



Toxoplasma gondii Infection in Marine Animal Species, as a Potential Source of Food Contamination: A Systematic Review and Meta-Analysis

Ehsan Ahmadpour^{1,2} · Mohamad Taghi Rahimi³ · Altin Ghoghji⁴ · Fatemeh Rezaei⁵ · Kareem Hatam-Nahavandi⁶ · Sónia M. R. Oliveira^{7,8} · Maria de Lourdes Pereira^{7,9} · Hamidreza Majidani¹⁰ · Abolghasem Siyadatpanah¹¹ · Samira Elhamirad¹² · Wei Cong¹³ · Abdol Sattar Pagheh¹²

Received: 30 August 2021 / Accepted: 9 December 2021 / Published online: 17 January 2022

© The Author(s) under exclusive licence to Witold Stefański Institute of Parasitology, Polish Academy of Sciences 2022

Abstract

Purpose Many marine animals are infected and susceptible to toxoplasmosis, which is considered as a potential transmission source of *Toxoplasma gondii* to other hosts, especially humans. The current systematic review and meta-analysis aimed to determine the prevalence of *T. gondii* infection among sea animal species worldwide and highlight the existing gaps.

Methods Data collection was systematically done through searching databases, including PubMed, Science Direct, Google Scholar, Scopus, and Web of Science from 1997 to July 2020.

Results Our search strategy resulted in the retrieval of 55 eligible studies reporting the prevalence of marine *T. gondii* infection. The highest prevalence belonged to mustelids (sea otter) with 54.8% (95% CI 34.21–74.57) and cetaceans (whale, dolphin, and porpoise) with 30.92% (95% CI 17.85–45.76). The microscopic agglutination test (MAT) with 41 records and indirect immunofluorescence assay (IFA) with 30 records were the most applied diagnostic techniques for *T. gondii* detection in marine species.

Conclusions Our results indicated the geographic distribution and spectrum of infected marine species with *T. gondii* in different parts of the world. The spread of *T. gondii* among marine animals can affect the health of humans and other animals; in addition, it is possible that marine mammals act as sentinels of environmental contamination, especially the parasites by consuming water or prey species.

✉ Abdol Sattar Pagheh
satar2011@gmail.com; pagheh.as@bums.ac.ir

¹ Infectious and Tropical Diseases Research Center, Tabriz University of Medical Sciences, Tabriz, Iran

² Department of Parasitology and Mycology, Faculty of Medicine, Tabriz University of Medical Sciences, Tabriz, Iran

³ School of Medicine, Shahroud University of Medical Sciences, Shahroud, Iran

⁴ Department of Fisheries, Gorgan University of Agricultural Sciences and Natural Resources, Gorgan, Iran

⁵ Islamic Azad University of Chalus Branch, Chalus, Iran

⁶ School of Medicine, Iranshahr University of Medical Sciences, Iranshahr, Iran

⁷ CICECO-Aveiro Institute of Materials, University of Aveiro, Aveiro, Portugal

⁸ Hunter Medical Research Institute (HMRI), New Lambton Heights, NSW, Australia

⁹ Department of Medical Sciences, University of Aveiro, Aveiro, Portugal

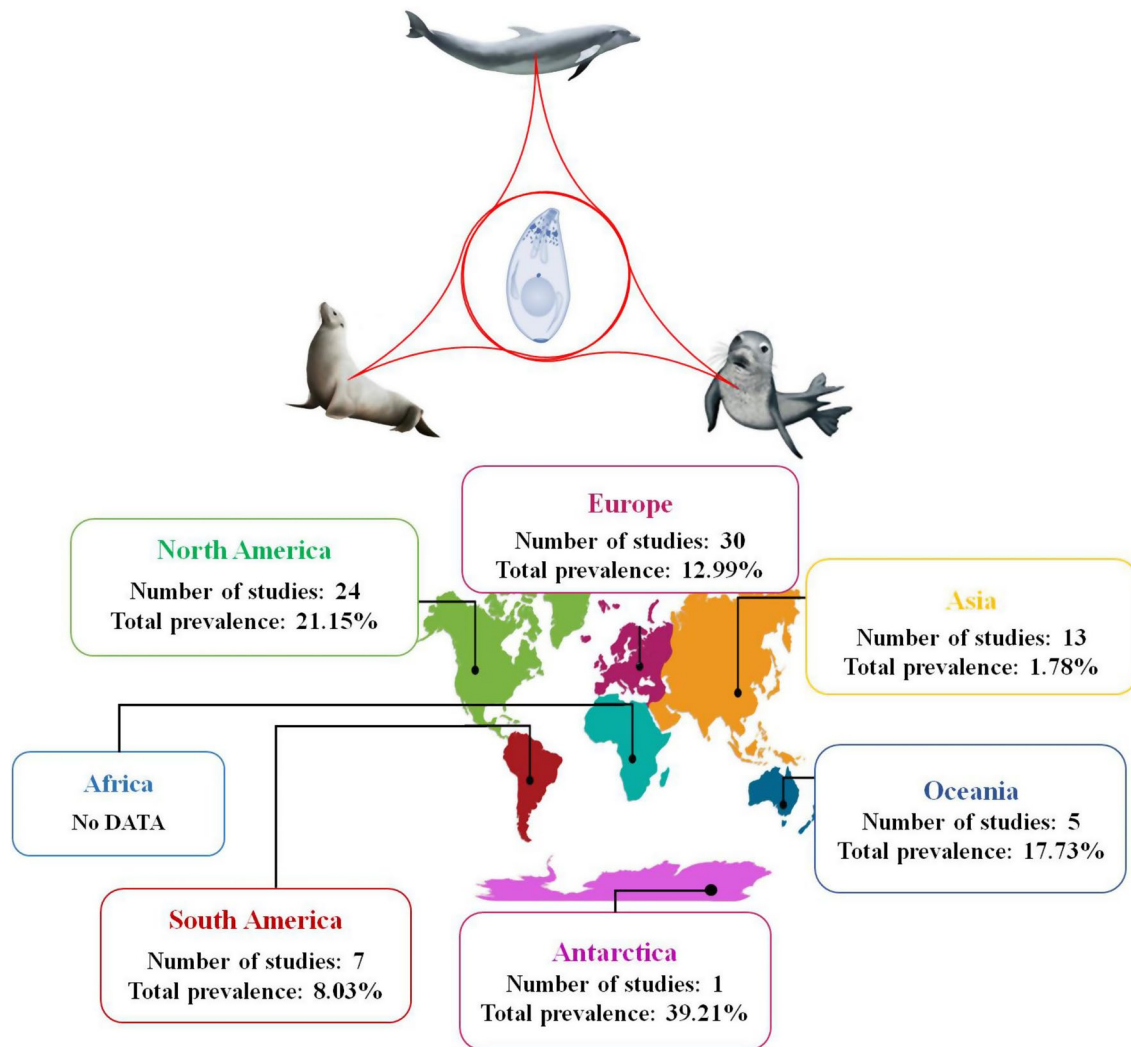
¹⁰ Department of Parasitology, Faculty of Medical Sciences, Tarbiat Modares University, Tehran, Iran

