually. Later, the studies mentioning mortality or stranding were assessed to
182 ensure they discussed these effects in the context of the study's findings. The parasite collection
183 methodology was also noted for each included full-text publication. Within the articles which met
184 the inclusion criteria, the geographical location(s) were recorded for 437 documented relationships
185 and the anatomical location(s) of the parasites were recorded in 371 documented relationships. We
186 further calculated the geographical dispersion of the 102 unique relationships between marine
187 mammals and metastrongyles.

188 For each documented relationship, data was also recorded on any reported pathogenic
189 effects (n=201). Pathogenic effects can be described as some biological impact on the host
190 associated with the presence of metastrongyle parasites. In cases where it was explicitly stated that
191 no pathogenic effect was associated with parasitism, this was recorded as well. Of the 101 articles
192 that assessed pathogenic effect, there were a total of 201 relationships in which attributes
193 describing a pathogenic effect or lack thereof were documented.

Between the 207 full-text publications which met our inclusion criteria, and the additional 35 publications we could not retrieve in full-text form, a total of 481 host-parasite relationships are documented. For each of these relationships, data was collected on their respective species taxonomy. Next, the frequency at which each metastrongyle parasite species appears in the literature, in the context of relationships with marine mammal hosts was recorded. For the purposes of frequency calculations, parasites described only to the genus level were excluded. The frequency at which marine mammal hosts appear in the literature, in the context of relationships with metastrongyle parasites was recorded in the same manner. For frequency calculations, hosts described only to the genus level were excluded. For the purposes of all diversity calculations, only relationships where both the host and parasite were described to the species level were considered. Finally, host diversity was calculated as a measure of the diversity of host species a metastrongyle species can infect, and parasite diversity was calculated as the diversity of metastrongyle species a marine mammal species can host.

To provide a metric by which the size of a host could be used as a predictor of pathogenic effects, host body mass was calculated by dividing the median weight in kilograms by the median length in centimetres for each host species. Median host measurements were compiled as the median of both genders from a variety of sources based on availability in the following order of priority: 1) World Register of Marine Species (WoRMS, *https://www.marinespecies.org*); 2) Society for Marine Mammalogy (*https://marinemammalscience.org/science-and-publications/species-information/facts/*); 3) National Oceanic and Atmospheric Administration (NOAA, *https://www.fisheries.noaa.gov/species-directory*); 4) Animal Diversity Web (ADW, *https://animaldiversity.org*). In cases where data on host size was not available through those four

216 sources, the median measurements of hosts documented during gross necropsy in articles which
217 met the inclusion criteria of this study were used.

218 Finally, we produced an up-to-date checklist of all known relationships concerning
219 metastrongyles in marine mammals, which is included in table 1, complete with information on
220 anatomical ranges documented for each relationship. The relationships documented are found
221 within the 207 articles included in this study or within the 35 articles that could not be acquired in
222 their full text form for inclusion in data analysis, provided the relationships they report are known
223 through prior citations in peer-reviewed journals.

224 Table 1: Checklist of all known relationships concerning metastrongyles in marine mammals,
225 complete with information on anatomical ranges documented for each relationship.

Host Family	**Host Species**	**Common Name**	**Parasite Family**	**Parasite species**	**Anatomical Location**	**Reference**
Balaenopteridae	Megaptera novaeangliae	*Humpback Whale*	Pseudaliidae	*Pharurus alatus*	N/A	(Raga and Balbuena, 1987)
Delphinidae	Cephalorhynchus commersonii	*Commerson's Dolphin*	Pseudaliidae	*Halocercus brasiliensis*	Lower respiratory	(Greenwood and Taylor, 1979)
				Halocercus sp.	Lower respiratory	(Goodall *et al.*, 1988; Dougnac and Fredes, 2012)
				Stenurus sp.	Lower respiratory	(Duignan, 2000)
	Cephalorhynchus hectori	*Hector's dolphin*	Pseudaliidae	*Halocercus sp.*	Lower respiratory	(McKenzie and Blair, 1983; Duignan, 2000)
	Delphinus delphis	*Short-beaked common dolphin*	Pseudaliidae	*Halocercus cryptocephalus*	N/A	(Delyamure, 1968)
				Halocercus delphini	Lower respiratory	(Abollo *et al.*, 1998; Gibson *et al.*, 1998; Davison *et al.*, 2013; Pool *et al.*, 2020b, 2021)
				Halocercus invaginatus	N/A	(Raga and Balbuena, 1987)
				Halocercus kleinenbergi	N/A	(Harris, 1982)
				Halocercus lagenorhynchi	Lower respiratory	(Tomo *et al.*, 2010)
				Halocercus sp.	Lower respiratory	(Zafra *et al.*, 2015b; Lehnert *et al.*, 2017)

				Stenurus minor	N/A	(Raga, 1994)
				Stenurus ovatus	Lower respiratory	(Pool *et al.*, 2021)
				Stenurus sp.	Lower respiratory	(DÍaz-Delgado *et al.*, 2012)
	Delphinus sp.	*Common dolphin*	Filaroididae	*Parafilaroides sp.*	Lower respiratory	(Stockin *et al.*, 2009)
	Feresa attenuata	*Pygmy killer whale*	Pseudaliidae	*Halocercus brasiliensis*	Lower respiratory	(Guimarães *et al.*, 2015)
				Halocercus sp.	Lower respiratory	(Mignucci-Giannoni *et al.*, 1998b)
				Stenurus globicephalae	Gastrointestinal, Lower respiratory, Otic apparatus	(Forrester *et al.*, 1980; Mignucci-Giannoni *et al.*, 1998b)
	Globicephala macrorhynchus	*Short-finned pilot whale*	Pseudaliidae	*Halocercus kleinenbergi*	Lower respiratory	(Carvalho *et al.*, 2010)
				Stenurus globicephalae	Gastrointestinal, Otic apparatus	(Arnold and Gaskin, 1975; Mignucci-Giannoni *et al.*, 1998b; Carvalho *et al.*, 2010)
				Stenurus minor	N/A	(Morales Vela and Olvera Gómez, 1993)
				Stenurus sp.	Otic apparatus	(Huertas and Lagueux, 2016)
				Torynurus convolutus	N/A	(Dougherty, 1943)
	Globicephala melas	*Long-finned pilot whale*	Pseudaliidae	*Stenurus globicephalae*	Lower respiratory, Otic apparatus	(Cowan, 1967; Arnold and Gaskin, 1975; McManus *et al.*, 1984; Abollo *et al.*, 1998; Gibson *et al.*, 1998; Lehnert *et al.*, 2017; Pool *et al.*, 2021)
				Torynurus convolutus	Lower respiratory	(Baylis and Daubney, 1925; Baylis, 1932)
	Grampus griseus	*Risso's dolphin*	Pseudaliidae	*Halocercus delphini*	Lower respiratory	(Pool *et al.*, 2021)
				Stenurus globicephalae	Gastrointestinal, Lower respiratory, Otic apparatus	(Arnold and Gaskin, 1975; Fernández *et al.*, 2003; Lehnert *et al.*, 2017; Pool *et al.*, 2021)
				Stenurus minor	N/A	(Tomilin, 1967)
	Lagenodelphis hosei	*Fraser's dolphin*	Pseudaliidae	*Stenurus ovatus*	Lower respiratory	(McColl and Obendorf, 1982)
	Lagenorhynchus acutus	*White sided dolphin*	Pseudaliidae	*Halocercus lagenorhynchi*	N/A	(Raga and Balbuena, 1987)
				Pseudalius inflexus	N/A	(Evans, 1991)
				Stenurus globicephalae	Gastrointestinal, Otic apparatus	(Arnold and Gaskin, 1975; Beverley-Burton, 1978; Rogan *et al.*, 1997; Schick *et al.*, 2020)
				Torynurus convolutus	N/A	(Gibson and Harris, 1979)

	Lagenorhynchus albirostris	*White-beaked dolphin*	Pseudaliidae	*Halocercus lagenorhynchi*	Lower respiratory	(Baylis and Daubney, 1925; Gibson and Harris, 1979)
	Lagenorhynchus obscurus	*Dusky dolphin*	Pseudaliidae	*Halocercus sp.*	Gastrointestinal	(von Waerebeek *et al.*, 1993)
				Stenurus sp.	Gastrointestinal	(de Castro *et al.*, 2014)
	Lissodelphis borealis	*Northern right whale dolphin*	Pseudaliidae	*Halocercus sp.*	N/A	(Moser and Rhinehart, 1993)
	Orcinus orca	*Killer whale (Orca)*	Pseudaliidae	*Halocercus sp.*	Lower respiratory	(Reckendorf *et al.*, 2018)
	Peponocephala electra	*Melon-headed whale*	Pseudaliidae	*Halocercus sp.*	N/A	(Dailey and Brownell, 1972)
				Stenurus globicephalae	Otic apparatus	(Cannon, 1977; Mignucci-Giannoni *et al.*, 1998a; b; Carvalho *et al.*, 2010)
	Pseudorca crassidens	*False killer whale*	Pseudaliidae	*Stenurus auditivus*	N/A	(Zam *et al.*, 1971)
				Stenurus globicephalae	Otic apparatus	(Zylber *et al.*, 2002)
	Sotalia fluviatilis	*Tucuxi*	Pseudaliidae	*Halocercus brasiliensis*	Lower respiratory	(Santos *et al.*, 1996; Di Beneditto and Ramos, 2004; Melo *et al.*, 2006; Rodrigues *et al.*, 2018)
	Sotalia guianensis	*Guiana dolphin*	Pseudaliidae	*Halocercus brasiliensis*	Gastrointestinal, Lower respiratory	(Marigo *et al.*, 2010; Carvalho *et al.*, 2010; Guimarães *et al.*, 2013, 2015; Domiciano *et al.*, 2016; Groch *et al.*, 2018, 2020b; Carvalho Demarque *et al.*, 2020)
				Halocercus sp.	Lower respiratory	(Carvalho *et al.*, 2010)
	Sousa chinensis	*Indo-Pacific humpback dolphin*	Pseudaliidae	*Halocercus pingi*	Lower respiratory	(Parsons and Jefferson, 2000; Parsons *et al.*, 2001)
	Sousa plumbea	*Indian Ocean humpback dolphin*	Pseudaliidae	*Halocercus sp.*	Lower respiratory	(Lane *et al.*, 2014)
	Stenella attenuata	*Pantropical spotted dolphin*	Pseudaliidae	*Halocercus delphini*	Lower respiratory	(Dailey and Perrin, 1973)
				Halocercus sp.	Lower respiratory	(Oliveira *et al.*, 2011)
	Stenella clymene	*Clymene dolphin*	Pseudaliidae	*Halocercus brasiliensis*	Lower respiratory	(Carvalho *et al.*, 2010; Guimarães *et al.*, 2015)
				Halocercus delphini	Lower respiratory, Upper respiratory	(Aguilar-Aguilar *et al.*, 2010; Hernández-Orts *et al.*, 2021)
				Halocercus sp.	Lower respiratory	(Carvalho *et al.*, 2010)
	Stenella coeruleoalba	*Striped dolphin*	Pseudaliidae	*Halocercus brasiliensis*	Lower respiratory	(Rosas *et al.*, 2002)
				Halocercus delphini	Lower respiratory	(Lehnert *et al.*, 2017; Pool *et al.*, 2020a; b, 2021; Terracciano *et al.*, 2020)

