Received: 24 March 2023 | Revised: 13 October 2023 | Accepted: 6 November 2023

DOI: 10.1002/ecs2.4781

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Disease Ecology

Meta-analysis suggests that, for marine mammals, the risk of parasitism by anisakids changed between 1978 and 2015

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Funding information
School of Aquatic and Fishery Sciences; Washington Sea Grant; National Science Foundation, Grant/Award Number: OCE-1829509; Alfred P. Sloan Foundation; University of Washington; Oceans Initiative; Univerisity of Washington Royalty Research Fund

Handling Editor: Andrew R. Wargo

Abstract

As gastrointestinal parasites affect the health of marine mammal species, they are a potentially consequential stressor. Although they are infrequently identified as a cause of mortality, gastrointestinal parasites could drive cryptic declines in individual fitness—including declines in nutritional status—by acting synergistically with other stressors. Nematodes in the family Anisakidae are ubiquitous throughout the world's oceans and are transmitted to marine mammal hosts through the consumption of fish and cephalopod prey. We sought to assess whether marine mammals face a rising risk of gastrointestinal infection due to an increase in anisakid burden of their prey species. We used data compiled from a recent meta-analysis of anisakid abundance in fish and invertebrates from 1967 to 2015. We reviewed the diets of 113 marine mammal species to identify their known prey species. We extracted data on anisakid burden for each of the prey species and tested whether anisakid abundance in these intermediate hosts had increased over time. Our findings suggest that *Anisakis* spp. abundance has increased over the past half-century, while *Pseudoterranova* spp. burden showed no significant change. Our findings suggest that the risk of *Anisakis* spp. infection is increasing for marine mammal hosts.

KEYWORDS
Anisakidae, historical ecology, marine mammal prey, parasites, sublethal stressors

INTRODUCTION

Marine mammals have faced substantial changes in anthropogenic stressors over the past 50 years. From that time, several pieces of legislation have reduced the burden of commercial harvest and placed protections on many marine mammal populations, including the US Marine Mammal Protection Act of 1972 (MMPA) and the International Whaling Commission's global moratorium on commercial whaling in 1986. At a global scale and among the 47 marine mammal species with at least 10 years or three generations of data, 61% have exhibited an increase (Magera et al., 2013). Within the United States and among the marine mammal species with sufficient data, there are reports of population recoveries over the past 40 years (Gulland & Hall, 2007; Roman et al., 2013). Since the enactment of the MMPA, 7%–21% of marine mammal stocks have increased in US waters (Roman et al., 2013). Despite these observed increases, 2% of marine mammal stocks in the United States have not recovered, and an additional 3% have exhibited declines; this is in addition to the 71% of stocks that lack sufficient data to detect a trend (Roman et al., 2013). Outside of the United States, many marine mammal species lack substantive protection (Roman et al., 2013). While direct mortality via harvest has declined, other anthropogenic stressors like fishing interactions, vessel strikes, and indirect effects of climate change, as well as less detectable sublethal stressors (i.e., stressors that do not cause direct mortality), threaten the recovery of many species (Roman et al., 2013).

Parasitic disease may be one factor contributing to reported marine mammal declines or recovery failures. Gastrointestinal nematodes are commonly reported during necropsies of cetaceans and pinnipeds (Dailey, 2001), including species in the family Anisakidae, which are among the most prevalent parasites in marine mammals (Dailey, 2001; Iñiguez et al., 2011). The anisakids include the genera *Anisakis* Dujardin, 1845, commonly known as whaleworm; *Pseudoterranova* Mozgovoi, 1951, commonly known as sealworm; and *Contracaecum* Railliet and Henry, 1912.

Anisakis and *Pseudoterranova* have complex life cycles (Figure 1). *Anisakis* spp. nematodes infect cetaceans as their definitive host, and *Pseudoterranova* spp. infect pinnipeds, though larval forms of *Pseudoterranova* have been found in cetaceans and larval *Anisakis* have been found in pinnipeds (Dailey, 2001; Dailey & Brownell, 1972). The life cycles involve four to five larval phases (summarized in Anderson, 1992; Klimpel & Palm, 2011; Mattiucci et al., 2018; McClelland, 2002). Unembryonated eggs are expelled from the marine mammal host via feces. They embryonate in seawater, maturing within the egg (Køie, 2001). The larvae molt once or twice and emerge as ensheathed, free-swimming larva (Køie et al., 1995; McClelland, 2002). Anisakid larvae continue their life cycle when ingested by the first intermediate host, a crustacean (Køie et al., 1995; McClelland, 1982). Fish and cephalopods that prey on this crustacean host can then act as paratenic hosts for *Anisakis* spp., which are not obligately required for the parasite's development but efficiently pass the parasite up the food web to their definitive marine mammal host (e.g., Klimpel & Palm, 2011). For *Pseudoterranova* spp., fish serve as an obligately required second intermediate host (McClelland, 1995; McClelland & Martell, 2001). When the larva is ingested, it either remains in the visceral cavity or organs or migrates to the muscle tissue, depending on the species (e.g., Cipriani et al., 2016; Karl & Levsen, 2011; Levsen et al., 2017; Levsen & Lunestad, 2010; Mattiucci et al., 2018; Roepstorff et al., 1993). Marine mammals become infected by ingesting a paratenic or intermediate host harboring one or more larvae, and the preadult larva reaches sexual maturity after 37–109 days (Klimpel & Palm, 2011; McClelland, 2002; Ugland et al., 2004).

Once inside their marine mammal definitive host, anisakids can cause both direct and indirect fitness costs. After being consumed with an intermediate host, the nematodes reproduce in the host stomach, inhabiting the stomach compartments either in gastric lumen or attached to the gastric or stomach wall mucosa (Dailey, 2001; Geraci & Aubin, 1987; Iñiguez et al., 2011). It is unknown what adult nematodes and subadult larvae feed on while in the gastrointestinal tract, but whether they consume the food of the host or the host itself, anisakids are an energy sink, sequestering nutrients away from their hosts (Combes, 2001). The proportion of host energy taken by these parasites is currently unknown. At the site of anisakid infection, the host immune system forms granulomas, often in the stomach lining, causing gastritis, ulceration, and secondary bacterial infections (Cattan et al., 1976; Dailey, 2001; Martineau et al., 2002). Individual worms cluster in groups of 50–100 with their anterior ends embedded in ulcers, which can reach up to 6 cm in diameter (Audicana et al., 2003; Geraci & Aubin, 1987; Motta et al., 2008). The ulcers may be acute and hemorrhagic, or chronic, and can be associated with edema (Haebler & Moeller, 2021; Motta et al., 2008; Raga et al., 2009). In stranded cetaceans off the coast of Brazil, six of eight animals with anisakid infections exhibited chronic lymphoplasmocytic gastritis (Motta et al., 2008). In severe infections, the perforations of the stomach wall can cause peritonitis, ultimately leading to hemorrhaging, anemia, and, rarely, death (Ballachey et al., 2002; Dailey, 1985; Dailey & Stroud, 1978; Margolis et al., 1997; Smith, 1989; Stroud & Roffe, 1979; van Beurden et al., 2015). Whether or not these infections result in disease or mortality, they reduce the hosts' fitness, which can have individual and population-level consequences (Shanebeck et al., 2022).