¹¹ Ferdows Paramedical School, Birjand University of Medical Sciences, Birjand, Iran

¹² Infectious Diseases Research Center, Birjand University of Medical Sciences, PO Box 9717853577, Birjand, Iran

¹³ Marine College, Shandong University, Weihai, China

Graphical Abstract



Keywords *Toxoplasma gondii* · Toxoplasmosis · Marine animals · Systematic review · Meta-analysis

Introduction

Marine species constitute a very diverse group of animals with global distribution, mostly along coastal regions or habitat [1]. The human population density in coastal areas greatly increased during the recent decades and zoonotic pathogens can be transmitted to humans directly or indirectly from marine animals [2]. Thus, the health of marine mammals can substantially influence human's well-being. Toxoplasmosis, caused by the intracellular protozoan *Toxoplasma gondii*, is a zoonotic infection with felids as definitive hosts, and a wide range of homeothermic vertebrates as intermediate hosts [3, 4]. Pregnant women and immunocompromised patients are at a higher

risk for developing the clinical disease with harsh outcomes, including congenital toxoplasmosis (hydrocephalus, chorioretinitis, and cerebral calcifications) and life-threatening encephalitis [5–7]. Understanding *T. gondii* transmission routes in wild, free-ranging marine mammals is problematic. There are three possible routes by which marine animals could become infected with *T. gondii*, including: ingestion of oocysts, ingestion of bradyzoites in tissue cysts of other intermediate hosts or vertically. Oocysts are shed via cat feces into the environment, which can readily infect several animal species [8, 9]. Small *T. gondii* oocysts show remarkable resistance to common disinfectants and remain alive in moist surroundings, even when exposed to a vast range of salinity and temperature

conditions. This environmental tolerance leads to in fast and extensive dispersal of infection, particularly following heavy rain falls. The runoff originated from rainfalls alongside wastewater outfalls being likely contaminated with stray/feral cat fecal material make a huge depot of infective oocysts, which are usually discharged into a water body, i.e., sea and ocean, posing potential risk of *T. gondii* infection in those species dwelling in marine habitats [10]. In another way, marine animals acquired infection through ingestion of *T. gondii* protozoal cyst containing numerous bradyzoites. In areas where definitive hosts are rare and the viability of oocysts are likely limited due to freezing conditions, such as the Canadian Arctic, this could explain how animals are exposed to *T. gondii*. A number of investigators have pointed out that oocysts and bradyzoites of *T. gondii* are concentrated by oysters, clams and mussels during filter-feeding activity. It is noteworthy that the role of vertical transmission of toxoplasmosis in marine animals is unknown [9]. These are highly promising findings, but the precise mode of transmission is still open to question. Experimentally, oocyst sporulation occurs in seawater, remaining infective for animals for 6–24 months, depending on the temperature [11, 12].

During the last decades, a number of studies have reported *T. gondii* infection in marine animals, such as cetaceans, pinnipeds, sirenians, and sea otters (*Enhydra lutris*) [13–16]. Disseminated clinical disease has also been documented in adult or sometimes neonate marine mammals from Europe, USA, and Australia [17–19], with some degree of morbidity observed, for example, in the sea otters [13, 20, 21] and in the Pacific harbor seal (*Phoca vitulina richardsi*) [22, 23]. Furthermore, it seems that some species have been threatened and endangered in part due to toxoplasmosis [3, 24].

The increasing amount of anthropogenic toxicants discharged into the marine environment, as well as morbillivirus infection, can suppress the immunity of marine mammals and give rise to clinical toxoplasmosis susceptibility, yet in others cases, no links to concurrent disease have been identified [25, 26]. Since *T. gondii* is a pronounced hallmark of aquatic pollution and marine species are superb sentinel animals in marine life [27–29], it would be beneficial to assess the status of *T. gondii* infection in these animals. Thus, the current systematic review and meta-analysis aimed to investigate the prevalence of *T. gondii* infection among marine animal species worldwide and highlight the existing gaps.

Materials and Methods

Search Strategy

This study was prepared and performed in accordance with the PRISMA (Preferred Reporting Items for Systematic

reviews and Meta-Analyses) statement [30]. Data were systematically searched and collected from English language databases including PubMed, Science Direct, Google Scholar, Scopus, ISI Web of Science, published from inception to 1 January, 2020 by two investigators (FR and ASP).