				Halocercus lagenorhynchi	Lower respiratory	(Ross and Bass, 1971; Gibson *et al.*, 1998; Oliveira *et al.*, 2011; Terracciano *et al.*, 2020)
				Halocercus sp.	Lower respiratory	(Abollo *et al.*, 1998; Carvalho *et al.*, 2010; Zafra *et al.*, 2015b; Lehnert *et al.*, 2017; Vargas-Castro *et al.*, 2020; García de los Ríos y Loshuertos *et al.*, 2021)
				Pharurus sp.	N/A	(García de los Ríos y Loshuertos *et al.*, 2021)
				Pseudalius sp.	N/A	(García de los Ríos y Loshuertos *et al.*, 2021)
				Stenurus minor	Gastrointestinal	(Aytemiz *et al.*, 2012)
				Stenurus ovatus	Lower respiratory	(Pool *et al.*, 2020a, 2021)
				Stenurus sp.	N/A	(García de los Ríos y Loshuertos *et al.*, 2021)
	Stenella frontalis	*Spotted dolphin*	Pseudaliidae	*Halocercus delphini*	N/A	(Perrin *et al.*, 1994)
				Halocercus lagenorhynchi	N/A	(Perrin *et al.*, 1987)
				Halocercus sp.	Lower respiratory	(Zafra *et al.*, 2015b)
				Pseudalius sp.	Lower respiratory	(Zafra *et al.*, 2015b)
	Stenella longirostris	*Spinner dolphin*	Pseudaliidae	*Halocercus brasiliensis*	Lower respiratory	(Carvalho *et al.*, 2010; Domiciano *et al.*, 2016)
				Halocercus delphini	Lower respiratory	(Dailey and Perrin, 1973)
				Halocercus sp.	Lower respiratory	(Carvalho *et al.*, 2010; Oliveira *et al.*, 2011)
	Steno bredanensis	*Rough-toothed dolphin*	Pseudaliidae	*Stenurus sp.*	Otic apparatus	(Ewing *et al.*, 2020)
	Tursiops aduncus	*Indo-Pacific bottlenose dolphin*	Pseudaliidae	*Halocercus lagenorhynchi*	Lower respiratory	(Tomo *et al.*, 2010)
				Halocercus sp.	Lower respiratory	(Stephens *et al.*, 2014; Lane *et al.*, 2014)
				Stenurus ovatus	Lower respiratory	(Tomo *et al.*, 2010)
	Tursiops truncatus	*Common bottlenose dolphin*	Pseudaliidae	*Halocercus cryptocephalus*	Lower respiratory	(Bowie, 1984; Fauquier *et al.*, 2009)
				Halocercus delphini	Lower respiratory	(Abollo *et al.*, 1998; Terracciano *et al.*, 2020; Pool *et al.*, 2021)
				Halocercus invaginatus	N/A	(Birkun and Krivokhizhin, 1996)

				Halocercus lagenorhynchi	Lower respiratory	(Woodard *et al.*, 1969; Dailey *et al.*, 1991b; Lipscomb *et al.*, 1996; Mazzariol *et al.*, 2007; McFee and Lipscomb, 2009; Fauquier *et al.*, 2009)
				Halocercus sp.	Lower respiratory	(Sierra *et al.*, 2014; Seguel *et al.*, 2020b)
				Pharurus alatus	Lower respiratory	(Tomo *et al.*, 2010)
				Stenurus minor	Lower respiratory	(Birincioğlu *et al.*, 2017)
				Stenurus ovatus	Lower respiratory	(Bowie, 1984; Kumazawa *et al.*, 2006; Kuwamura *et al.*, 2007; Tomo *et al.*, 2010; Terracciano *et al.*, 2020; Pool *et al.*, 2021)
				Stenurus sp.	Lower respiratory	(Sierra *et al.*, 2014)
Iniidae	Inia geoffrensis	*Amazon river dolphin*	Pseudaliidae	*Halocercus brasiliensis*	Lower respiratory	(Rodrigues *et al.*, 2018)
				Halocercus sp.	N/A	(Dailey and Brownell, 1972)
Kogiidae	Kogia breviceps	*Pygmy sperm whale*	Pseudaliidae	*Halocercus sp.*	Lower respiratory	(Carvalho *et al.*, 2010)
Monodontidae	Delphinapterus leucas	*Beluga whale*	Pseudaliidae	*Halocercus monoceris*	Cardiovascular, Lower respiratory, Upper respiratory	(Measures *et al.*, 1995)
				Halocercus taurica	Cardiovascular, Lower respiratory, Upper respiratory	(Measures *et al.*, 1995)
				Pharurus pallasii	Central Nervous System, Lower respiratory, Otic apparatus	(Babero and Thomas, 1960; Arnold and Gaskin, 1975; Kenyon and Kenyon, 1977; Wazura *et al.*, 1986; Measures *et al.*, 1995; Houde *et al.*, 2003)
				Stenurus arctomarinus	Cardiovascular, Lower respiratory, Upper respiratory	(Arnold and Gaskin, 1975; Measures *et al.*, 1995; Burek-Huntington *et al.*, 2015)
				Stenurus minor	N/A	(Kühn, 1829)
	Monodon monoceros	*Narwhal*	Pseudaliidae	*Halocercus monoceris*	Lower respiratory	(Webster *et al.*, 1973; MacNeill *et al.*, 1975)
				Pharurus alatus	N/A	(Arnold and Gaskin, 1975)
Otariidae	Arctocephalus australis	*South american fur seal*	Filaroididae	*Parafilaroides sp.*	Lower respiratory	(Jacobus *et al.*, 2016)
				Parafilaroides normani	Lower respiratory	(Echenique *et al.*, 2020)
	Arctocephalus forsteri	*New zealand fur seal*	Filaroididae	*Parafilaroides normani*	Lower respiratory	(Dailey, 2009)
	Arctocephalus gazella	*Antarctic fur seal*	Filaroididae	*Parafilaroides normani*	Lower respiratory	(Jacobus *et al.*, 2016)

	Arctocephalus philippii	*Guadalupe Fur seal*	Filaroididae	*Parafilaroides decorus*	Cardiovascular, Lower respiratory	(Seguel *et al.*, 2018a; Williams *et al.*, 2020)
	Arctocephalus pusillus	*Australian fur seal*	Filaroididae	*Parafilaroides normani*	Lower respiratory	(Dailey, 2009; Jabbar *et al.*, 2014)
	Arctocephalus tropicalis	*Sub-antarctic fur seal*	Filaroididae	*Parafilaroides sp.*	Lower respiratory	(Reisfeld *et al.*, 2019)
				Parafilaroides normani	Lower respiratory	(Dailey, 2009)
	Callorhinus ursinus	*Northern fur seal*	Filaroididae	*Parafilaroides decorus*	N/A	(Gerber *et al.*, 1993)
	Eumetopias jubatus	*Stellar sea lion*	Filaroididae	*Parafilaroides decorus*	Lower respiratory	(Stroud, 1978; Stroud and Roffe, 1979)
				Parafilaroides nanus	N/A	(Dougherty and Herman, 1947)
				Parafilaroides prolificus	N/A	(Dougherty and Herman, 1947)
	Neophoca cinerea	*Australian sea lion*	Filaroididae	*Parafilaroides sp.*	Lower respiratory	(Nicholson and Fanning, 1981)
	Otaria flavescens	*South American sea lion*	Crenosomatidae	*Otostrongylus circumlitus*	N/A	(Ebmer *et al.*, 2020)
				Otostrongylus sp.	N/A	(Hermosilla *et al.*, 2016)
			Filaroididae	*Parafilaroides sp.*	N/A	(Hermosilla *et al.*, 2016)
	Phocarctos hookeri	*New zealand sea lion*	Filaroididae	*Parafilaroides decorus*	N/A	(Duignan, 2000)
	Zalophus californianus	*Californian sea lion*	Crenosomatidae	*Otostrongylus circumlitus*	Cardiovascular, Lower respiratory	(Kelly *et al.*, 2005; Goldstein *et al.*, 2011)
			Filaroididae	*Parafilaroides sp.*	Lower respiratory	(Gulland *et al.*, 2012)
				Parafilaroides decorus	Lower respiratory	(Johnston and Ridgway, 1969; Dailey, 1970b; Fleischman and Squire, 1970; Migaki *et al.*, 1971; Sweeney and Gilmartin, 1974; Stroud, 1978; Gerber *et al.*, 1993; Haulena and Gulland, 2001; Fauquier *et al.*, 2004; Greig *et al.*, 2005; Dennison *et al.*, 2007; Evans, 2011; Kuzmina *et al.*, 2018; Williams *et al.*, 2020; Liu *et al.*, 2021)
	Zalophus wollebaeki	*Galapagos sea lion*	Crenosomatidae	*Otostrongylus sp.*	N/A	(Walden *et al.*, 2018)
			Filaroididae	*Parafilaroides sp.*	N/A	(Walden *et al.*, 2018)
Phocidae	Cystophora cristata	*Hooded seal*	Crenosomatidae	*Otostrongylus circumlitus*	Lower respiratory	(Lucas *et al.*, 2003)
			Filaroididae	*Parafilaroides gymnurus*	Lower respiratory	(Lucas *et al.*, 2003)