With some marine mammals increasing while others languish or decline, threats that can cross species barriers become especially salient for conservation. As some marine mammals recover, they increase in density and facilitate parasite transmission (Anderson & May, 1978; Arneberg et al., 1998), increasing the availability of parasite propagules in the environment and the potential for infection among at-risk marine mammal species. Marine mammals have high energetic demands (Berta, 2020; McNab, 2012), and populations that are declining due to persistent sublethal stressors, like acoustic or physical disturbance, entanglement, or bioaccumulation of pollutants, are likely to face elevated energy demands (Berta, 2020; King et al., 2015; McNab, 1989, 2012). This can result in individuals having less energy available to devote to immune response, making them more susceptible to infection (Beldomenico et al., 2008; Shanebeck et al., 2022; e.g., Colegrove et al., 2016; Lair et al., 2016; Seguel et al., 2018). It also leaves less energy to spare, meaning that the energetic costs of parasite infection could have population-level consequences (Beldomenico et al., 2008; King et al., 2015; May et al., 2019; Shanebeck et al., 2022). Meanwhile, healthy marine mammal populations with few stressors may increase in abundance and continue to tolerate parasite infections, further serving as breeding grounds for parasites and possibly increasing the population

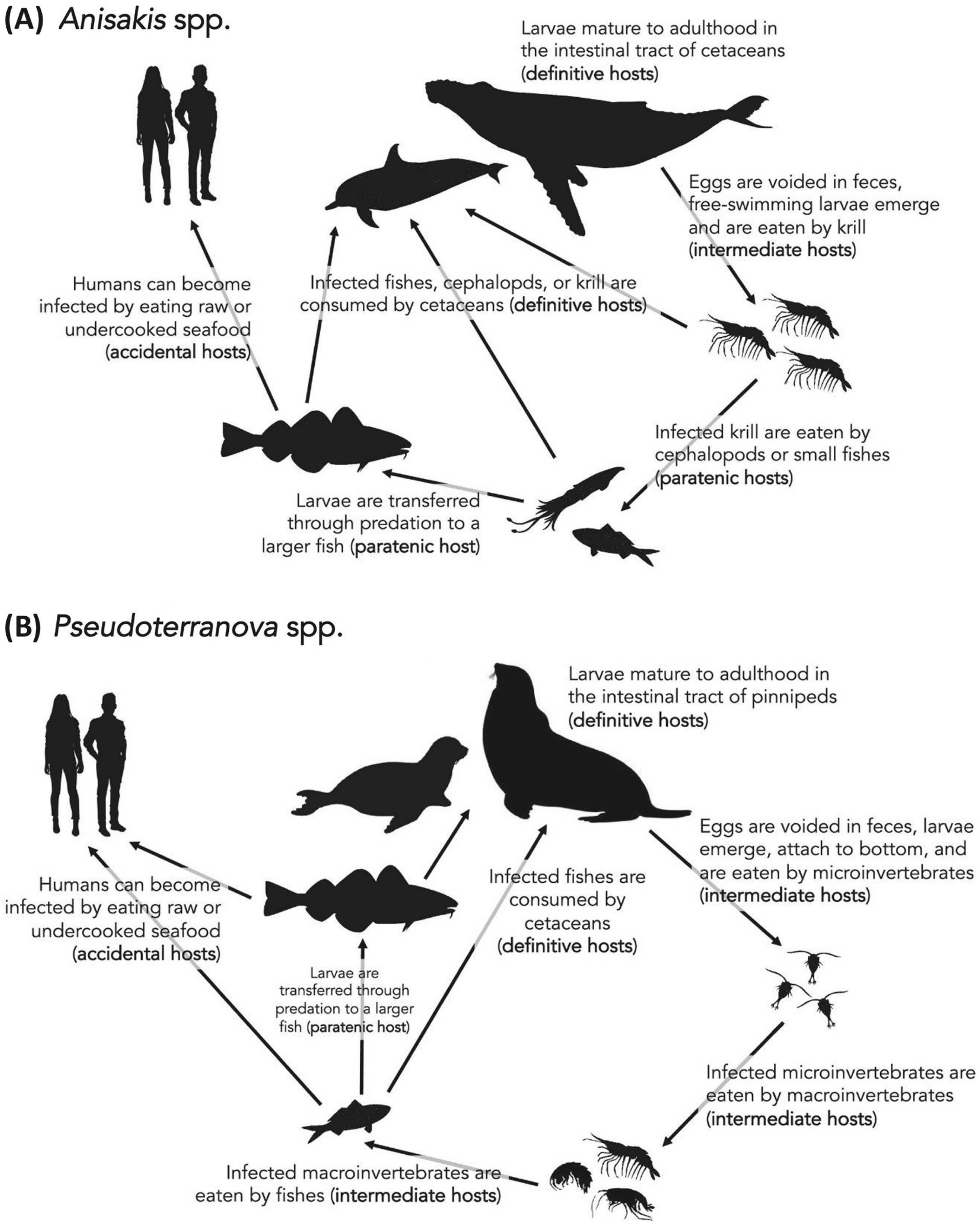

FIGURE 1 Legend on next page.

of infectious helminths available to infect more vulnerable hosts.

Recently, Fiorenza et al. (2020a) demonstrated a global increase in the abundance of *Anisakis* sp. in fish and cephalopod intermediate hosts. The authors conducted a meta-analysis of records of *Anisakis* and *Pseudoterranova* spp. in fish and squid host species published in peer-reviewed literature from 1967 to 2017. They found that there was a 283-fold increase in *Anisakis* spp. between 1978 and 2015 and no change in the abundance of *Pseudoterranova* spp. Does this finding mean that cetaceans are at greater risk of *Anisakis* infections today than they were in the past? Fiorenza et al. (2020a) could not answer this question, because they included in their meta-analysis all species of fish and invertebrates that were sampled and screened for anisakid infections. They did not take into account which species of fish sampled are components of the diet for marine mammal hosts. While Fiorenza et al. (2020a) found a global increase in *Anisakis* spp., they could not determine whether this represented an increase in risk to marine mammal definitive hosts.

We sought to determine whether marine mammals face an increased risk of anisakid infection by assessing how anisakid prevalence has changed in prey species of marine mammals over four decades (1967–2007). This time period is especially important, as this 35-year window immediately followed the passage of the MMPA and the Endangered Species Act (1973) in the United States and encompasses the beginning of the international moratorium on commercial whaling. We made use of Fiorenza et al.'s (2020a) existing meta-analytic database by extracting those records that pertained to (1) marine mammal prey species that (2) geographically overlapped with the range of their marine mammal predator.

We used anisakid burden within prey species as a proxy for marine mammal risk rather than obtaining infection data directly from marine mammals for a number of reasons. While there is evidence from direct sampling of hosts that viral and bacterial diseases of marine mammals have increased from 1966 to 2007, metazoan parasites, which were well studied in the 1960s, have not received much research attention in recent years, so the temporal trend in helminth burden is currently unknown (Gulland & Hall, 2007). Direct parasitological examinations can only be conducted on difficult-to-obtain fecal samples from wild animals or necropsy samples from deceased individuals, the latter typically being skewed toward overrepresentation of unhealthy individuals which may not represent the burden of parasites in healthy animals (Aguilar & Borrell, 1994; Dailey & Stroud, 1978; Hermosilla et al., 2018; Ten Doeschate et al., 2017). Gastrointestinal helminths rarely cause mortality, but may contribute to poor marine mammal health in vulnerable species threatened by multiple stressors. By investigating how anisakid burden has changed in marine mammal prey over time, we were able to quantify temporal trends in infection risk for marine mammals. We sought to answer the following questions: (1) Have *Anisakis* spp. and *Pseudoterranova* spp. abundance increased over time in the prey species marine mammals commonly eat? And (2) does the trajectory of change in anisakid abundance differ between two major marine mammal groups (i.e., cetaceans vs. pinnipeds)?

METHODS

Data collection

Literature search and data extraction

We used a publicly available and published dataset (Fiorenza et al., 2020b) to obtain estimates of *Anisakis* spp. and *Pseudoterranova* spp. abundance from 1978 to 2015.