The search process was performed using the following keywords and medical subject headings (MeSH) terms: “*Toxoplasma gondii*”, “*Toxoplasmosis*”, “*T. gondii*” in combination with “fishes”, “marine mammals”; “oyster”, “Shellfish”, “mussels”, “dolphin”, “shark”, “crab”, “seal”, “sea lion”, “whale”, “sea otter”, “porpoise”, “shrimp”, “Manatees”, “Walruses”, “Eel”, “crayfish”, and “turtle”. To avoid missing of any paper, the reference list of relevant papers was screened manually.

Study Selection

For the first screening, the two independent authors (ASP and FR) surveyed the title and the abstract of all papers returned from the search process. To ensure the eligibility for inclusion to the systematic review, full texts of papers were also reviewed by investigators (ASP and FR), and any disagreement on articles selected was resolved.

Quality Evaluation

Selected articles were assessed according to a checklist used in previous studies [31]. This checklist was based on contents of the strengthening the reporting of observational studies in epidemiology (STROBE) checklist containing questions about various methodological aspects such as type of study, sample size, study population, data collection approaches and tools, sampling methods, variables estimation status, methodology, research objectives and demonstration of results according to the objectives [32]. For each question, a score was attributed and articles with a score of at least seven were selected articles. In addition, any disagreements with selected papers were reviewed by another author.

Selection Criteria and Data Extraction

Papers were included in the meta-analysis with the following criteria: (1) original articles; (2) studies in English language; (2) articles available in full-text; (3) studies that evaluated the prevalence of *T. gondii* infection in marine animals. On the other hand, the exclusion criteria entailed: case reports, review articles, letter to the editor, unclear or not technically acceptable diagnostic criteria, insufficient information, congress articles, as well as those with unavailable full-text. After reviewing all articles, papers without sufficient information and that did not obtain the minimum quality score were excluded.

Meta-Analysis

In this study, a forest plot was used to visualize the summarized results and heterogeneity among the included studies. The size of every square indicated the weight of every study as well as crossed lines presented confidence intervals, CI. To assess heterogeneity index, Cochran's Q test and I^2 statistics were applied. Additionally, a funnel plot was designed to determine the small study effects and their publication bias, based on Egger's regression test. The meta-analysis was conducted using Stats Direct statistical software (<http://www.statsdirect.com>). A P value less than 0.05 was considered statistically significant. Additional meta-analysis was performed based on the type of host, location and diagnostic method.

Results

A total of 5175 papers were analyzed by exploration of PubMed, Science Direct, Scopus, Google Scholar, and ISI Web of Science databases, and finally 55 records were found to be eligible for the current systematic review and meta-analysis. The searching and study selection procedures are illustrated in Fig. 1. Based on Continent, the highest number of investigations was from Europe (30 studies) with a total prevalence of 12.99%, and marine mustelids were the most infected group with 53.12%. It is also worth noting that 24 studies from North America were included in this systematic review, indicating a total prevalence of 21.15%, and an exceptionally high infection rate among cetaceans was observed in this continent (80.85%). In Asian countries, a low prevalence rate of 1.78% was reported and the pinnipeds were the most infected group with 29.2%. In South America,