	Erignathus barbatus	*Bearded seal*	Crenosomatidae	*Otostrongylus circumlitus*	N/A	(Antonelis *et al.*, 1994)
			Filaroididae	*Parafilaroides sp.*	Cardiovascular, Lower respiratory	(Walden *et al.*, 2020)
				Parafilaroides gymnurus	Lower respiratory	(Gosselin *et al.*, 1998; Walden *et al.*, 2020)
	Halichoerus grypus	*Grey seal*	Crenosomatidae	*Otostrongylus circumlitus*	Cardiovascular, Lower respiratory	(Gosselin *et al.*, 1998; Ulrich *et al.*, 2015; Barnett *et al.*, 2019a, 2021)
				Otostrongylus sp.	Lower respiratory	(Baker, 1987)
			Filaroididae	*Parafilaroides sp.*	Lower respiratory	(Baker, 1987; Barnett *et al.*, 2019a, 2021)
				Parafilaroides gymnurus	Lower respiratory	(Gosselin and Measures, 1997; Gosselin *et al.*, 1998; Ulrich *et al.*, 2015)
				Parafilaroides hispidus	Lower respiratory	(Gosselin and Measures, 1997; Gosselin *et al.*, 1998)
	Histriophoca fasciata	*Ribbon seal*	Crenosomatidae	*Otostrongylus circumlitus*	N/A	(Walden *et al.*, 2020)
				Otostrongylus sp.	N/A	(Walden *et al.*, 2020)
			Filaroididae	*Parafilaroides gymnurus*	Lower respiratory	(Walden *et al.*, 2020)
	Hydrurga leptonyx	*Leopard seal*	Filaroididae	*Parafilaroides hydrurgae*	Lower respiratory	(Mawson, 1953)
	Mirounga angustirostris	*Northern elephant seal*	Crenosomatidae	*Otostrongylus circumlitus*	Cardiovascular, Gastrointestinal, Lower respiratory	(Stroud, 1978; Stroud and Roffe, 1979; Gulland *et al.*, 1997a; Elson-Riggins *et al.*, 2001; Fauquier *et al.*, 2003; Elson-Riggins *et al.*, 2004; Colegrove *et al.*, 2005; Kaye *et al.*, 2016; Sheldon *et al.*, 2017; Kaye *et al.*, 2017; Sheldon *et al.*, 2019)
				Otostrongylus sp.	N/A	(Gerber *et al.*, 1993)
			Filaroididae	*Parafilaroides sp.*	Lower respiratory	(Stroud, 1978; Stroud and Roffe, 1979)
				Parafilaroides decorus	N/A	(Gerber *et al.*, 1993)
				Parafilaroides measuresae	Lower respiratory	(Dailey, 2006b)
	Pagophilus groenlandicus	*Harp seal*	Crenosomatidae	*Otostrongylus circumlitus*	Lower respiratory, Upper respiratory	(Lucas *et al.*, 2003; Piché *et al.*, 2010)
			Filaroididae	*Parafilaroides gymnurus*	Lower respiratory	(Gosselin and Measures, 1997; Gosselin *et al.*, 1998; Lucas *et al.*, 2003)
	Phoca largha	*Spotted seal*	Crenosomatidae	*Otostrongylus circumlitus*	N/A	(Delyamure *et al.*, 1984; Walden *et al.*, 2020)
			Filaroididae	*Parafilaroides gymnurus*	Lower respiratory	(Delyamure *et al.*, 1984; Walden *et al.*, 2020)

	Phoca vitulina	*Harbour seal*	Crenosomatidae	*Otostrongylus circumlitus*	Cardiovascular, Lower respiratory	(Dunn and Wolke, 1976; Kennedy *et al.*, 1989; Claussen *et al.*, 1991; Borgsteede *et al.*, 1991; Gerber *et al.*, 1993; Gosselin *et al.*, 1998; Elson-Riggins *et al.*, 2001, 2004; Fouchier *et al.*, 2001; Vercruysse *et al.*, 2003; Colegrove *et al.*, 2005; McKnight *et al.*, 2005; Lehnert *et al.*, 2007, 2010; Leidenberger and Boström, 2009; Lambourn *et al.*, 2013; Osinga *et al.*, 2015; Ulrich *et al.*, 2015, 2016; Kroese *et al.*, 2018)
				Otostrongylus sp.	N/A	(Herreman *et al.*, 2011)
			Filaroididae	*Parafilaroides sp.*	Lower respiratory	(Garner *et al.*, 1997; Prenger-Berninghoff *et al.*, 2008; Herreman *et al.*, 2011; Lambourn *et al.*, 2013; Rhyan *et al.*, 2018b)
				Parafilaroides decorus	Lower respiratory	(Greig *et al.*, 2014)
				Parafilaroides gullandae	Lower respiratory	(Dailey, 2006b)
				Parafilaroides gymnurus	Lower respiratory, Reproductive	(Schumacher *et al.*, 1990; Claussen *et al.*, 1991; Borgsteede *et al.*, 1991; Gosselin and Measures, 1997; Gosselin *et al.*, 1998; Fouchier *et al.*, 2001; Vercruysse *et al.*, 2003; Lehnert *et al.*, 2007, 2010; Osinga *et al.*, 2015; Ulrich *et al.*, 2015; Elson-Riggins *et al.*, 2020)
	Pusa caspica	*Caspian seal*	Filaroididae	*Parafilaroides caspicus*	N/A	(Kurochkin and Zablotsky, 1958)
	Pusa hispida	*Ringed seal*	Crenosomatidae	*Otostrongylus circumlitus*	Lower respiratory	(Onderka, 1989; Measures and Gosselin, 1994; Bergeron *et al.*, 1997a; b; Walden *et al.*, 2020)
			Filaroididae	*Parafilaroides sp.*	Lower respiratory	(Walden *et al.*, 2020)
				Parafilaroides gymnurus	Gastrointestinal, Lower respiratory	(Measures and Gosselin, 1994; Gosselin and Measures, 1997; Gosselin *et al.*, 1998; Walden *et al.*, 2020)
				Parafilaroides hispidus	Lower respiratory	(Kennedy, 1986; Onderka, 1989; Gosselin and Measures, 1997; Gosselin *et al.*, 1998)
	Pusa sibirica	*Baikal seal*	Crenosomatidae	*Otostrongylus circumlitus*	Lower respiratory	(Suvorova and Prokushina, 2021)
			Filaroididae	*Parafilaroides gymnurus*	Lower respiratory	(Kontrimavichus and Delyamure, 1979; Suvorova and Prokushina, 2021)
Phocoenidae	Neophocaena asiaeorientalis	*Narrow-ridged finless porpoise*	Pseudaliidae	*Halocercus pingi*	Lower respiratory, Reproductive	(Shiozaki and Amano, 2017)
				Halocercus sp.	Lower respiratory	(Wan *et al.*, 2017; Gui *et al.*, 2018)

				Halocercus sunameri	Lower respiratory	(Shiozaki and Amano, 2017)
				Halocercus taurica	Lower respiratory	(Shiozaki and Amano, 2017)
				Pharurus asiaeorientalis	Lower respiratory, Otic apparatus	(Shiozaki and Amano, 2017)
				Pharurus sunameri	Lower respiratory, Otic apparatus	(Shiozaki and Amano, 2017)
				Stenurus nanjingensis	Otic apparatus	(Shiozaki and Amano, 2017)
	Neophocaena phocaenoides	*Indo-Pacific finless porpoise*	Crenosomatidae	*Otostrongylus circumlitus*	N/A	(Yu *et al.*, 2009)
			Pseudaliidae	*Halocercus pingi*	Lower respiratory	(Wu, 1929; Parsons and Jefferson, 2000; Parsons *et al.*, 2001)
				Halocercus sp.	Lower respiratory	(Gui *et al.*, 2018)
				Halocercus sunameri	N/A	(Yamaguti, 1951)
				Halocercus taurica	N/A	(Kuramochi *et al.*, 2000)
				Pharurus asiaeorientalis	N/A	(Petter and Pilleri, 1982)
				Pharurus sunameri	N/A	(Yamaguti, 1951)
				Stenurus auditivus	N/A	(Hsü and Hoeppli, 1933)
				Stenurus nanjingensis	N/A	(Tao, 1983)
	Phocoena dioptrica	*Spectacled porpoise*	Pseudaliidae	*Stenurus minor*	Otic apparatus	(Lehnert *et al.*, 2017)
	Phocoena phocoena	*Harbour Porpoise*	Pseudaliidae	*Halocercus invaginatus*	Cardiovascular, Lower respiratory, Upper respiratory	(Smith and Threlfall, 1973; Andersen, 1974; Arnold and Gaskin, 1975; Dailey and Stroud, 1978; Stroud and Roffe, 1979; Kastelein and Lavaleije, 1992; Moser and Rhinehart, 1993; Balbuena *et al.*, 1994; Abollo *et al.*, 1998; Gibson *et al.*, 1998; Jepson *et al.*, 2000; Rogan *et al.*, 2001; Lehnert *et al.*, 2005, 2010, 2014; Siebert *et al.*, 2006, 2020; Veryeri, 2012; Pekmezci *et al.*, 2013)
				Halocercus kirbyi	N/A	(Dougherty, 1944)
				Halocercus sp.	Lower respiratory	(Smith and Threlfall, 1973; Wunschimann *et al.*, 2001; Jauniaux *et al.*, 2002; Dagleish *et al.*, 2008; Valderrama Vasquez *et al.*, 2008; Fenton *et al.*, 2017; van Elk *et al.*, 2019)

				Halocercus taurica	Lower respiratory	(Arnold and Gaskin, 1975; Gibson *et al.*, 1998; Jepson *et al.*, 2000; Rogan *et al.*, 2001; Pekmezci *et al.*, 2013)
				Pharurus dalli	Lower respiratory, Otic apparatus	(Smith and Threlfall, 1973; Colón-Llavina *et al.*, 2019)
				Pharurus sp.	N/A	(Smith and Threlfall, 1973)
				Pseudalius inflexus	Cardiovascular, Gastrointestinal, Lower respiratory, Otic apparatus	(Andersen, 1974; Arnold and Gaskin, 1975; Kastelein and Lavaleije, 1992; Balbuena *et al.*, 1994; Brosens *et al.*, 1996; Szefer *et al.*, 1998; Gibson *et al.*, 1998; Wünschmann *et al.*, 1999; Jepson *et al.*, 2000; Siebert *et al.*, 2001, 2006, 2013, 2020; Wunschimann *et al.*, 2001; Rogan *et al.*, 2001; Jauniaux *et al.*, 2002; Lehnert *et al.*, 2005, 2010; Dawson *et al.*, 2008; Dagleish *et al.*, 2008; Valderrama Vasquez *et al.*, 2008; Davison *et al.*, 2010a; b; Seibel *et al.*, 2010; Fenton *et al.*, 2017; van Elk *et al.*, 2019; Gabel *et al.*, 2021)
				Stenurus minor	Gastrointestinal, Lower respiratory, Otic apparatus, Upper Respiratory	(Andersen, 1974; Arnold and Gaskin, 1975; Dailey and Stroud, 1978; Stroud and Roffe, 1979; Faulkner, 1995; Brosens *et al.*, 1996; Faulkner *et al.*, 1998; Gibson *et al.*, 1998; Wünschmann *et al.*, 1999; Jepson *et al.*, 2000; Siebert *et al.*, 2001, 2006, 2013, 2020; Wunschimann *et al.*, 2001; Rogan *et al.*, 2001; Jauniaux *et al.*, 2002; Kijewska *et al.*, 2003; Lehnert *et al.*, 2005, 2010, 2014; Prahl *et al.*, 2008; Valderrama Vasquez *et al.*, 2008; Seibel *et al.*, 2010; Pekmezci *et al.*, 2013; Fenton *et al.*, 2017; Morell *et al.*, 2017; Wohlsein *et al.*, 2019b; van Elk *et al.*, 2019; Colón-Llavina *et al.*, 2019; Gabel *et al.*, 2021)
				Stenurus sp.	Lower respiratory	(Fenton *et al.*, 2017)
				Torynurus convolutus	Cardiovascular, Gastrointestinal, Lower respiratory, Otic apparatus, Upper respiratory	(Arnold and Gaskin, 1975; Dailey and Stroud, 1978; Kastelein and Lavaleije, 1992; Balbuena *et al.*, 1994; Brosens *et al.*, 1996; Faulkner *et al.*, 1998; Gibson *et al.*, 1998; Wünschmann *et al.*, 1999; Jepson *et al.*, 2000; Siebert *et al.*, 2001, 2006, 2013, 2020; Wunschimann *et al.*, 2001; Rogan *et al.*, 2001; Jauniaux *et al.*, 2002; Lehnert *et al.*, 2005, 2010; Valderrama Vasquez *et al.*, 2008; Davison *et al.*, 2010a; Seibel *et al.*, 2010; Fenton *et al.*, 2017; van Elk *et al.*, 2019)
	Phocoena spinipinnis	*Burmeister's porpoise*	Pseudaliidae	*Halocercus sp.*	Lower respiratory	(Reyes and van Waerebeek, 1995)