FIGURE 1 General life cycle of *Anisakis* species (A) and *Pseudoterranova* species (B) nematodes. The *Anisakis* spp. life cycles involve four larval phases (L1–L4) that take place mainly in the pelagic environment (Klimpel & Palm, 2011). L1 through L3 take place inside the egg, which is released into the ocean through a cetacean's scat. The L3 larvae are eaten by the first intermediate host, a pelagic crustacean, which breaks the larva's cuticle, and they penetrate the intestinal tract into the hemocoel (Køie et al., 1995). The crustacean host is eaten by a paratenic intermediate host, which can be a larger copepod, euphausiid, or small fish. Larger fish or copepods can serve as additional paratenic hosts by preying on the second intermediate hosts, and in turn being preyed on by the definitive host. Cetaceans become infected by consuming an intermediate or paratenic host, at which time the L4 develop into the adult stage and reproduce within the digestive tract (Klimpel & Palm, 2011). The *Pseudoterranova* spp. life cycle begins with eggs defecated by an infected pinniped. The egg sinks to the seafloor and develops through L1–L2, and hatches to L3. L3 larvae are eaten by their first intermediate host, a microinvertebrate, in which the larvae penetrate the digestive tract and enter the hemocoel. The invertebrate is consumed by a benthic macroinvertebrate second intermediate host (Anderson, 2000; McClelland, 2002, 2005). Unlike *Anisakis* spp., *Pseudoterranova* spp. require a third intermediate fish host, which is generally a benthic teleost juvenile fish. The third intermediate host can be consumed by piscivorous paratenic hosts before ultimately reaching their final pinniped host (Anderson, 2000; McClelland, 2002, 2005; Palm, 1999). There they reach their L4 stage, embed in the gastric mucosa, and develop into their adult stage and reproduce (Klimpel & Palm, 2011). Humans can be infected by consuming larval anisakids, though not all *Anisakis* and *Pseudoterranova* species are pathogenic. Reproduced with permission from Fiorenza et al. (2020a).

To compile their meta-analytic dataset, Fiorenza et al. (2020a) conducted a search in Web of Science in October 2017 using the search terms anisak* or "herring worm" or "herringworm" or Pseudoterranova or whaleworm or "whale worm" or phocanema or "whale-worm" (Figure 2). The search resulted in 2284 papers, which were then screened for suitability using their titles (2284 papers), abstracts (1336 papers), and full text (576 papers). In this process, the authors removed any papers that focused on non-fish/non-cephalopod hosts or nontarget parasites, experimental manipulation studies, and reviews. The final pool of papers (123) reported host and parasite species identity, location and year of collection, size of host, how parasitological examinations were conducted, and prevalence and intensity or abundance of infection with an error estimate. From these papers, the authors extracted 755 data points, or unique estimates of parasite abundance for a host species in a particular location at a particular time. Of these data points, 69.7% represented *Anisakis* spp. and 30.3% *Pseudoterranova* spp. (Fiorenza et al., 2020a).

Identifying records pertinent to marine mammal health

To extract the records from the Fiorenza et al. (2020b) dataset that were germane to marine mammal health, we sought the subset of records from marine mammal prey species in geographic areas where their marine mammal predators occur. We first compiled all marine mammals included in the International Union for Conservation of Nature (IUCN) database (IUCN, 2018), regardless of Red List status, including all marine species in the genera *Arctocephalus*, *Callorhinus*, *Enhydra*, *Eumetopias*, *Lontra*, *Neophoca*, *Otaria*, *Phocarctos*, and *Zalophus* and families Balaenidae, Balaenopteridae, Delphinidae, Dugongidae, Eschrichtiidae, Iniidae, Monodontidae, Neobalaenidae, Odobenidae, Phocidae, Phocoenidae, Physeteridae, Pontoporiidae, Trichechidae, Ursidae, and Ziphiidae. We used IUCN range maps for each species, which were the most detailed and up-to-date maps available at the time of our analysis (IUCN, 2020). Many marine mammal species are subdivided into distinct populations, but because IUCN range data are available only at the species level, our analysis was conducted at the species level. We only considered extant ranges—that is, areas where the species is known or thought to occur in the present day (IUCN, 2020). This includes areas with current or recent (past 30 years) records of suitable habitat. As habitat records for each species were developed using sighting data from about 75% of the meta-analysis data period, we found these habitat ranges suitable for our filtering process. We then determined which marine mammal species ranges overlapped with the data points from the meta-analysis through visual identification and filtered out marine mammal species whose ranges did not overlap with any data points.

We compiled diet data for each of the remaining marine mammal species. Many of these data were derived from species summaries through the IUCN Red List, which contains detailed diet information from literature reviews compiled by experts on each species (IUCN, 2020). For marine mammal species whose diet data were not included in IUCN species summaries, we compiled diet data by reviewing the published literature for each species, searching Google Scholar for publications including the species and region of interest, which surveyed the prey species eaten through any method (e.g., stable isotopes, necropsy, and fecal samples). In some cases, prey data were only reported at the prey family level. In these instances, we reviewed each prey family in FishBase (Froese & Pauly, 2000) and determined which species of those families had ranges that overlapped geographically with the marine mammal's range. Through this effort, we generated a list of potential prey species for each marine mammal. Then, we filtered the Fiorenza et al. (2020a) records to include only those records that fell within both the geographic and diet range of at least one marine mammal species. We then performed a final filter to ensure that the remaining prey species were collected in the geographic range of the marine mammal that preys upon it. This was completed by visually comparing the specific location where the intermediate host from Fiorenza et al. (2020a) was caught to ensure that the definitive host could have theoretically consumed that prey item. We obtained 396 overlapping data points, including 278 *Anisakis* spp. data points and 118 *Pseudoterranova* spp. data points, which were then used in the analysis.

Analysis

Data standardization

We standardized the data prior to analysis using the methods described in Fiorenza et al. (2020a). Briefly, the dataset included information on host species; collection location and year; portion of the host examined and examination method; parasite genus, prevalence, intensity, and abundance; and error associated with intensity and abundance. Some, especially older, articles only identified parasites to the genus level (e.g., *Anisakis* sp.). In order to maximize the proportion of available data that we could use, maximize the temporal scope of our analysis, and increase the sample size and power for our