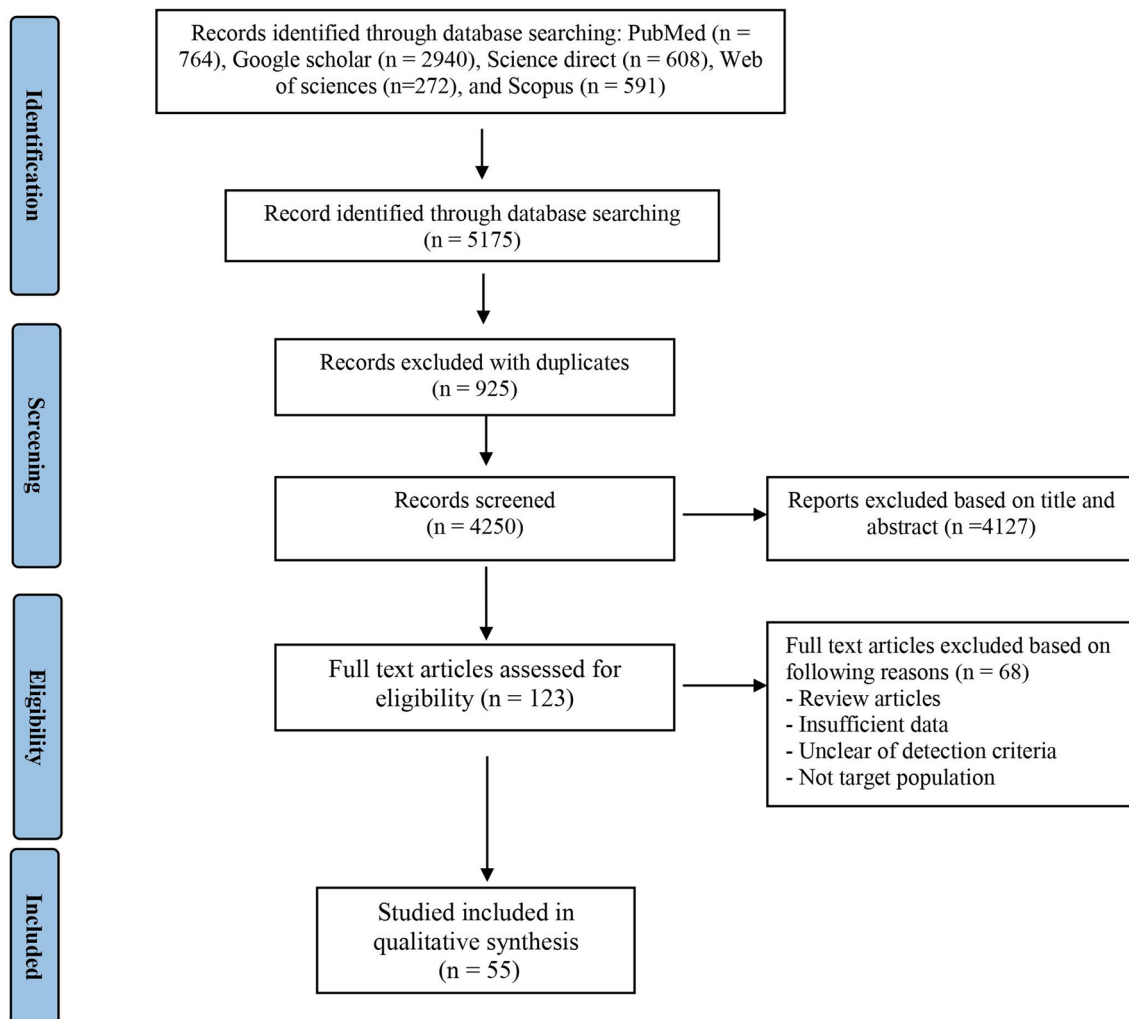


Fig. 1 Flowchart describing the study design process

a pooled prevalence of 8.03% was reported with the highest infection in cetaceans (30.35%). In Oceania, the pooled prevalence was 17.73% and cetaceans were the most infected species (26.12%). In addition, the pooled prevalence rate in Antarctica was 39.21% in pinnipeds. On the other hand, no reports were found for the North Pole and the African continent (Fig. 2).

According to Table 1, *T. gondii* infection was detected in dolphins (45 entries), whales (29 entries), seals (31 entries), sea lions (5 entries), sea otters (10 entries), porpoise (3 entries), oysters/mussels/shellfish (11 entries), fishes (4 entries), shrimp (2 entries), manatees (2 entries), walruses, eel and crayfish (single record for each) using serological and/or molecular techniques. Most reports were from the USA and Brazil with 24 records for each country, followed by Scotland (15 records), Italy (13 records), China (10 records), Spain (9 records), Canada and United Kingdom (8 records for each), Mexico (5 records), Norway and Russia (4 records for each), New Zealand (3 records), Japan (2 records) as well as single records from Iran, Turkey, Portugal, Netherlands, Peru, Australia and Solomon Islands. Altogether, eight serological methods were employed to determine *T. gondii* infection among marine animals. These include the modified agglutination test (MAT) as the most used technique (41 records), followed by immunofluorescence

antibody test (IFA) (30 records) and immunohistochemistry (IHC) (21 records). Moreover, 17 entries used conventional polymerase chain reaction (PCR), being this the most used molecular technique, followed by nested-PCR (7 records) and quantitative PCR (qPCR) (4 records). Subgroup analysis (Table 2) showed that most studies were focused on cetaceans (whale, dolphin and porpoise) (36 studies), whereas the highest prevalence rate of *T. gondii* infection belonged to marine mustelids (sea otter, 10 studies) with 54.8% (95% CI 34.21–74.57%). Pooled proportion of *T. gondii* infection in dolphin species was of 51.07%. According to Egger's test, the prevalence rates in cetaceans (P value = 0.0489) and pinnipeds (P value = 0.0004) were statistically significant.

Discussion

The present systematic review and meta-analysis aimed to determine the prevalence rate of *T. gondii* infection worldwide. The obtained data were categorized based on the species of marine animals, continents, and diagnostic techniques. Among marine animals, the prevalence of *T. gondii* infection was higher in the population of sea otters (54.8%). In a study, Miller *et al.* [33] suggested that coastal freshwater runoff is a risk factor for toxoplasmosis in southern sea otters

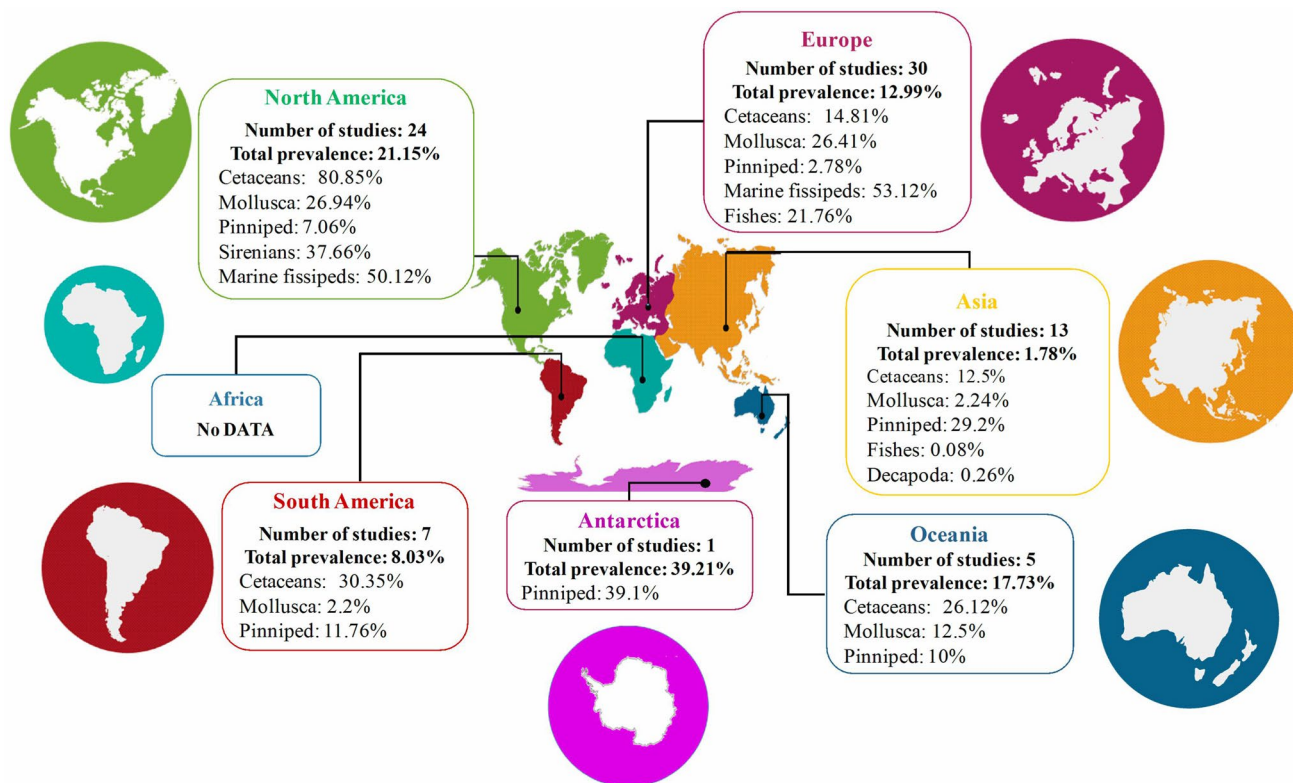


Fig. 2 Pooled prevalence of *T. gondii* in marine animal species in different continents