				Pseudalius inflexus	Lower respiratory	(Corcuera *et al.*, 1995; Reyes and van Waerebeek, 1995; Alvarado-Rybak *et al.*, 2020b)
				Stenurus australis	Lower respiratory, Otic apparatus	(Torres *et al.*, 1994; Alvarado-Rybak *et al.*, 2020b)
				Stenurus minor	Otic apparatus	(Corcuera *et al.*, 1995)
				Stenurus sp.	Otic apparatus	(Reyes and van Waerebeek, 1995)
	Phocoenoides dalli	*Dall's porpoise*	Pseudaliidae	*Halocercus dalli*	Lower respiratory	(Conlogue *et al.*, 1985)
				Halocercus kirbyi	N/A	(Dougherty, 1944)
				Halocercus sp.	Lower respiratory	(Migaki *et al.*, 1971)
				Pharurus dalli	Otic apparatus	(Arnold and Gaskin, 1975; Dailey and Walker, 1978; Kuramochi *et al.*, 1990)
				Pharurus sp.	N/A	(Walker, 1975)
				Stenurus minor	Lower respiratory, Otic apparatus	(Johnston and Ridgway, 1969; Migaki *et al.*, 1971; Dailey and Walker, 1978)
				Stenurus truei	Otic apparatus	(Kuramochi *et al.*, 1990)
				Stenurus yamagutii	Otic apparatus	(Kuramochi *et al.*, 1990)
Physteridae	Physeter macrocephalus	*Sperm whale*	Pseudaliidae	*Stenurus ovatus*	N/A	(Raga and Balbuena, 1987)
Ziphiidae	Berardius bairdii	*Baird's beaked whale*	Pseudaliidae	*Halocercus hyperoodoni*	N/A	(Delyamure, 1968)
	Mesoplodon sp.	*Unidentified whale*	Pseudaliidae	*Halocercus sp.*	Lower respiratory	(Moser and Rhinehart, 1993)
	Mesoplodon stejnegeri	*Stejneger's beaked whale*	Pseudaliidae	*Halocercus sp.*	Lower respiratory	(Savage *et al.*, 2021)

2.2 Data management and analyses

When assessing the relative host and parasite diversities, corrections were made for literature and intra-study biases which arose from non-uniform sampling efforts. We used a modified approach, based previously published methods (Nunn *et al.*, 2003; Ezenwa *et al.*, 2006; Seguel and Gottdenker, 2017), to create a bias penalization index for each host and parasite species. To

232 do this, we searched scientific names of each host and parasite species individually on Google
233 Scholar and the number of hits was recorded. The number of hits for each species was then
234 multiplied by the number of studies that both met our inclusion criteria and contained mentions of
235 a relationship concerning that respective species. The natural logarithm of these products was then
236 taken, and the result constitutes our penalization index for each species study bias (correction-
237 index). The resulting corrected diversity indexes were plotted using frequency plots constructed in
238 the R package "ggplo2".

239 We explored the predictors of pathogenic effects among different host parasite interactions
240 using binomial generalized linear mixed effects models (GLMMs) with the restricted maximum
241 likelihood fitted using the R package "glmmTMB" (Brooks *et al.*, 2017). Although this method
242 can estimate positively biased odds ratios for binary outcomes in metadata, these are usually more
243 problematic for smaller samples sizes and alternative methods for the analysis of binary metadata
244 present similar issues (Stijnen *et al.*, 2010; Bakbergenuly and Kulinskaya, 2018). We used
245 corrected host diversity, corrected parasite diversity, and host body size as predictors for the
246 presence or absence of pathogenic effects. Study ID was added as a random effect to account for
247 studies documenting multiple host-parasite relationships with their respective outcomes. For each
248 documented host-parasite relationship, with both the host and parasite specified to the species level
249 and for which pathogenic effect was assessed (n=165), binomial GLMMs for the presence or
250 absence of pathogenic effect were fit. A second model was fit to exclusively assess the presence
251 or absence of respiratory specific effect (bronchopneumonia or bronchitis). For the respiratory
252 specific effect model, each documented host-parasite relationship was included if the host and
253 parasite were specified to the species level, pathogenic effect was assessed, and the presence of
254 the parasite was documented in either the upper or lower respiratory system (n=134). We attempted

to fit cardiovascular specific effect (DIC, thrombosis, vasculitis, hemorrhage, endocarditis) (n=11) and otic apparatus specific effect (sinusitis, otitis, otic metaplasia) (n=24) models using the same method as for respiratory specific effect but were unable because the small sample size affected model convergence. In both the full and respiratory specific models, we included interaction effects between the corrected host diversity, corrected parasite diversity, and body size predictors terms to account for individual permissiveness of host species to parasite species as well as individual pervasiveness of parasite species to host species.

2.3 Discrepancies in the literature

Hermosilla, C., et al. (2015) reports *Stenurus sp*. in sei whale (*Balaenoptera borealis*), blue whale (*Balaenoptera musculus*), and fin whale (*Balaenoptera physalus*) as non-primary findings, however we could not identify a primary source of these relationships (Hermosilla *et al.*, 2015). Lehnert, K., et al. (2019) reports *Pharurus alatus* as a parasite of short-beaked common dolphin (*Delphinus delphis*) citing Tomo, I., et al. (2010) (Tomo *et al.*, 2010; Lehnert *et al.*, 2019). Upon reviewing Tomo, I., et al. (2010), it does not appear to include this relationship (Tomo *et al.*, 2010). The World Register of Marine Species (WoRMS) documents *Halocercus taurica* in of short-beaked common dolphin (*Delphinus delphis*) and *Halocercus hyperoodoni* in northern bottlenose whale (*Hyperoodon ampullatus*), however primary sources could not be identified for either of these relationships (WoRMS Editorial Board, 2022). Measures, L.N. (2001) documents *Halocercus pingi* in Dall's porpoise (*Phocoenoides dalli*) as a non-primary finding, however we could not find a primary source for this relationship (Measures, 2001). Three (n=3) additional publications document relationships that were not specified to the genus level (Giorda *et al.*, 2017; Reckendorf *et al.*, 2021; van Wijngaarden *et al.*, 2021).

3. Results

At least 40 species of metastrongyles have been described in 66 marine mammal host species. Most metastrongyle species parasitize multiple host species, with a total of 213 unique host-metastrongyle relationships recorded (table 1).

3.1 Characterization of studies

The mean publication year of the 207 articles which met the inclusion criteria was 2003, with the distribution of publication years skewed towards the most recent decade (Figure 1). For each of the articles which met the inclusion criteria, 48.88% (n=101/207) assessed pathogenic effect. Additionally, 78.74% (n=163/207) of studies mentioned stranding and 43.48% (n=90/207) of articles mentioned mortality as potentially related to lungworm infection. Gross necropsy is the predominant parasite collection method for metastrongyles in marine mammals with 92.27% (n=191/207) of the studies using this as the only method of collection. The next most common method of collection was, fecal sampling, in 6.28% (n=13/207) of the studies (Figure 2).

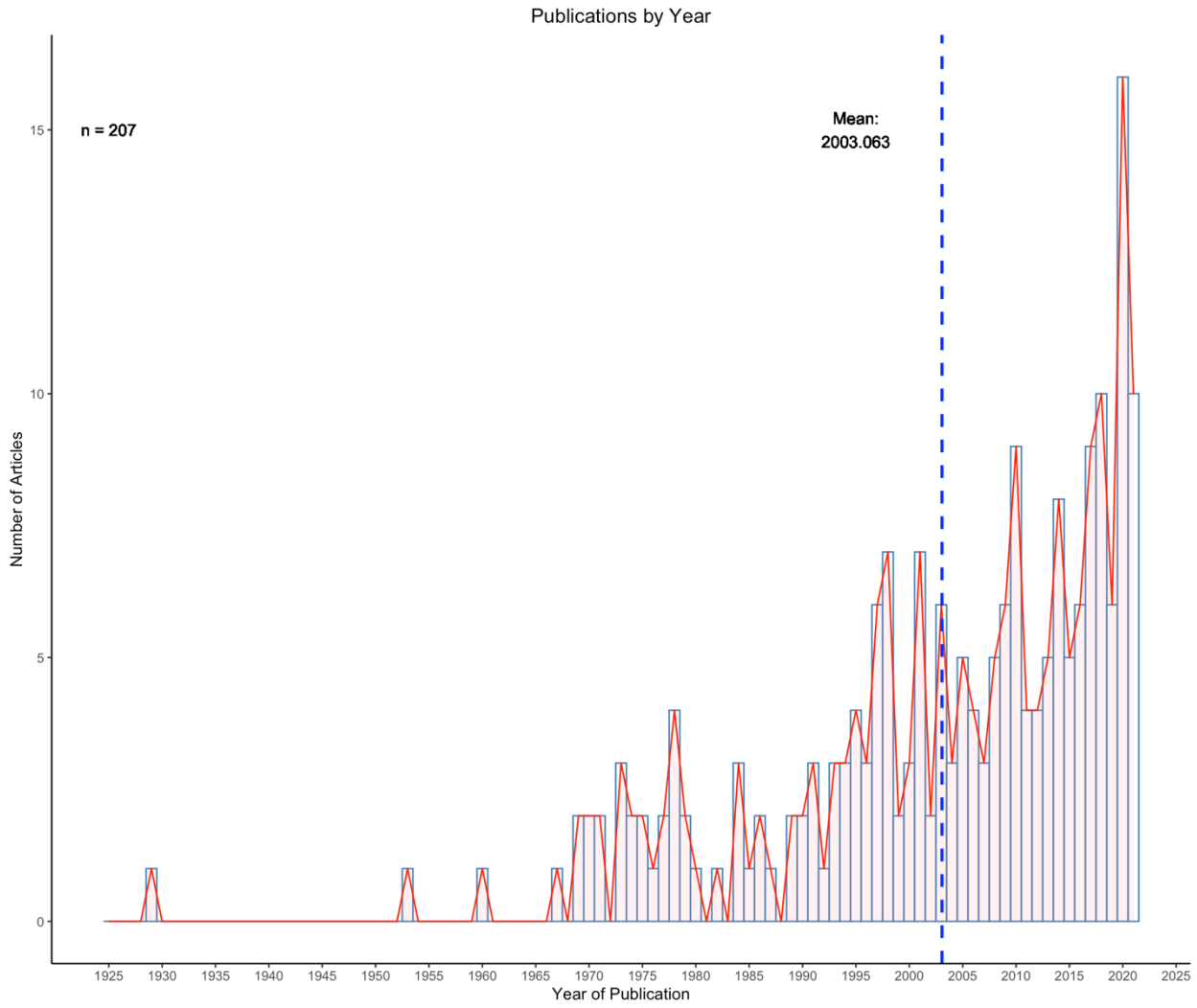


Figure 1: Distribution of publication year for articles which met the inclusion criteria of this study. The mean year of publication was 2003.