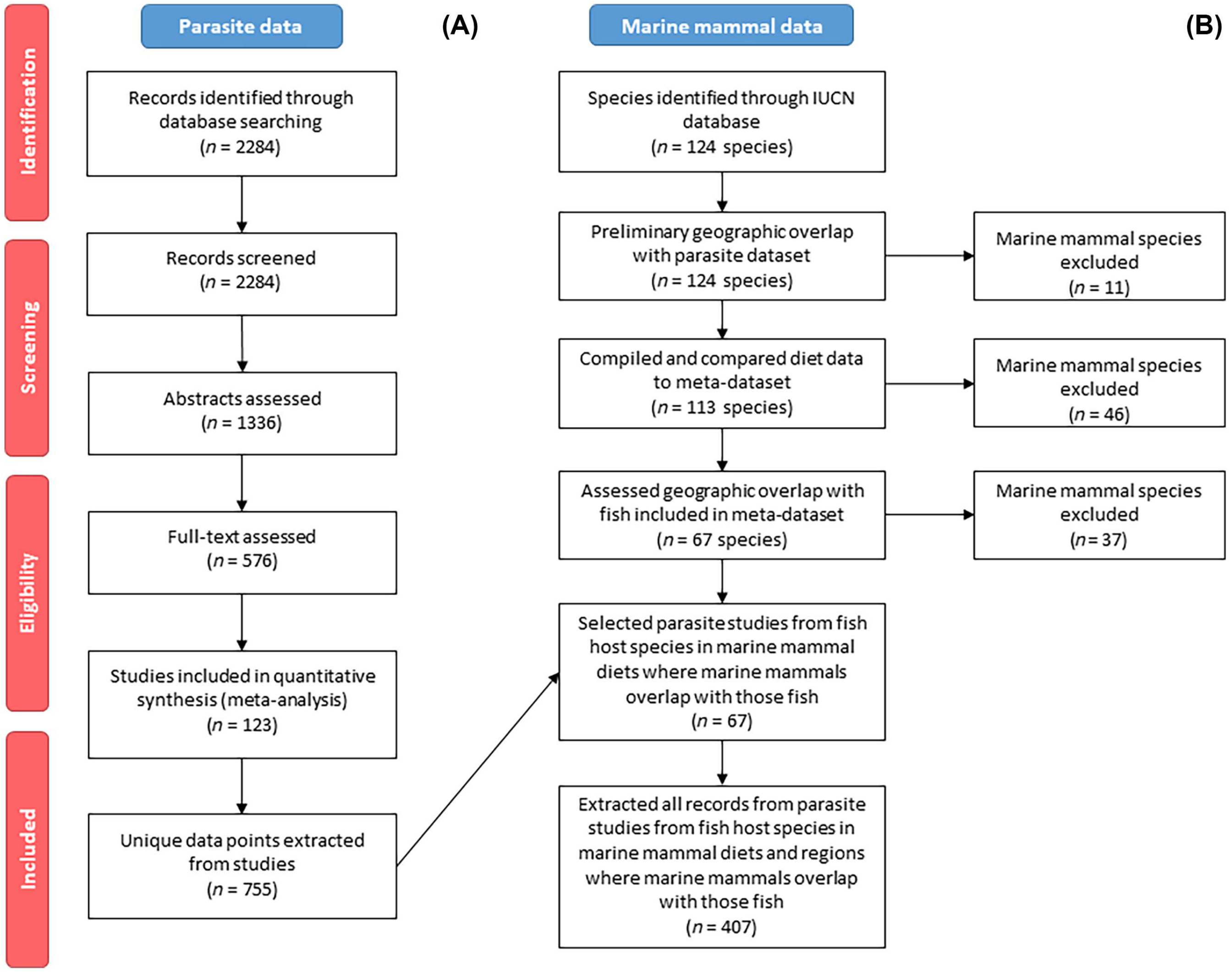

FIGURE 2 A PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) flow diagram of the process of determining inclusion of parasite publications for the meta-analysis (A) and marine mammal diet species with which to filter the meta-dataset (B). The process of screening papers for the meta-analysis (A) was conducted by Fiorenza et al. (2020a). All full-text articles were assessed for eligibility of inclusion, resulting in 123 articles with 755 unique records of anisakid abundance. The process of screening marine mammal diet and ranges (B) began with compiling 124 marine mammal species from the International Union for Conservation of Nature (IUCN) and then we completed a preliminary screening to exclude any species that did not overlap geographically with the dataset compiled by Fiorenza et al. (2020b; e.g., excluding freshwater species or species that live in oceans not represented by the meta-analysis dataset). We then compiled all species that marine mammals are confirmed or likely to eat, and filtered those data based on fish species included in the meta-dataset. Finally, we assessed the remaining data to ensure that each marine mammal range actually overlapped with the species from the meta-dataset. This process resulted in 30 marine mammal species and encompassed 67 articles that included data on parasite abundance in these fish species, and 407 unique records of anisakid abundance for prey eaten by marine mammals.

analysis, we grouped parasites by genus. Because fish length was reported in different ways across studies, we standardized values using a standard linear conversion equation $\text{Length}_{\text{standard}} = a + b \times \text{Length}_{\text{reported}}$ using a and b values, or length–weight parameters, for each species from FishBase (Froese & Pauly, 2000). The mean parameter values were calculated and when multiple values were reported (Froese & Pauly, 2000). Parasite abundance, if not reported, was calculated from parasite intensity and prevalence by multiplying intensity and prevalence and propagating the error through in quadrature (the square root of the sum of squares; Fiorenza et al., 2020a). Locations were grouped based on FAO fishing region (FAO, 2008) using ESRI ArcGIS (ESRI, 2011). As SD was required for the meta-analytic framework, if a study reported other forms of error (SE, CIs, or range), we calculated SD using formulae (Fiorenza et al., 2020a). If the range of parasite abundance was provided, we estimated SD by using the properties of the negative binomial distribution (Shaw et al., 1998). We optimized the negative binomial distribution for the dispersion parameter, assuming that the maximum value was the 95th quantile of the negative binomial distribution, and the mean value as the mean of the negative binomial distribution (Shaw et al., 1998). An optimization algorithm was used to estimate the best-fit dispersion parameter, which was then used to calculate the error of the mean. If other forms of error were reported, they were converted back to SD. For example, SE was multiplied by the square root of sample size, and, for CIs, we took the difference of the upper bound and the mean and then divided it by the appropriate *z*-score and then multiplied by the square root of the sample size, as in Fiorenza et al. (2020a).

Data analysis

We generated columns for definitive host species, definitive host suborder/infraorder (Pinnipedia or Cetacea), parasite genus (*Anisakis* spp. or *Pseudoterranova* spp.), and paper ID (i.e., the paper from which the datum arose) to group the data for analysis. There was one instance in which multiple marine mammal definitive hosts had the same intermediate host species in their diet. In that instance, we chose to include the intermediate host row for the definitive host with the smaller sample size, as duplicating the row would complicate interpretation of the analysis. Anisakid abundance and SD were fourth-root-transformed to fit normality assumptions (Ekstam et al., 2011; Mandonnet et al., 2001; Stevens & Connolly, 2005). We corrected for SEs that were equal to zero (e.g., when only one sample was taken) by adding 1 to every variance to prevent overweighting, as meta-regression uses the inverse of variance to weight observations (Fiorenza et al., 2020a). We subset the data into two datasets based on parasite species occurrence, one for *Anisakis* spp. and one for *Pseudoterranova* spp., to run separate models on each genus.

We ran four generalized linear mixed-effects models on the data to determine whether (1) there has been a change in the abundance of (1a) *Anisakis* spp. or (1b) *Pseudoterranova* spp. in prey species of marine mammals over time and (2) there has been a change in the abundance of (2a) *Anisakis* spp. or (2b) *Pseudoterranova* spp. in prey species of each marine mammal host sub/infraorder (Table 1). Each model was run using rma.mv() in the metafor package (Viechtbauer, 2010) in R (version 4.0.0, R Core Team, 2020).

Models 1a and 1b tested whether the abundance of *Anisakis* spp. and *Pseudoterranova* spp. changed over time. The models included parasite abundance of *Anisakis* or *Pseudoterranova* spp. as the response variable. Year and host length were included as fixed effects. As we expected that host species, fishing region, the portion of fish analyzed for parasites, and method of detection could all influence the count of anisakids differently, we included random effects of portion of fish sampled nested within intermediate host species, FAO region, method of detection, and paper ID. This resulted in the following model:

$$\begin{aligned}\left(\text{Parasite\_abundance}_{ijkl}\right)^{1/4} &\sim \text{Host\_length}_{ijkl} + \text{Year}_{ijkl} \\ &+ \left(1|\text{Host\_species}_{l}/\text{Portion\_of\_fish}_{ijkl}\right) \\ &+ \left(1|\text{FAO\_region}_{j}\right) \\ &+ \left(1|\text{Method\_of\_detection}_{ijkl}\right) \\ &+ \left(1|\text{Paper\_ID}_{i}\right), \qquad (1)\end{aligned}$$

where the response variable$_{ijkl}$ represents a measurement of parasite abundance from the ith study in the jth location at the kth time in the lth intermediate host species. Models 2a and 2b tested whether the change over time in *Anisakis* spp. or *Pseudoterranova* spp. differed between those prey items consumed by cetaceans versus those consumed by pinnipeds. Model 2 was identical to Model 1, except that it also included an interaction term of $\text{Year}_{ijkl} \times \text{Definitive\_host\_suborder}_{l}$. To assess the interaction between time and definitive host order (Model 2), we ran identical models, changing the host

TABLE 1 The research questions and the generalized linear mixed-effects models run separately for a subset of data with *Anisakis* species (spp.) and *Pseudoterranova* species (spp.) to detect a change in anisakid prevalence over time for (1) all marine mammal prey species and (2) prey species grouped by marine mammal order.