Table 1 Detection of *Toxoplasma gondii* in marine animals (sorted by scientific name and publication date)

Species	Location	Continent	Test	Sample size	Positive (%)	References
Dolphin						
<i>Tursiops truncatus</i>	USA	North America	MAT	141	138 (97.9)	Dubey <i>et al.</i> [17]
<i>Sousa chinensis</i>	Australia	Australia	IHC	4	4 (100)	Bowater <i>et al.</i> [47]
<i>Stenella coeruleoalba</i>	Spain	Europe	MAT	36	4 (11.1)	Cabezón <i>et al.</i> [48]
<i>Delphinus delphis</i>	Spain	Europe	MAT	4	2 (50)	Cabezón <i>et al.</i> [48]
<i>Tursiops truncatus</i>	Spain	Europe	MAT	7	4 (57.1)	Cabezón <i>et al.</i> [48]
<i>Phocoena phocoena</i>	Spain	Europe	MAT	1	1 (100)	Cabezón <i>et al.</i> [48]
<i>Grampus griseus</i>	Spain	Europe	MAT	9	0	Cabezón <i>et al.</i> [48]
<i>Tursiops aduncus</i>	Solomon Islands	Oceania	Immunoblotting	58	8 (13.8)	Omata <i>et al.</i> [49]
<i>Tursiops truncatus ponticus</i>	Russia	Europe	ELISA	59	27 (45.7)	Alekseev <i>et al.</i> [50]
<i>Tursiops truncatus</i>	USA	North America	MAT	52	27 (51.9)	Dubey <i>et al.</i> [44]
<i>Tursiops truncatus ponticus</i>	Russia	Europe	ELISA	74	39 (52.7)	Alekseev <i>et al.</i> [51]
<i>Tursiops truncatus</i>	USA	North America	MAT	7	7 (100)	Dubey <i>et al.</i> [18]
<i>Delphinus delphis</i>	United Kingdom	Europe	Sabin Feldman	21	6 (28.5)	Forman <i>et al.</i> [52]
<i>Grampus griseus</i>	United Kingdom	Europe	Sabin Feldman	1	0	Forman <i>et al.</i> [52]
<i>Lagenorhynchus acutus</i>	United Kingdom	Europe	Sabin Feldman	1	0	Forman <i>et al.</i> [52]
<i>Tursiops truncatus</i>	United Kingdom	Europe	Sabin Feldman	1	0	Forman <i>et al.</i> [52]
<i>Stenella coeruleoalba</i>	United Kingdom	Europe	Sabin Feldman	5	0	Forman <i>et al.</i> [52]
<i>Stenella coeruleoalba</i>	Italy	Europe	IFA	8	4 (50)	Di Guardo <i>et al.</i> [53]
<i>Tursiops truncatus</i>	Italy	Europe	Nested-PCR and MAT	8	7 (87.5)	Pretti <i>et al.</i> [54]
<i>Stenella coeruleoalba</i>	Italy	Europe	Nested-PCR and MAT	6	6 (100)	Pretti <i>et al.</i> [54]
<i>Inia geoffrensis</i>	Brazil	South America	MAT	95	82 (86.3)	Santos <i>et al.</i> [55]
<i>Tursiops truncatus truncatus</i>	Mexico	North America	MAT	63	55 (87.3)	Alvarado-Esquivel <i>et al.</i> [56]
<i>Tursiops truncatus gillii</i>	Mexico	North America	MAT	3	3 (100)	Alvarado-Esquivel <i>et al.</i> [56]
<i>Cephalorhynchus hectori</i>	New Zealand	Oceania	PCR	49	17 (34.7)	Roe <i>et al.</i> [57]
<i>Tursiops truncatus</i>	Spain	Europe	IFA	24	2 (8.3)	Bernal-Guadarrama <i>et al.</i> [58]
<i>Stenella coeruleoalba</i>	Italy	Europe	IFA	18	8 (44.4)	Profeta <i>et al.</i> [59]
<i>Tursiops truncatus</i>	Italy	Europe	IFA	3	2 (66.6)	Profeta <i>et al.</i> [59]
<i>Grampus griseus</i>	Scotland	Europe	IFA	7	2 (28.5)	<i>et al.</i> [26]
<i>Delphinus delphis</i>	Scotland	Europe	IFA	13	2 (15.4)	van de Velde <i>et al.</i> [26]
<i>Stenella coeruleoalba</i>	Scotland	Europe	IFA	9	0	van de Velde <i>et al.</i> [26]
<i>Lagenorhynchus albirostris</i>	Scotland	Europe	IFA	6	1 (16.6)	van de Velde <i>et al.</i> [26]
<i>Stenella coeruleoalba</i>	Italy	Europe	PCR	10	6 (60)	Pintore <i>et al.</i> [60]
<i>Tursiops truncatus</i>	Italy	Europe	PCR	1	1 (100)	Pintore <i>et al.</i> [60]
<i>Steno bredanensis</i>	Brazil	South America	IHC	3	0	Costa-Silva <i>et al.</i> [61]
<i>Lagenodelphis hosei</i>	Brazil	South America	IHC	2	0	Costa-Silva <i>et al.</i> [61]
<i>Sotalia guianensis</i>	Brazil	South America	IHC	27	1 (3.7)	Costa-Silva <i>et al.</i> [61]
<i>Tursiops truncatus</i>	Brazil	South America	IHC	4	1 (25)	Costa-Silva <i>et al.</i> [61]
<i>Pontoporia blainvillei</i>	Brazil	South America	IHC	102	0	Costa-Silva <i>et al.</i> [61]
<i>Stenella frontalis</i>	Brazil	South America	IHC	6	0	Costa-Silva <i>et al.</i> [61]
<i>Stenella longirostris</i>	Brazil	South America	IHC	5	0	Costa-Silva <i>et al.</i> [61]
<i>Stenella clymene</i>	Brazil	South America	IHC	6	0	Costa-Silva <i>et al.</i> [61]
<i>Stenella coeruleoalba</i>	Brazil	South America	IHC	2	0	Costa-Silva <i>et al.</i> [61]
<i>Delphinus delphis</i>	Brazil	South America	IHC	1	0	Costa-Silva <i>et al.</i> [61]