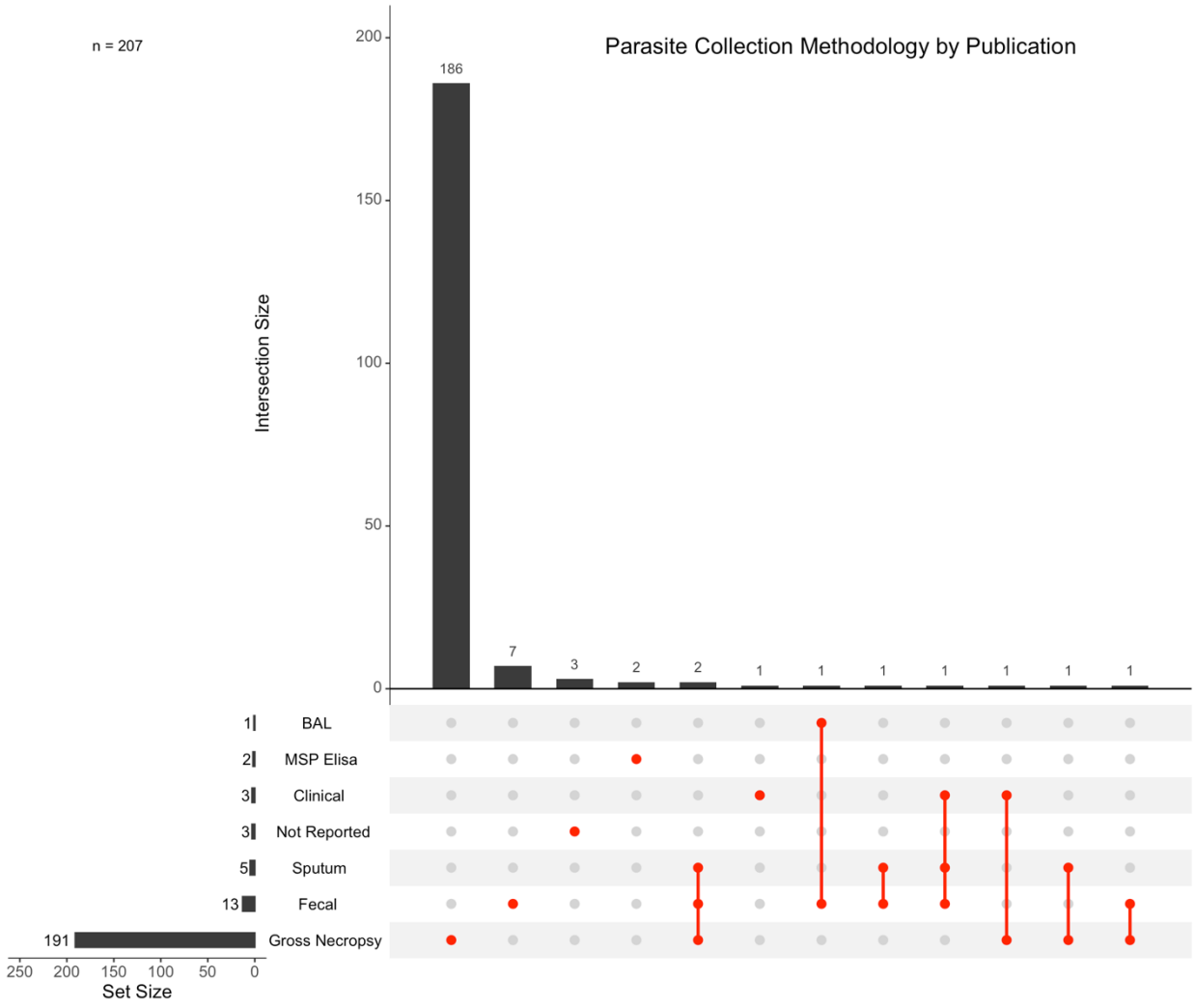


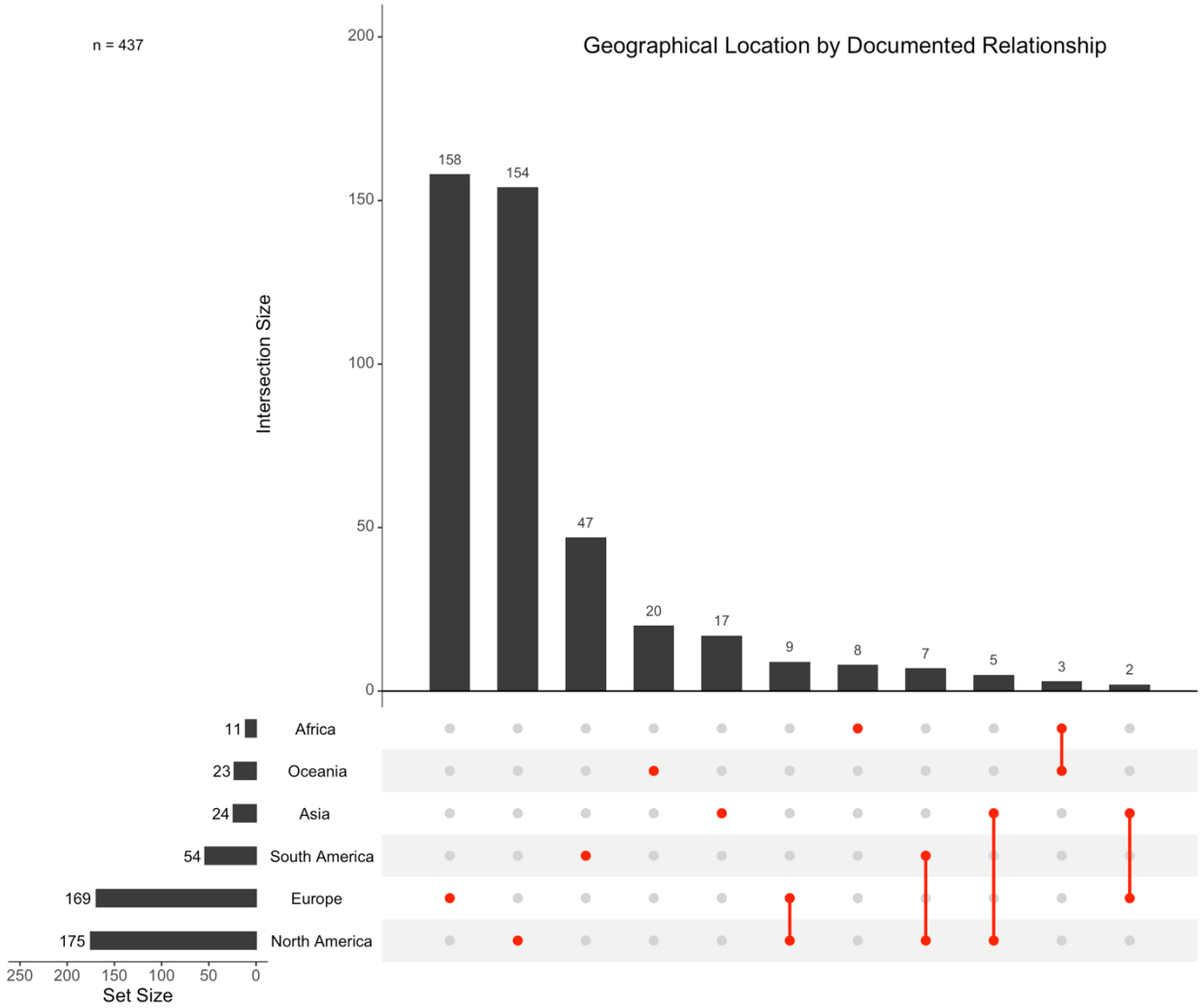
Figure 2: Parasite collection methodologies documented, with intersections between the methodologies shown to represent studies that utilize more than one methodology. Articles that did not report a collection methodology are designated as “Not Reported”.

A total of 175 host-metastrongyle relationships were reported in North America (including the commonly referenced Central America region), and 169 relationships were reported in Europe. North America and Europe are the most common locations reported for metastrongyle infections in marine mammals, followed by 54 relationships in South America, 24 in Asia, 23 in Oceania and 11 in Africa (Figure 3). Exactly half (50.00%, n=51/102) of all unique relationships are reported

306 in North America, with 29.41% (n=30/102) of these relationships being reported exclusively in

307 North America (Figure 4).

308



309

310 Figure 3: Geographical location(s), denoted by continent, of documented relationships between

311 metastrongyles and marine mammals. Documented relationships include duplicates of unique

312 relationships published independently. Intersections are shown for studies which report

313 individual host species to parasite species relationships occurring in multiple locations.