Has anisakid prevalence changed over time in …	Model no.	Model
… marine mammal prey species generally?	1	[Parasite abundance]$^{1/4}$ ~ Std length + Year + (1|Intermediate host/Portion of Body) + (1|FAO) + (1|Method of Counting) + (1|Paper ID)
… pinniped versus cetacean prey species?	2	[Parasite abundance]$^{1/4}$ ~ Std length + Definitive Host Order × Year + (1|Intermediate host/Portion of Body) + (1|FAO) + (1|Method of Counting) + (1|Paper ID)

order in the reference position and recording the coefficient for each as represented by the intercept in its respective model.

For Models 1 and 2, all marine mammal-definitive hosts were used, regardless of the temporal range or sample size of their prey data. While *Pseudoterranova* spp. and *Anisakis* spp. have different definitive hosts, we included both *Pseudoterranova* spp. and *Anisakis* spp. data points for the analysis of all species of marine mammal definitive host regardless of preferred host, as there is evidence that larval forms of parasites can infect non-preferred hosts (*Anisakis* spp. in pinnipeds, *Pseudoterranova* spp. in cetaceans; Dailey, 2001).

As in Fiorenza et al. (2020a), we were interested in determining whether certain fish species or regions contributed disproportionately to the observed patterns. We performed two sub-analyses of Models 1a and 1b: one to investigate whether any one intermediate host species was responsible for driving patterns and another to investigate whether any one FAO region was responsible for driving patterns. We sequentially excluded single host species or FAO regions and then reran the model on the reduced dataset. We extracted an estimate of the change over time for each iteration to assess whether a single host or region was responsible for the observed change over time. When the significant influence of a particular species or region was detected, we ran the model (excluding the random effect of either FAO or intermediate host species) on the subset of data for the influential FAO region/intermediate host species, to determine whether a significant trend would be observed within that subset of the data.

RESULTS

We compiled and reviewed diet data for 113 marine mammal species listed in the IUCN database (Figure 2). After compiling range data for each species, we compared ranges with the data points extracted in the meta-analysis and found that 30 marine mammal species overlapped spatially with the records collected in the Fiorenza et al. (2020b) dataset (Appendix S1: Table S1). The number of fish or invertebrates analyzed totaled 46,359, representing 66 wild prey species collected in 64 studies from 1978 to 2015 (Appendix S1: Figure S1).

In Model 1, we detected a significant increase (estimate = 0.0234, SE = 0.0067, $Z = 3.5055$, $p = 0.0005$) in the abundance of *Anisakis* spp. over time and no significant change (estimate = −0.0115, SE = 0.0109, $Z = -1.0573$, $p = 0.2904$) in the abundance of *Pseudoterranova* spp. (Figure 3, Table 2). In Model 2, there was a significant increase in the abundance of *Aniskais* spp. (estimate for effect of year = 0.0218, SE = 0.0113, $Z = 1.9249$, $p = 0.0542$) detected in the prey species consumed by both cetaceans and pinnipeds (estimate for effect of year × definitive host suborder = 0.0086, SE = 0.0142, $Z = 0.6084$, $p = 0.5429$). We detected no difference in the rate of change in *Pseudoterranova* spp. abundance (estimate for effect of year = 0.0054, SE = 0.0214, $Z = 0.2503$, $p = 0.8023$) in the prey species of cetaceans versus pinnipeds (estimate for effect of year × definitive host suborder = −0.0134, SE = 0.0248, $Z = -0.5402$, $p = 0.5891$; Figure 4, Table 3).

When testing whether particular intermediate host species drove the trend observed in Model 1, we found that the prey species *Aphanopus carbo* was the most influential intermediate host driving the temporal increase in *Anisakis* spp.; however, once this species was removed and the model was rerun, the trend remained significant for *Anisakis* spp. (estimate = 0.0169, SE = 0.0071, $Z = 2.3648$, $p = 0.0180$). The prey species that was most influential for *Pseudoterranova* spp. was *Reinhardtius hippoglossoides*, and when this intermediate host species was removed, the overall trend for *Pseudoterranova* spp. was significantly negative (estimate = −0.0281, SE = 0.0104, $Z = -2.6955$, $p = 0.0070$). When the model was run on *R. hippoglossoides* exclusively, the temporal trend was nonsignificant (estimate = 0.1046, SE = 0.2826, $Z = 0.3701$, $p = 0.7113$). When testing which FAO region contributed most to the observed pattern in Model 1, the model failed to converge when we removed region 57 (the Eastern Indian Ocean), so we were unable to evaluate whether this region drove the observed pattern. We were able to proceed with sequential removal of the remaining FAO regions, and we found that FAO region 37 (the Mediterranean and Black Seas) had the greatest effect on *Anisakis* spp.; although when it was removed, the trend remained significantly positive (estimate = 0.0292, SE = 0.0077, $Z = 3.8104$, $p = 0.0001$; Appendix S1: Figures S2–S4). The FAO region 21, the Northwest Atlantic, had the biggest effect on *Pseudoterranova* spp., and when removed, the trend became significantly negative (estimate = −0.0279, SE = 0.0105, $Z = -2.6495$, $p = 0.0081$). When run independently, the trend for *Pseudoterranova* spp. in the Northwest Atlantic was nonsignificantly positive (estimate = 0.0692, SE = 0.0429, $Z = 1.6145$, $p = 0.1064$).

DISCUSSION

We detected a significant increase in the abundance of *Anisakis* spp. in the prey species of marine mammals over a 36-year period (Figure 3). At the same time, there was no change in the abundance of *Pseudoterranova* spp. in these prey species over the