Table 1 (continued)

Species	Location	Continent	Test	Sample size	Positive (%)	References
<i>Delphinus delphis</i>	Brazil	South America	IHC	1	0	Costa-Silva <i>et al.</i> [61]
<i>Inia geoffrensis</i>	Brazil	South America	IHC	1	0	Costa-Silva <i>et al.</i> [61]
Whale						
<i>Balaenoptera acuto-rostrata</i>	Norway	Europe	MAT	202	0	Oksanen <i>et al.</i> [62]
<i>Delphinapterus leucas</i>	USA	North America	MAT	3	0	Dubey <i>et al.</i> [17]
<i>Globicephala melas</i>	Spain	Europe	MAT	1	0	Cabezón <i>et al.</i> [48]
<i>Orcinus orca</i>	Japan	Asia	PCR	8	1 (12.5)	Omata <i>et al.</i> [49]
<i>Delphinapterus leucas</i>	Russia	Europe	ELISA	147	7 (4.7)	Alekseev <i>et al.</i> [51]
<i>Megaptera novaeangliae</i>	United Kingdom	Europe	Sabin Feldman	1	1 (100)	Forman <i>et al.</i> [52]
<i>Ziphius cavirostris</i>	United Kingdom	Europe	Sabin Feldman	1	0	Forman <i>et al.</i> [52]
<i>Physeter macrocephalus</i>	Portugal	Europe	qPCR	5	0	Hermosilla <i>et al.</i> [63]
<i>Balaenoptera physalus</i>	Italy	Europe	IFA	1	0	van de Velde <i>et al.</i> [26]
<i>Globicephala melas</i>	Italy	Europe	IFA	1	0	van de Velde <i>et al.</i> [26]
<i>Balaenoptera physalus</i>	Scotland	Europe	IFA	1	0	van de Velde <i>et al.</i> [26]
<i>Orcinus orca</i>	Scotland	Europe	IFA	3	0	van de Velde <i>et al.</i> [26]
<i>Globicephala melas</i>	Scotland	Europe	IFA	10	4 (40)	van de Velde <i>et al.</i> [26]
<i>Balaenoptera acuto-rostrata</i>	Scotland	Europe	IFA	5	0	van de Velde <i>et al.</i> [26]
<i>Mesoplodon bidens</i>	Scotland	Europe	IFA	4	0	van de Velde <i>et al.</i> [26]
<i>Physeter macrocephalus</i>	Scotland	Europe	IFA	2	0	Alekseev <i>et al.</i> 2017 [64]
<i>Balaenoptera borealis</i>	Scotland	Europe	IFA	1	0	Iqbal <i>et al.</i> [65]
<i>Delphinapterus leucas</i>	Russia	Europe	ELISA	87	10 (11.5)	Profeta <i>et al.</i> [59]
<i>Delphinapterus leucas</i>	Canada	North America	PCR	34	15 (44.1)	Profeta <i>et al.</i> [59]
<i>Globicephala melas</i>	Italy	Europe	PCR	1	0	Pintore <i>et al.</i> [60]
<i>Kogia sima</i>	Brazil	South America	IHC	7	0	Costa-Silva <i>et al.</i> [61]
<i>Peponocephala electra</i>	Brazil	South America	IHC	5	0	Costa-Silva <i>et al.</i> [61]
<i>Globicephala macro-rhynchus</i>	Brazil	South America	IHC	3	0	Costa-Silva <i>et al.</i> [61]
<i>Physeter macrocephalus</i>	Brazil	South America	IHC	3	0	Costa-Silva <i>et al.</i> [61]
<i>Kogia breviceps</i>	Brazil	South America	IHC	2	0	Costa-Silva <i>et al.</i> [61]
<i>Megaptera novaeangliae</i>	Brazil	South America	IHC	2	0	Costa-Silva <i>et al.</i> [61]
<i>Orcinus orca</i>	Brazil	South America	IHC	2	1 (50)	Costa-Silva <i>et al.</i> [61]
<i>Mesoplodon europaeus</i>	Brazil	South America	IHC	1	0	Costa-Silva <i>et al.</i> [61]
<i>Balaenoptera physalus</i>	Italy	Europe	PCR	7	1 (14.2)	Marcet <i>et al.</i> [66]
Seals						
<i>Phoca groenlandica</i>	Norway	Europe	MAT	316	0	Oksanen <i>et al.</i> [62]
<i>Phoca hispida</i>	Norway	Europe	MAT	48	0	Oksanen <i>et al.</i> [62]
<i>Cystophora cristata</i>	Norway	Europe	MAT	78	0	Oksanen <i>et al.</i> [62]
<i>Phoca vitulina</i>	USA	North America	MAT	380	29 (7.6)	Lambourn <i>et al.</i> [67]
<i>Phoca vitulina</i>	USA	North America	MAT	311	51 (16.4)	Dubey <i>et al.</i> [17]
<i>Phoca hispida</i>	USA	North America	MAT	32	5 (15.6)	Dubey <i>et al.</i> [17]
<i>Erignathus barbatus</i>	USA	North America	MAT	8	4 (50)	Dubey <i>et al.</i> [17]
<i>Phoca largha</i>	USA	North America	MAT	9	1 (11.1)	Dubey <i>et al.</i> [17]
<i>Phoca fasciata</i>	USA	North America	MAT	14	0	Dubey <i>et al.</i> [17]
<i>Phoca groenlandica</i>	Canada	North America	MAT	112	0	Measures <i>et al.</i> [68]