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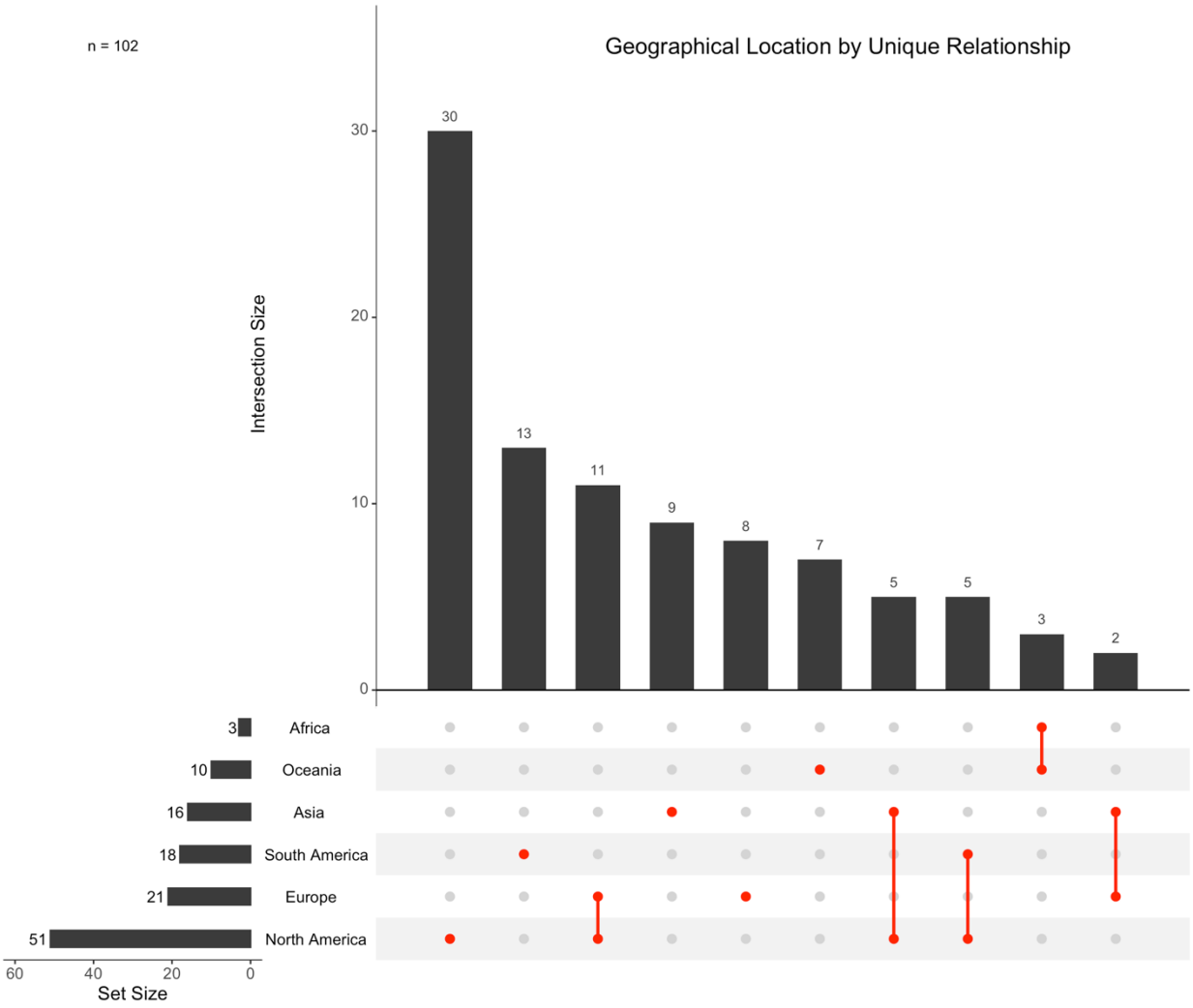


Figure 4: Geographical location(s), denoted by continent, of all unique relationships between metastrongyles and marine mammals. Intersections are shown for studies which report individual host species to parasite species relationships occurring in multiple locations.

3.2 Frequencies and diversities of metastrongyle infections in marine mammals

Pseudaliidae was the most reported metastrongyle family in marine mammals (n=331), followed by Filaroididae (n=90), and Crenosomatidae (n=58). At the host family level, Delphinidae (n=159), Phocoenidae (n=150), and Phocidae (n=107) are most frequently parasitized

by metastrongyles. Further, metastrongyles from the Pseudaliidae family are reported in hosts from the Delphinidae (n=158), Phocoenidae (n=148), Monodontidae (n=15), Ziphiidae (n=3), Iniidae (n=2), Balaenopteridae (n=1), Kogiidae (n=1), and Physeteridae (n=1) families. Metastrongyles from the Crenosomatidae family are reported to parasitize hosts from the Phocidae (n=52), Otariidae (n=5), and Phocoenidae (n=1) families. Metastrongyles from the Filaroididae family are reported to parasitize hosts from the Phocidae (n=54), Otariidae (n=35), and Delphinidae (n=1) families.

Otostrongylus circumlitus (n=52) is the most reported metastrongyle species followed by *Stenurus minor* (n=42) and *Pseudalius inflexus* (n=31) (Supplementary Figure 1). The harbour porpoise (*Phocoena phocoena*) (n=118) is the most reported host, followed by harbour seal (*Phoca vitulina*) (n=41) and bottlenose dolphin (*Tursiops truncat*us) (n=23) (Supplementary Figure 2).

Before penalizing for literature and intra-study biases, the host species harbouring the largest number of metastrongyle species (parasite diversity) were: indo-pacific finless porpoise (*Neophocaena phocaenoides*) (n=8), short-beaked common dolphin (*Delphinus delphis*) (n=7), harbour porpoise (*Phocoena phocoena*) (n=7), and bottlenose dolphin (*Tursiops truncatus*) (n=7) (Supplementary Figure 3). After correction for publication bias, indo-pacific finless porpoise (*Neophocaena phocaenoides*) remained the most permissive host (Figure 5.). Before penalization, the metastrongyle species with the broader host diversity were: *Otostrongylus circumlitus* (n=13), *Stenurus min*or (n=10), *Parafilaroides gymnurus* (n=9), *Halocercus brasiliensis* (n=8), and *Halocercus delphini* (n=8) (Supplementary Figure 4). After correction for publication bias, *Halocercus hyperdooni* emerged as the most generalist lungworm species, followed closely by *Otostrongylus circumlitus* and *Parafilaroides gymnurus* (Figure 6.).

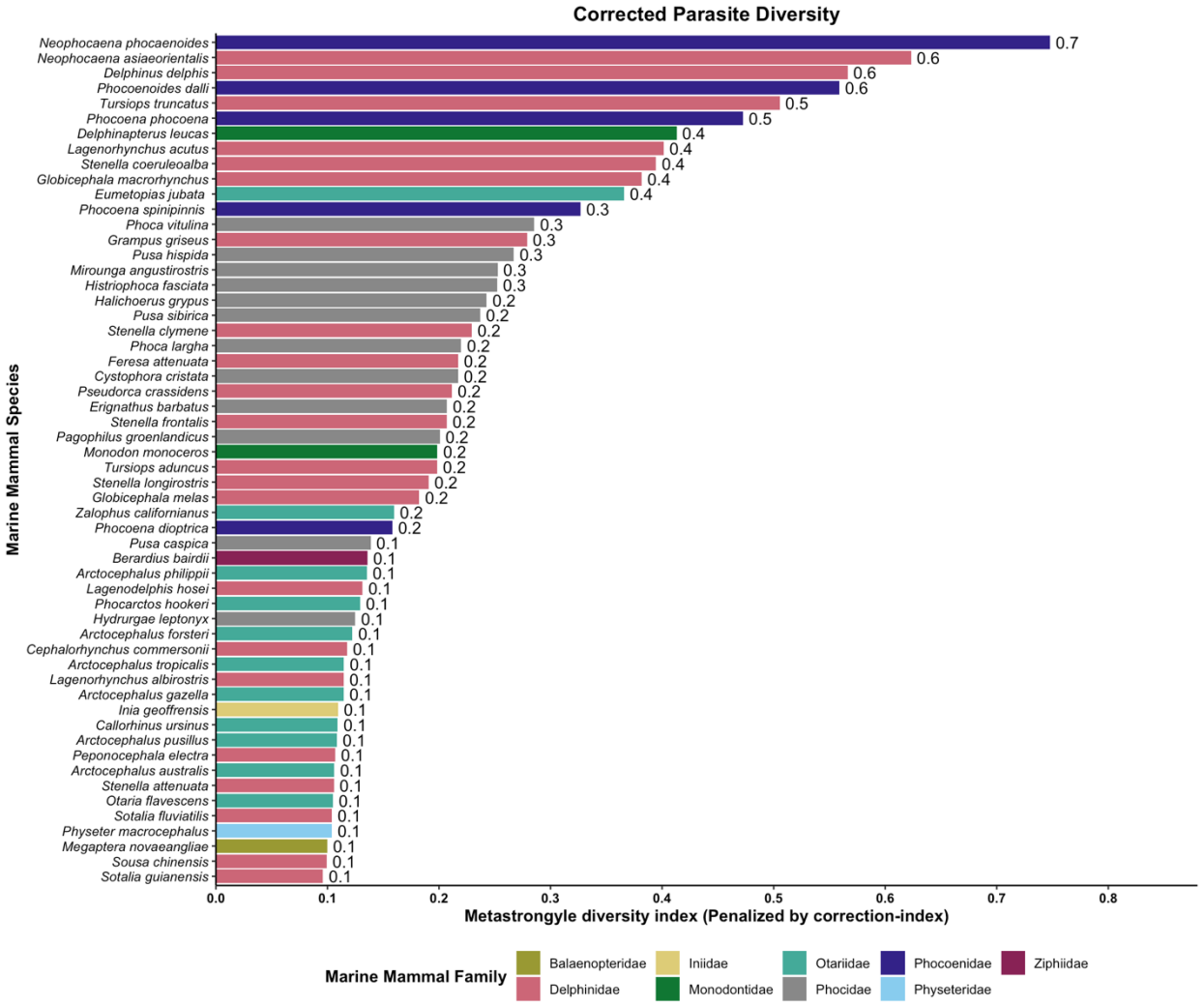


Figure 5: Parasite diversity for metastrongyles in marine mammals, corrected for publication bias (correction-index).