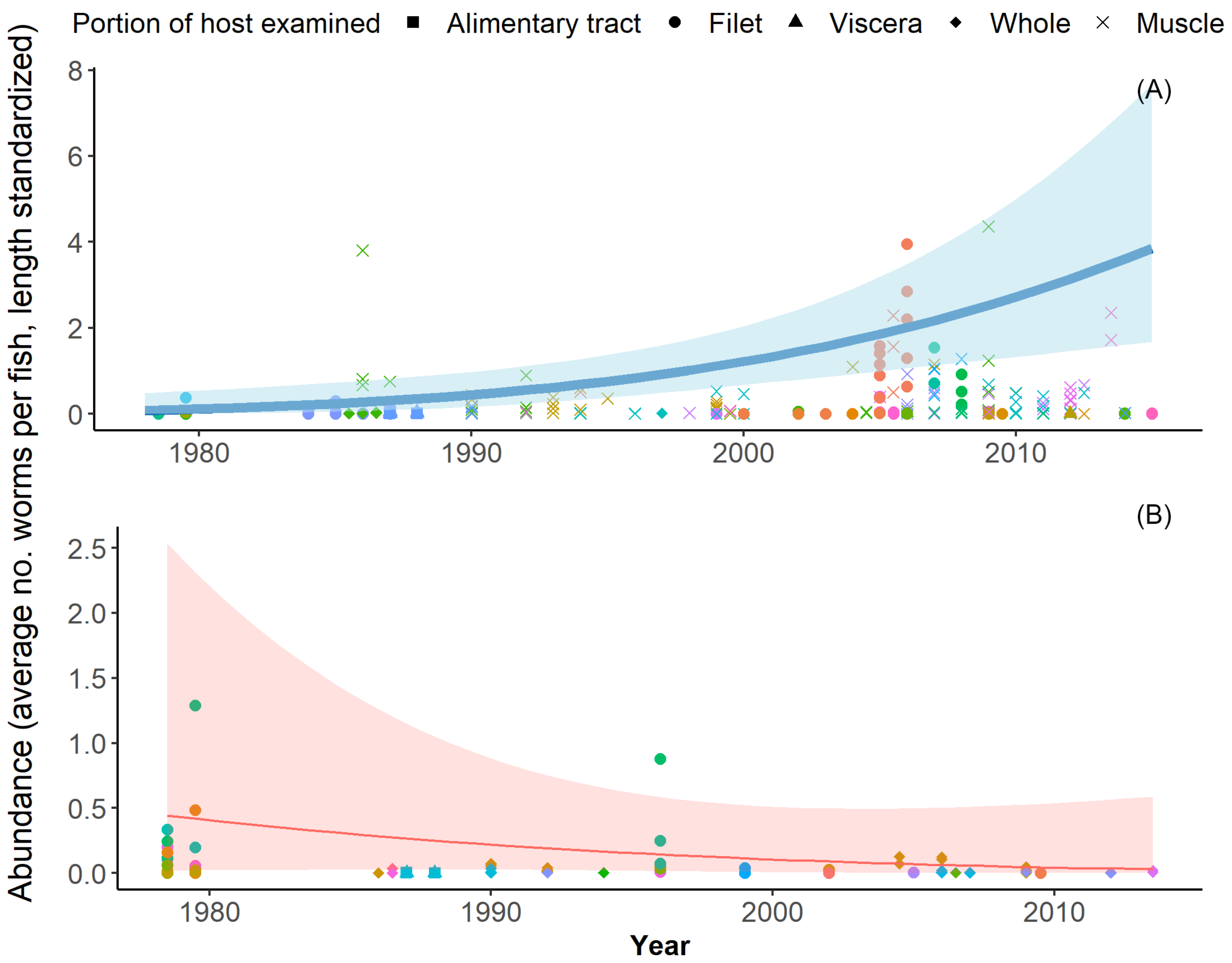

FIGURE 3 The trend in *Anisakis* species (A) and *Pseudoterranova* species (B) abundance, corrected for host length and colored by the intermediate (fish) host species, as predicted from Model 1. Predictions were derived in the predict.rma() function in the metafor package in R and are based on the average standard length of the hosts in the dataset.

TABLE 2 Results of Model 1—assessing the effect of year on *Anisakis* species (spp., 1a) and *Pseudoterranova* species (spp., 1b) independently.

Model	Coefficient	Estimate	SE	z	p
Model 1a, *Anisakis* spp.	Intercept	−46.7131	13.3812	−3.491	0.0005
	Standard length	0.0246	0.0031	7.9789	<0.0001
	Year	0.0234	0.0067	3.5055	0.0005
Model 1b, *Psuedoterranova* spp.	Intercept	23.3783	21.6688	1.0789	0.2806
	Standard length	0.004	0.0059	0.6882	0.4913
	Year	−0.0115	0.0109	−1.0573	0.2904

focal time period. Both prey species eaten by cetaceans and pinnipeds showed an increase in *Anisakis* spp. This study is retrospective and correlational, constraining our ability to identify causal drivers of the patterns observed. With the caveat that our data cannot discriminate among competing hypotheses to explain these patterns, we offer some potential explanations below.

The observed increase in *Anisakis* spp. over time is consistent with findings for the broader dataset in Fiorenza et al. (2020b) and may correspond to a number of drivers. One possible driver is the recovery of some

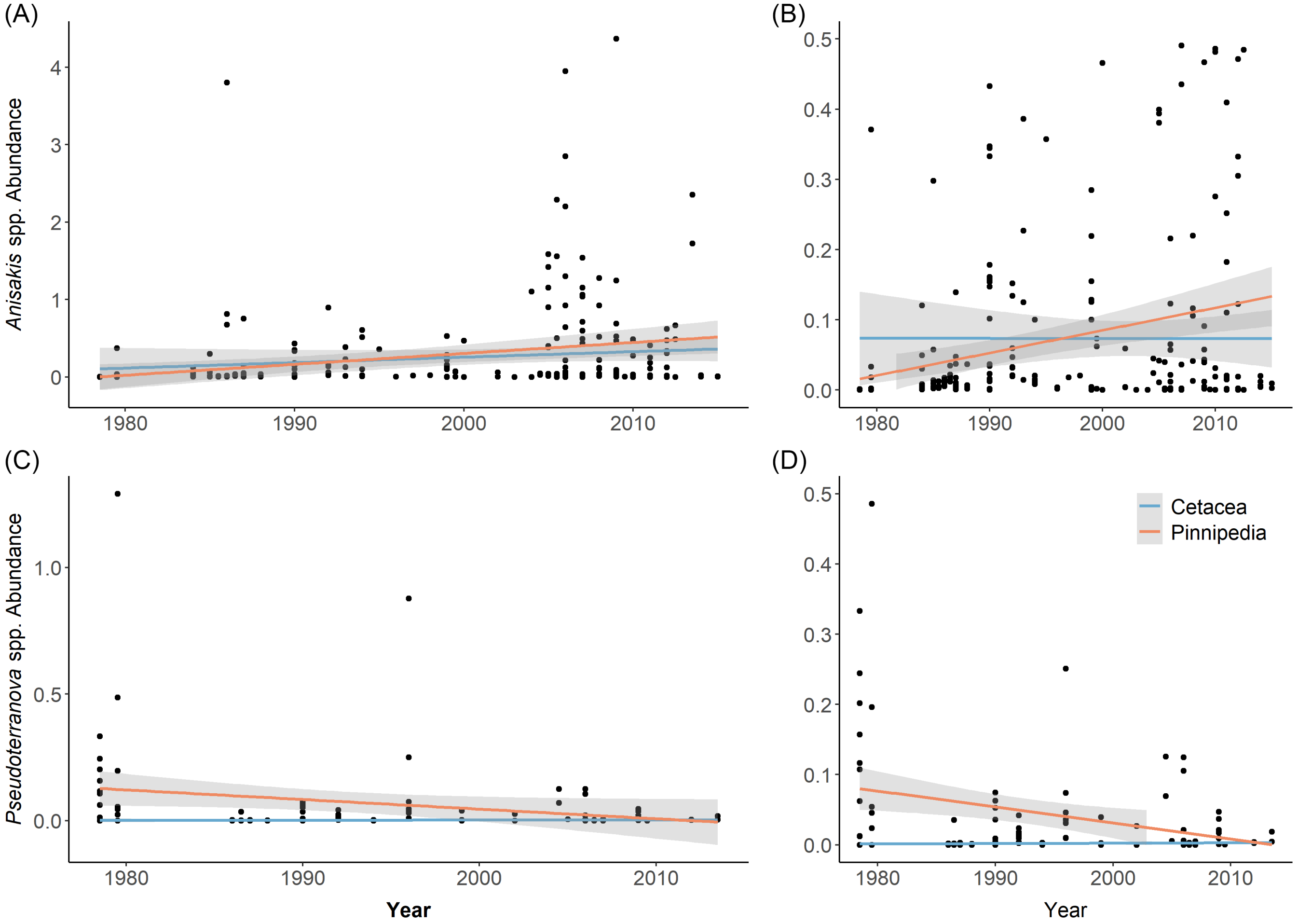

FIGURE 4 Trends in *Anisakis* species (A, B) and *Pseudoterranova* species (C, D) abundance over time in cetaceans and pinnipeds using raw data. In plots B and D, the *y*-axis is truncated to make the temporal relationship more apparent. Lines represent smoothed conditional means of parasite abundance to time by order, calculated in the ggplot2 package in R using the glm method in the geom_smooth() function. Shaded areas represent CIs around the generalized linear model regression line, generated by the geom_smooth() function, which constructed the normal CI on the link scale and back-transformed it to the response scale, parasite abundance. These data were used in Model 2.

TABLE 3 Coefficients for the effect of time on each order (Model 2) for both *Anisakis* species (spp., 2a) and *Pseudoterranova* species (spp., 2b), where estimates represent the effect of order × year when cetacea is in the reference position.