Table 1 (continued)

Species	Location	Continent	Test	Sample size	Positive (%)	References
<i>Cystophora cristata</i>	Canada	North America	MAT	60	1 (1.6)	Measures <i>et al.</i> [68]
<i>Halichoerus grypus</i>	Canada	North America	MAT	122	11 (9)	Measures <i>et al.</i> [68]
<i>Phoca vitulina</i>	Canada	North America	MAT	34	3 (8.8)	Measures <i>et al.</i> [68]
<i>Phoca vitulina stejnegeri</i>	Japan	Asia	ELISA	77	3 (3.9)	Fujii <i>et al.</i> [9]
<i>Phoca vitulina vitulina</i>	Spain	Europe	MAT	56	3 (5.3)	Cabezón <i>et al.</i> [48]
<i>Halichoerus grypus</i>	Spain	Europe	MAT	47	11 (23.4)	Cabezón <i>et al.</i> [48]
<i>Pusa hispida</i>	Canada	North America	DAT	788	80 (10.1)	Simon <i>et al.</i> [69]
<i>Erignathus barbatus</i>	Canada	North America	DAT	20	2 (10)	Simon <i>et al.</i> [69]
<i>Phoca vitulina</i>	Canada	North America	DAT	9	2 (22.2)	Simon <i>et al.</i> [69]
<i>Leptonychotes weddellii</i>	Antarctic Peninsula	South America	DAT	31	13 (41.9)	Rengifo-Herrera <i>et al.</i> [70]
<i>Mirounga leonina</i>	Antarctic Peninsula	South America	DAT	13	10 (76.9)	Rengifo-Herrera <i>et al.</i> [70]
<i>Lobodon carcinophaga</i>	Antarctic Peninsula	South America	DAT	2	1 (50)	Rengifo-Herrera <i>et al.</i> [70]
<i>Arctocephalus gazella</i>	Antarctic Peninsula	South America	DAT	165	4 (2.4)	Rengifo-Herrera <i>et al.</i> [70]
<i>Arctocephalus gazella</i>	Antarctica	Antarctica	DAT	21	12 (57.1)	Jensen <i>et al.</i> [71]
<i>Leptonychotes weddellii</i>	Antarctica	Antarctica	DAT	33	17 (51.5)	Jensen <i>et al.</i> [71]
<i>Mirounga leonina</i>	Antarctica	Antarctica	DAT	48	11 (22.9)	Jensen <i>et al.</i> [71]
<i>Arctocephalus australis</i>	Peru	South America	IFA	27	0	Jankowski <i>et al.</i> [72]
<i>Halichoerus grypus</i>	Scotland	Europe	IFA	13	0	van de Velde <i>et al.</i> [26]
<i>Phoca vitulina</i>	Scotland	Europe	IFA	17	2 (11.7)	van de Velde <i>et al.</i> [26]
<i>Phoca vitulina richardsi</i>	Alaska	North America	IFA	34	0	Bauer <i>et al.</i> [73]
<i>Pusa caspica</i>	Iran	Asia	MAT	36	30 (83.3)	Namroodi <i>et al.</i> [74]
Sea lions						
<i>Zalophus californianus</i>	USA	North America	MAT	45	19 (42.2)	Dubey <i>et al.</i> [17]
<i>Otaria flavescens</i>	Mexico	North America	MAT	2	0	Alvarado-Esquivel <i>et al.</i> [56]
<i>Zalophus californianus</i>	Mexico	North America	MAT	4	2 (50)	Alvarado-Esquivel <i>et al.</i> [56]
<i>Zalophus californianus</i>	USA	North America	IFA	1630	46 (2.8)	Carlson-Bremer <i>et al.</i> [75]
<i>Phocartos hookeri</i>	New Zealand	Oceania	ELISA	50	5 (10)	Michael <i>et al.</i> [76]
Sea otters						
<i>Lontra canadensis</i>	USA	North America	LAT	103	46 (44.6)	Tocidlowski <i>et al.</i> [77]
<i>Enhydra lutris nereis</i>	USA	North America	IFA	223	115 (51.5)	Miller <i>et al.</i> [78]
<i>Enhydra lutris nereis</i>	USA	North America	IFA	80	29 (36.2)	Miller <i>et al.</i> [78]
<i>Enhydra lutris kenyoni</i>	USA	North America	IFA	21	8 (38.1)	Miller <i>et al.</i> [78]
<i>Enhydra lutris kenyoni</i>	USA	North America	IFA	65	0	Miller <i>et al.</i> [78]
<i>Enhydra lutris nereis</i>	USA	North America	Microscopic test	35	15 (42.8)	Miller <i>et al.</i> [79]
<i>Enhydra lutris</i>	USA	North America	MAT	145	107 (73.7)	Dubey <i>et al.</i> [17]
<i>Lontra canadensis</i>	USA	North America	IFA	40	7 (17.5)	Gaydos <i>et al.</i> [80]
<i>Lutra lutra</i>	Scotland	Europe	IFA	32	17 (53.1)	van de Velde <i>et al.</i> [26]
<i>Enhydra lutris kenyoni</i>	USA	North America	MAT	70	65 (92.8)	Verma <i>et al.</i> [81]
Porpoise						
<i>Phocoena phocoena</i>	United Kingdom	Europe	Sabin Feldman	70	1 (1.4)	Forman <i>et al.</i> [52]
<i>Phocoena phocoena</i>	Netherlands	Europe	MAT	31	4 (12.9)	van de Velde <i>et al.</i> [26]
<i>Phocoena phocoena</i>	Scotland	Europe	IFA	98	2 (2)	van de Velde <i>et al.</i> [26]
Oysters/mussels/shellfish						
<i>Mytella guyanensis</i>	Brazil	South America	Nested PCR	300	0	Esmerini <i>et al.</i> [82]