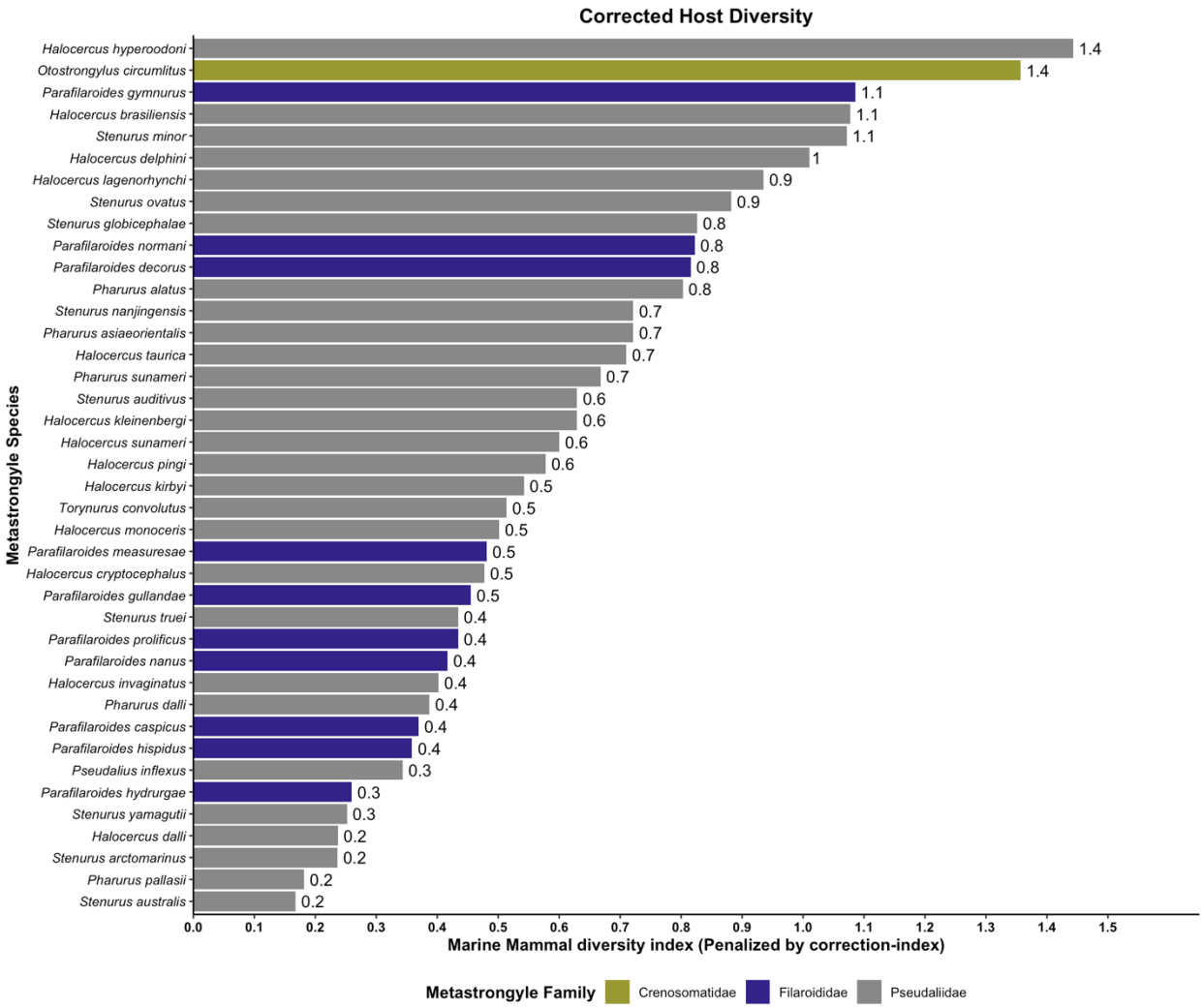
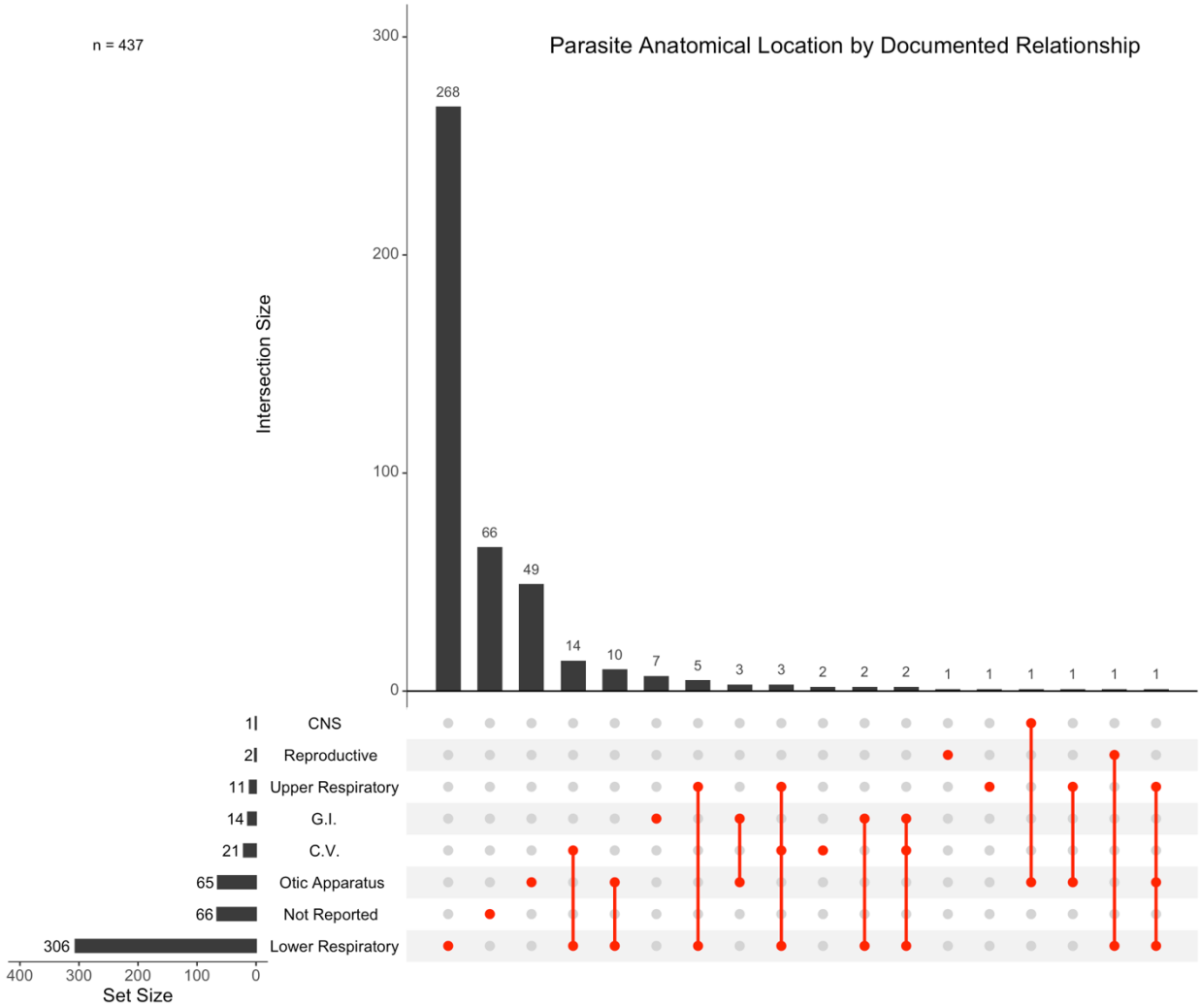


Figure 6: Host diversity for metastrongyles in marine mammals, corrected for publication bias (correction-index).

3.3 The impact of metastrongyle infections on marine mammals

Of the 481 host parasite relationships documented, 371 (77.13%) reported an anatomical location. Lungworms were found in the lower respiratory system in 82.48% (n=306/371) of cases, while parasites were found in the otic apparatus in 17.52% (n=65/371) of cases. In 11.59%

359 (n=43/371) of cases, a single species of parasite parasitized an individual host in multiple
360 anatomical locations (Figure 7).
361



362

363 Figure 7: Anatomical location(s) of documented relationships between metastrongyles and
364 marine mammals. Intersections are shown for studies which report individual host species to
365 parasite species relationships occurring in multiple locations. Relationships that did not report an
366 anatomical location are designated as “Not Reported”. (CNS= Central nervous system, G.I=
367 Gastrointestinal tract, C.V= Cardiovascular system).
368

369 Out of the 201 unique host-parasite relationships assessed, 44.77% (n=90/201) mentioned
370 mortality as “possible” or “potential” contributory cause of death and only 10.44% (n=21/201)
371 studies considered metastrongyle infection as the primary cause of death. Of the 201 host-parasite
372 relationships for which pathogenic effect was assessed, bronchopneumonia was described in
373 71.64% (n=144/201) of the relationships, indicating a high prevalence of bronchopneumonia in
374 hosts infected with metastrongyles (Figure 8). Other reported pathogenic effects included edema
375 (10.95%, n=22/201), vasculitis (7.46%, n=15/201), thrombosis (5.97%, n=12/201), and
376 hemorrhage (5.97%, n=12/201). Lungworm parasitism resulted in no discernible pathogenic effect
377 on the host in 16.42% (n=33/201) of the relationships.

378

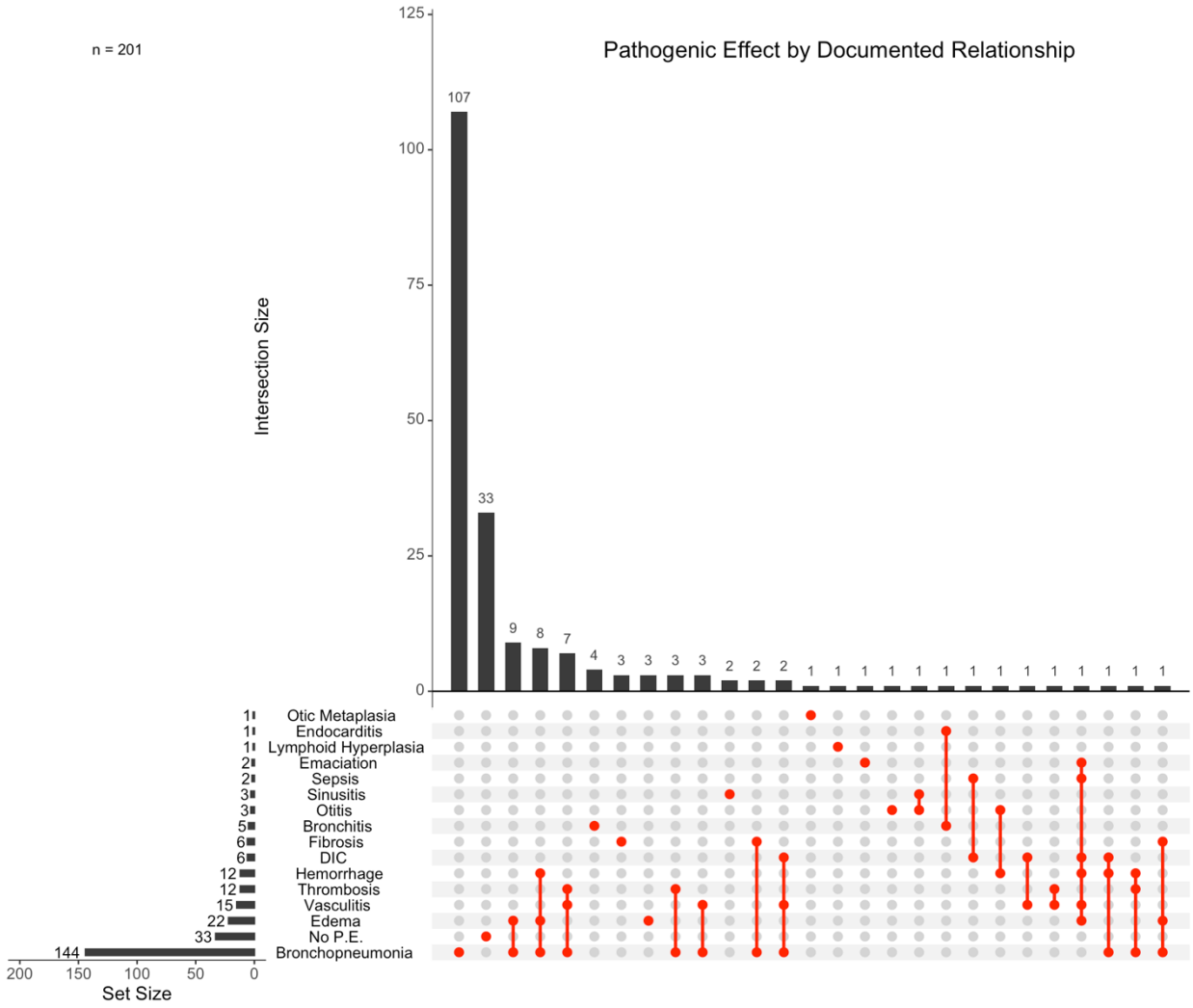


Figure 8: Pathogenic effect(s) of documented relationships between metastrongyles and marine mammals. Intersections are shown for studies which report individual host species to parasite species relationships causing multiple pathogenic effects. Relationships were designated as "No. P.E." when pathogenic effect was assessed and was determined to be negligible. (DIC= Disseminated Intravascular Coagulation).