Model	Coefficient	Estimate	SE	z	p
Model 2a, *Anisakis* spp.	Intercept	−43.5278	22.714	−1.9163	0.0553
	Standard length	0.0245	0.0031	7.9844	<0.0001
	Pinnipedia	−17.0561	28.2814	−0.6031	0.5465
	Year	0.0218	0.0113	1.9249	0.0542
	Pinnipedia × year	0.0086	0.0142	0.6084	0.5429
Model 2b, *Pseudoterranova* spp.	Intercept	−10.6582	42.8568	−0.2487	0.8036
	Standard length	0.0035	0.0057	0.6178	0.5367
	Pinnipedia	27.3422	49.4813	0.5526	0.5806
	Year	0.0054	0.0214	0.2503	0.8023
	Pinnipedia × year	−0.0134	0.0248	−0.5402	0.5891

marine mammal species following protections. Our filtered meta-analysis dataset spanned from 1978 and 2015. This period immediately follows the passage of the MMPA in the United States in 1972 and encompasses the enactment of the International Whaling Commission's global moratorium on commercial whaling in 1986. While the MMPA protected only marine mammals in US waters, the moratorium was an international protection on great whale species. Prior to the moratorium, many whale species were heavily overexploited, some nearly to the point of extirpation (Clapham et al., 1999; Thomas et al., 2016). Following the moratorium, some cetacean species, especially small coastal species, have increased and even recovered to historical levels (Magera et al., 2013; Roman et al., 2013). This recovery in some cetaceans, the definitive hosts of *Anisakis* spp., could lead to increased prevalence of *Anisakis* spp. in the prey species of the many marine mammals surveyed in this meta-analysis, including the prey of pinnipeds. Our analysis showed a greater increase in *Anisakis* spp. in pinniped prey over time, which may be a product of the time profile we had available for each definitive host. The data of cetacean prey were collected from the mid-1980s to 2015, whereas the data of pinniped prey species cover a broader span of time (1978–2013), including the passage of the IWC moratorium on whaling, which is a period that is more likely to show a change in anisakid burden. We posit that increasing *Anisakis* spp. burdens driven by marine mammal populations that are increasing in abundance could spill over into data-deficient and declining marine mammal species.

As these parasites have complex life cycles with multiple hosts, it is possible that the observed increase in *Anisakis* spp. is attributable to changes in intermediate hosts as well. Increased nutrient inputs drive plankton blooms (Beman et al., 2005), thus increasing the number of copepod intermediate hosts (Siokou-Frangou & Papathanassiou, 1991; Uriarte & Villate, 2004) available for marine mammal parasites to infect, as suggested in Fiorenza et al. (2020a). If copepods or other low-trophic-level crustaceans were previously the bottleneck in marine mammal parasite life cycles (Lafferty, 2012), this increased nutrient input could release that constraint, allowing anisakids more opportunities to survive to transmit to paratenic and definitive hosts. Similarly, fish paratenic hosts could drive the increase in several ways. Changing fishing pressures away from preferred paratenic hosts could result in a greater number of infected fish available for marine mammals to eat (Dobson & May, 1987; McCallum et al., 2005). Such a change would increase paratenic host density and could then increase infection if these hosts were previously a limiting factor (Dobson & May, 1987; Wood et al., 2010). Furthermore, if fish have moved into ranges that they previously did not inhabit due to climate change or species introductions, they could potentially increase overlap with novel marine mammal hosts, thus increasing the number of exploitable hosts in the ecosystem for marine mammal parasites (Brooks & Hoberg, 2007; Marcogliese, 2001). As anisakids include many species that collectively infect a wide range of intermediate and paratenic hosts, this could increase their prevalence (Klimpel & Palm, 2011).

Climate change could drive the observed changes in a number of ways. Increased temperatures associated with climate change are predicted to increase growth and decrease generation time in fishes (Magnuson et al., 1997), which could speed up the development of their parasites as well (Marcogliese, 2001), as suggested by Fiorenza et al. (2020a). With increasing temperatures, earlier onset of spring, and longer growing seasons, parasites with complex life cycles could increase the number of generations produced annually (Magnuson et al., 1997; Marcogliese, 2001; Measures, 1996). The resulting increase in the fecundity of some parasite species could be responsible for the increase in *Anisakis* spp. prevalence observed in this study. Increasing temperature can also reduce immunocompetence or behavioral resistance of fish hosts, which could lead to increases in abundance in anisakids (Burgess et al., 2013; Claar & Wood, 2020; Harvell et al., 2002). These predicted trends could be species-specific; however, if certain parasite species or their requisite hosts are adapted to colder climates, climate change could have the opposite effect, which may in part explain the observed differences in trends in *Anisakis* and *Pseudoterranova* spp. Additionally, climate change could result in one species succeeding over another. In general, *Anisakis* spp. use pelagic hosts (Klimpel & Palm, 2011), which could mean that, in areas that face increases in pelagic productivity (Lannuzel et al., 2020; Meier et al., 2014), *Anisakis* spp. have more hosts available to exploit. Regions that have experienced a loss of multiyear ice, like the Arctic, have the potential to increase primary productivity in pelagic environments (Lannuzel et al., 2020; Meier et al., 2014). Decreases in multiyear ice have led to a greater prevalence of younger ice, which is more permeable to light and drives phytoplankton blooms (Meier et al., 2014). These blooms may in turn increase the number of pelagic intermediate hosts in some regions (Lannuzel et al., 2020). This could serve to increase the hosts available for *Anisakis* spp., while the more benthic *Pseudoterranova* spp. (Klimpel & Palm, 2011) would not experience the same increase.

The global trend in *Pseudoterranova* spp. was nonsignificant, but fragile; it changed depending on the species and regions included in the model. When we tested for intermediate host species and FAO regions that heavily influenced the observed trend, we found that removing data for Greenland halibut (*R. hippoglossoides*) and the Northwest Atlantic resulted in significant declines in *Pseudoterranova* spp. abundance through time. When examined independently, the temporal trend for Greenland halibut showed no significant trend. *R. hippoglossoides* stocks were fished heavily until the 1990s, with catches in the Northeast Atlantic exceeding the advised limit and catches in the Northwest Atlantic proceeding relatively uncontrolled (Bowering & Nedreaas, 2000). Since then, recruitment has increased in both locations (MFRI, 2021; Treble & Nogueira, 2020), which would have allowed *R. hippoglossoides* and their parasites to increase or remain stable, which may have masked the declining trend observed across the other host species. When the data from the Northwest Atlantic were examined independently, there was a nonsignificant increase in *Pseudoterranova* spp. This suggests that the Northwest Atlantic may have experienced a slight increase in *Pseudoterranova* spp., which, when combined with global data, masks a significant decline observed across other regions. The Northwest Atlantic has experienced an increase in harbor seals and gray seals on the Atlantic coast of the United States since the enactment of the MMPA (Roman et al., 2013), and in other systems, increasing abundances of gray seals have correspondingly increased the local prevalence of anisakids in intermediate hosts (Buchmann & Kania, 2012; Galatius & Olsen, 2014; Hiby et al., 2007; Horbowy et al., 2016; Mehrdana et al., 2014). It is possible the federal protections put in place have increased the density of definitive hosts of *Pseudoterranova* spp. in the Northwest Atlantic. A similar trend is not detectable on the west coast of the United States, where pinnipeds have also been increasing, but this region of the Pacific was not well represented in our dataset.

Of the two anisakid genera, we expected *Pseudoterranova* spp. to fare better than *Anisakis* spp., given the strong recoveries of pinniped compared with cetacean populations (Magera et al., 2013). Globally, half of the pinniped populations assessed by Magera et al. (2013) were found to be significantly increasing. However, the lack of protections in place for pinniped species on an international level and a myriad of additional threats may drive an opposite trend in other, less-monitored pinniped populations, resulting in the appearance of *Pseudoterranova* spp. remaining unchanged. Pinnipeds are often caught in conflict with fisheries and have been subject to culls (Bowen & Lidgard, 2011; Olsen et al., 2018; Roman et al., 2013). Pinnipeds are also subject to harvest in some countries, a threat that many cetaceans do not face as pelagic species (Kovacs et al., 2011). Many of the Arctic seals, which overlap in range with the meta-analysis dataset, face habitat loss and other threats rooted in climate change, which may cause declines in pinniped populations (Kovacs et al., 2011). Declines in these species may go unnoticed; for example, a decline in any ice-obligate pinniped species would be difficult to detect without concerted survey efforts (Taylor et al., 2007). The lack of protections for pinnipeds on a global scale and the cumulative threats from climate change and other anthropogenic stressors may leave them more vulnerable to undetected declines, reducing the number of pinniped definitive hosts. This, in tandem with regional increases in pinnipeds in the Northwest Atlantic and elsewhere, may have leveled out the prevalence of *Pseudoterranova* spp. in the marine environment, leading to the nonsignificant trend detected in our analysis.

The prey species that both cetaceans and pinnipeds are eating have experienced an increase in *Anisakis* spp. prevalence over the past 40 years. We did not account for changes in marine mammal abundance in our analysis due to a deficit of data on population trends of all marine mammals; therefore, we could not determine whether the risk of *Anisakis* infections has increased. However, this increase suggests not only marine mammals may be facing mounting risks of *Anisakis* infections, especially cetaceans (the appropriate definitive hosts), but also pinnipeds and other dead-end hosts can nonetheless become infected (Dailey, 2001). The fragile trend in *Pseudoterranova* spp. suggests pinnipeds may face less of a burden of gastrointestinal nematodes than in the past 40 years depending on the region (i.e., outside of the Northwest Atlantic); however, the detected increase in *Anisakis* abundance in pinniped prey indicates that pinnipeds may have a greater risk of the pathology associated with *Anisakis* (Dailey, 2001). Importantly, the study period encompasses an era immediately following the protection of marine mammals from extensive hunting. The changes we detected in this study may be very different from a baseline prior to the removal of marine mammals from much of the world's oceans—it is possible that anisakids were much more abundant pre-whaling, when their definitive hosts were much more abundant. At this moment, this remains an untested hypothesis. Regardless of the past burden of anisakids, the persistent sublethal stressors on many contemporary marine mammal populations may make anisakid infection more dangerous than it would have been in the past. Marine mammals should be monitored for digestive tract helminth burdens when conducting health assessments using fecal samples, or at necropsy, to determine whether burdens of anisakids are changing accordingly. Future research using population-based models to assess the impacts of multiple stressors on endangered cetacean species could incorporate the energetic impact of gastrointestinal parasites on their hosts via increased prevalence in key prey species.

We used the information available for 113 marine mammal species, but the data used to inform these analyses are limited by low study effort for many marine mammal species. Thorough diet analyses for marine mammals over their entire range are difficult to conduct for some species and nearly impossible for others; in order to determine diet, adequate sample sizes from a representative population are required, which can be difficult to obtain, especially in pelagic cetaceans that eat and defecate at depth and rarely strand (Pauly, 1998; Trites & Spitz, 2017). As a result, for many marine mammal species, only the family of prey items is known, and we were therefore compelled to include all intermediate host species that fell within the reported family, some of which will not actually be prey of the marine mammal species in question. Additionally, it is known that geographical ranges of marine mammals can be biased by the survey method (Tyne et al., 2016; Williams et al., 2014). While density maps would have given a more accurate account of where marine mammals concentrate within their ranges, because these were not available for all species considered in this analysis, we instead chose to use the most recent range maps compiled by species experts for IUCN (2020).

For our analysis, we compiled data dating back to the 1960s and 1970s, and over this period, techniques in parasite detection and identification improved significantly (Wood & Vanhove, 2022). To achieve the statistical power needed to detect a trend in these two genera, and to include older data on parasite abundance collected at the genus level with older techniques, we performed our analysis by genus and accounted for any potential differences in detection methods in our models. However, it is important to note that we grouped together species with diverse ecologies, specific life cycles, and varying pathology. As such, we cannot detect changes in individual species, and the general trends observed in our analysis may mask differences in trends among species that are not ecologically equivalent.

While our aim was to be inclusive when determining which intermediate host species were likely to fall within marine mammal diets, there were factors we did not take into account in preparing the dataset for analysis. We did not consider shifts in marine mammal range over the 36-year period, either short term (migration) or long term (changes in range as species recover or decline). While it would have been possible to incorporate these long-term shifts for some well-studied marine mammal species, many more species are data-deficient. We therefore used the most up-to-date marine mammal ranges from IUCN (2020). Instead of incorporating seasonality in migration patterns, we erred on the side of inclusivity—if a prey species was sampled in the marine mammal's range, it was included regardless of the time of year sampled. This may be an issue in calving grounds where cetaceans are known to fast. Similarly, we did not consider seasonal or temporal shifts in diet, nor proportion of diet. Some species have had documented shifts in their diet as fish stocks change (e.g., humpback whales in the Southern Gulf of Maine). It is likely that the prey species of the marine mammals surveyed make up varying portions of their diet and may carry varying weights of importance and thus infection risk. However, as many understudied marine mammals do not include this level of detail in their diet data, we included any diet species or families each species is documented to eat regardless of the period documented and assumed each prey species was equally weighted.

CONCLUSION

We found an increase in *Anisakis* spp. and no change in *Pseudoterranova* spp. prevalence in the fish that marine mammals consume using a long-term, global meta-analysis dataset spanning nearly four decades. This period encompasses the 1986 moratorium on commercial whaling and immediately follows the 1972 enactment of the US MMPA. The observed increase in *Anisakis* spp. may reflect a global trend of increasing cetacean abundance, powered by international conservation efforts, while the lack of change in *Pseudoterranova* spp. suggests variable changes in pinniped host recovery, driven by changes in definitive host abundance or the availability of requisite intermediate hosts. The observed increase in *Anisakis* spp. should be considered when assessing the threats to marine mammals globally. Parasitism may not be the primary source of mortality in marine mammals, but it is an additional stressor in the growing list of threats that marine mammals face. The additional health and energetic burden of *Anisakis* spp. nematodes, a threat that is currently unrecognized, will be important to include when considering the impact of multiple stressors on marine mammal conservation going forward.

ACKNOWLEDGMENTS

Catrin Wendt, Katie Dobkowski, and Hyejoo Ro helped to assemble the meta-analytic database. Rob Williams and Erin Ashe contributed to the development of the analysis for geographic overlap of marine mammals and prey. Natalie C. Mastick was supported by a UW Innovation Award (to Chelsea L. Wood), a contract from Oceans Initiative (to Chelsea L. Wood), a Program

Development Grant from Washington Sea Grant (to Chelsea L. Wood), and an SAFS Scholarship from the University of Washington School of Aquatic and Fishery Sciences. Evan Fiorenza was supported by a Program Development Grant from Washington Sea Grant (to Chelsea L. Wood) and an SAFS Scholarship from the University of Washington School of Aquatic and Fishery Sciences. Chelsea L. Wood was supported by a grant from the National Science Foundation (OCE-1829509), a Sloan Research Fellowship from the Alfred P. Sloan Foundation, a UW Innovation Award, and the Univeristy of Washington Royalty Research Fund.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Fiorenza et al., 2020b) are available from Dryad: https://doi.org/10.5061/dryad.kwh70rz0z.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Mastick, Natalie C., Evan Fiorenza, and Chelsea L. Wood. 2024. “Meta-Analysis Suggests That, for Marine Mammals, the Risk of Parasitism by Anisakids Changed between 1978 and 2015.” *Ecosphere* 15(3): e4781. https://doi.org/10.1002/ecs2.4781