386 Pathogenic effect was assessed for 166 host-parasite relationships in the respiratory system,
387 with respiratory specific pathology reported in 80.12% (n=133/166) of these cases. In contrast, 26
388 host-parasite relationships assessed pathogenic effect in the otic apparatus, with otic specific
389 lesions reported in only 23.08% (n=6/26) of these relationships.

390 In the binomial GLMM that assessed pathogenic effect, host body size, corrected host
391 diversity and corrected parasite diversity were all significant predictors of the presence of
392 metastrongyle pathogenic effect in marine mammals, with a significant effect of the interaction
393 between host and parasite diversity indexes (table 2). For respiratory specific effects, corrected
394 parasite diversity and corrected host diversity main effects and their interaction were significant
395 predictors of metastrongyle respiratory specific effect in marine mammals, but host body size was
396 not a significant predictor of respiratory specific effect (table 3).

397

398 Table 2: Binomial generalized linear mixed effects model (GLMM) for presence of pathogenic
399 effect. Presented are predictors estimates, standard error (SE), statistic (Z) and P values. The
400 model used study ID as a random effect (total observations n=165, study ID n=89).

Predictor	**Estimate**	**SE**	**Z**	**P**
(Intercept)	-189.93	65.03	-2.921	0.00349
Corrected Parasite Diversity	523.62	165.18	3.170	0.00152
Corrected Host Diversity	232.05	88.44	2.624	0.00869
Host Body Size	166.90	83.04	2.010	0.04444
Corrected Parasite Diversity : Corrected Host Diversity	-625.90	250.44	-2.499	0.01245
Corrected Parasite Diversity : Host Body Size	-435.38	220.87	-1.971	0.04870
Corrected Host Diversity : Host Body Size	-189.10	131.22	-1.441	0.14953
Corrected Parasite Diversity : Corrected Host Diversity : Host Body Size	581.44	438.86	1.325	0.18521

Table 3: Binomial generalized linear mixed effects model (GLMM) for respiratory pathogenic effects. Presented are predictors estimates, standard error (SE), statistic (Z) and P values. The model used study ID as a random effect (total observations n=134, study ID n=76).

Predictor	Estimate	SE	Z	P
(Intercept)	0.09403	12.65860	0.007	0.99407
Corrected Parasite Diversity	88.93332	41.43432	2.146	0.03184
Corrected Host Diversity	74.10991	26.73963	2.772	0.00558
Host Body Size	-18.39291	13.61594	-1.351	0.17675
Corrected Parasite Diversity : Corrected Host Diversity	-244.76967	87.16180	-2.808	0.00498
Corrected Parasite Diversity : Host Body Size	8.03858	38.70274	0.208	0.83546
Corrected Host Diversity : Host Body Size	-29.25975	24.54618	-1.192	0.23325
Corrected Parasite Diversity : Corrected Host Diversity : Host Body Size	154.98741	93.04556	1.666	0.09577

4. Discussion and Conclusions

Metastrongyles are common helminth parasites of the respiratory and cardiovascular system of mammals. Given the importance of these body systems for the survival of diving animals, it was expected that the health impacts of metastrongyles would be particularly significant in marine mammals. Our findings confirm that pathogenic effects, mainly bronchopneumonia, are common in marine mammals infected with metastrongyles, although association of metastrongyle parasites and mortality is usually not definitive. Importantly, our review suggests that pathogenic host-parasite relationships are associated to hosts that can harbor a wider range of metastrongyle species (parasite diversity). From the parasite perspective, metastrongyle species with a broader host diversity tend to be more pathogenic. These results emphasize the importance of host and parasite diversity with regards to the virulence of metastrongyles in marine ecosystems.

417 Most parasitology studies in marine mammals have been conducted through the opportunistic
418 collection and examination of stranded carcasses. This probably explains in part why in most cases
419 metastrongyle infections are suggested or considered as a contributory cause of death but rarely
420 confirmed as the primary cause of mortality. Determining cause of death in stranded marine
421 mammals is challenging, amid the rapid rate of postmortem changes in these species and little
422 background information for most cases (Arbelo *et al.*, 2013; Alvarado-Rybak *et al.*, 2020a).
423 Additionally, access to carcasses is sometimes difficult (*e.g.*, tides), limiting proper dissection
424 techniques and tissue sampling. As with other host-parasite systems, the use of longitudinal
425 assessments and experimental manipulation of infection could give new perspectives on the impact
426 of metastrongyles in marine mammal health. Recently, the sampling of living species through the
427 collection of feces and body fluids has been implemented in cetaceans (Williams *et al.*, 2020).
428 Further, the development of molecular techniques such as major sperm protein (MSP) ELISAs to
429 test for serum antibodies to metastrongyles aid in illuminating metastrongyle seroprevalence
430 (Ulrich *et al.*, 2015, 2016). The continued use of approaches other than opportunistic necropsies
431 may substantially contribute to the understanding of the drivers and consequences of
432 metastrongyle infection in marine mammals.

433 As with many wildlife parasites (Haddaway and Watson, 2016; Seguel and Gottdenker, 2017),
434 most studies on metastrongyles in marine mammals are conducted in North America and Europe,
435 leading to overrepresentation of North American and European marine mammal and metastrongyle
436 species in the literature. Therefore, cosmopolitan coastal marine mammals in these regions such
437 as the harbor porpoise and the harbor seal along with their parasites were among the most assessed
438 species. Despite our intended penalization for these study biases, our results should be interpreted
439 with caution since more studies from different regions of the world and in cryptic and/or pelagic

440 marine mammal species could influence inferences on the role of host and parasite factors driving
441 pathogenic effects. For instance, PCBs and other persistent organic pollutants (POPs) are found in
442 higher concentrations in marine mammals in more industrialized regions of North America and
443 Europe (Fair *et al.*, 2010; Jepson *et al.*, 2016; Durante *et al.*, 2016; Seguel *et al.*, 2020a). These
444 immunosuppressive pollutants are thought to increase susceptibility to metastrongyles, facilitating
445 their pathogenic effects (Jepson *et al.*, 2016). Therefore, more studies from regions of the world
446 with lower POP concentrations or where new or underrepresented host-parasite relationships occur
447 could modify our understanding of the health impacts of metastrongyles in marine mammals.

448 As in domestic and land mammals, bronchopneumonia is the most common pathogenic
449 outcome of lungworm infection in marine mammals. The presence of lungworms in airways or
450 pulmonary parenchyma causes tissue damage, eliciting an inflammatory response that also
451 facilitates colonization by bacteria (Measures, 2001). Therefore, in most of the assessed studies,
452 verminous bronchopneumonia was usually complicated by secondary bacterial infection. The
453 impact of metastrongyles in other tissues such as blood vessels, heart or otic apparatus is probably
454 more direct, since in these tissues bacteria colonization secondary to helminth infection is rare. In
455 the cardiovascular system, the impact of lungworm infection can be serious with vasculitis,
456 localized or systemic thrombosis and coagulopathy (Gulland *et al.*, 1997b; Seguel *et al.*, 2018b;
457 Barnett *et al.*, 2019b). In these cases, there is clear link between metastrongyle infection and
458 mortality. Interestingly, invasion of the cardiovascular system is usually associated to
459 metastrongyle species that are not the most common definitive host for that parasite species,
460 highlighting the role of host specificity in the most pathogenic interactions between metastrongyles
461 and marine mammals.

462 Parasite and host diversity increase the chances for a for a pathogenic outcome in
463 metastrongyle-marine mammal relationships. This finding is supported by general hypotheses on
464 parasite virulence that suggests that a parasite species with a greater diversity of potential hosts
465 can evolve to be more pathogenic, as the sustainability of the parasite population is less dependent
466 on the survival of individual hosts (Poulin, 2011; Schmid-Hempel, 2021). Similarly, a host species
467 that harbors a greater diversity of parasites may see a greater propensity for pathogenic outcomes
468 from individual parasite species due to an increase in the stress on the immune and respiratory
469 systems resulting from co-infections (Seguel *et al.*, 2023). Our results also suggest that larger hosts
470 are more likely to sustain pathogenic outcomes because of metastrongyle parasitism. Since marine
471 metastrongyles are transmitted through intermediate hosts that represent food items for marine
472 mammals (Dailey, 1970a), this result could indicate that increased food consumption leads to a
473 greater larvae intake and subsequently a higher parasite burden. Similarly, a larger host body size
474 could correlate with access to different prey items, contributing to a greater diversity of
475 metastrongyle infections.

476 A comprehensive understanding of the drivers of the negative physiological effects
477 associated with metastrongyle parasitism in marine mammal hosts is challenged by a presumably
478 strong bias towards reporting only positive findings. The available literature clearly elucidates a
479 multitude of host-parasite relationships in which metastrongyles produce a definable pathological
480 effect, howbeit it is inadequate in clarifying why these effects are observed in some species or
481 populations and not in others. However, general host and parasite traits associated with pathogenic
482 outcomes are like those of other helminth and microbial parasites, including host permissiveness
483 of infection by multiple species and parasite capacity to infect multiple host species. In this context,
484 the rapidly changing marine environment with generalized loss of biomass could favor parasites

and hosts with a diversified trophic network, potentially selecting for more pathogenic relationships between metastrongyles and their marine mammal hosts.

5. Supplementary Data

Supplementary figures are submitted as electronic supplementary files. Review protocol not registered.

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