Table 1 (continued)

Species	Location	Continent	Test	Sample size	Positive (%)	References
<i>Crassostrea rhizophorae</i>	Brazil	South America	Nested PCR	300	10 (3.3)	Esmerini <i>et al.</i> [82]
<i>Mytilus galloprovincialis</i>	Turkey	Europe	HRM	53	21 (39.6)	Aksoy <i>et al.</i> [37]
<i>Ostrea concha</i>	China	Asia	PCR	398	0	Zhang <i>et al.</i> [83]
<i>Mytilus galloprovincialis</i>	Italy	Europe	qPCR	53	7 (13.2)	Marangi <i>et al.</i> [84]
<i>Crassostrea virginica</i>	USA	North America	PCR	230	4 (1.7)	Marquis <i>et al.</i> [85]
<i>Crassostrea rhizophorae</i>	Brazil	South America	PCR	624	17 (2.7)	Ribeiro <i>et al.</i> [86]
Oysters	China	Asia	Nested PCR	998	26 (2.6)	Cong <i>et al.</i> [87]
<i>Perna canaliculus</i>	New Zealand	Oceania	Nested PCR	104	13 (12.5)	Coupe <i>et al.</i> [88]
<i>Mytilus edulis</i>	China	Asia	Nested PCR	2215	55 (2.4)	Cong <i>et al.</i> [89]
<i>Crassostrea virginica</i>	USA	North America	qPCR	1440	446 (30.9)	Marquis <i>et al.</i> [90]
Fishes						
<i>Carassius auratus</i>	China	Asia	PCR	309	0	Zhang <i>et al.</i> [83]
<i>Cyprinus carpio</i>	China	Asia	PCR	309	0	Zhang <i>et al.</i> [83]
<i>Hypophthalmichthys molitrix</i>	China	Asia	PCR	456	1 (0.2)	Zhang <i>et al.</i> [83]
Fishes	Italy	Europe	qPCR	147	32 (21.7)	Marino <i>et al.</i> [91]
Shrimp						
<i>Penaeus monodon</i> Fabricius	China	Asia	PCR	426	0	Zhang <i>et al.</i> [83]
<i>Macrobrachium nipponense</i>	China	Asia	PCR	813	1 (0.1)	Zhang <i>et al.</i> [83]
Manatees						
<i>Trichechus manatus</i>	Mexico	North America	MAT	3	0	Alvarado-Esquivel <i>et al.</i> [56]
<i>Trichechus inunguis</i>			MAT	74	29 (39.1)	Mathews <i>et al.</i> [15]
Walruses						
<i>Odobenus rosmarus</i>	USA	North America	MAT	53	3 (5.6)	Dubey <i>et al.</i> [17]
Eel						
<i>Monopterus albus</i>	China	Asia	PCR	98	0	Zhang <i>et al.</i> [83]
Crayfish						
<i>Procambarus clarkii</i>	China	Asia	PCR	618	4 (0.64)	Zhang <i>et al.</i> [83]

IHC immunohistochemistry, IFA immunofluorescence antibody test, DAT direct agglutination test, LAT latex agglutination test, HRM real time PCR/high-resolution melting analysis, IHAT indirect hemagglutination test

(*Enhydra lutris nereis*) in southern California. Furthermore, it has been shown that exposure to *T. gondii* among sea otters was highly influenced by individual animal prey choice and habitat use [34]. Toxoplasmosis had considerable morbidity and mortality rates in the sea otter [35]. *T. gondii* encephalitis in sea otters causes high mortality rate and is responsible for slow population recovery, particularly for the endangered Southern sea otter [27]. In addition, cetaceans were the most infected animals in North America, South America, and Oceania.

Modified agglutination test (MAT) was the most applied diagnostic assay for *T. gondii* detection in marine animals. This technique is widely employed in research of toxoplasmosis in humans and in all species of animals because it is considered as a rapid and simple approach without the requirement for special facilities [36]. Molecular methods, particularly polymerase chain reaction (PCR) and nested PCR, were used in marine animals usually as a food source for humans like fishes, shrimp, oysters, and crayfish, amongst others. Some studies indicate that consumption of contaminated raw shellfish and mussels can be considered a

Table 2 Pooled prevalence of *Toxoplasma* infection in marine animals and subgroup analyses

Types of animals (species)	No. of studies	Prevalence (95% CI)	Heterogeneity		Egger's test	
			I_2	Q	T	P value
<i>Cetaceans</i> (whale, dolphin, porpoise)	36	30.92 (17.85–45.76)	97.5	1377.98	4.87	0.0489
<i>Pinniped</i> (seals, sea lions, walrus)	18	12.16 (7.28–18.09)	96.3	460.63	4.59	0.0004
<i>Sirenians</i> (manatees)	2	26.51 (2.46–63.69)	–	2.62	–	–
<i>Marine fissipeds</i> (sea otter)	6	54.8 (34.21–74.57)	96.6	147.12	–0.42	0.9593
<i>Fishes</i> (fish, eel)	5	1.64 (0.02–7.22)	96.2	105.71	4.34	0.1065
<i>Decapoda</i> (crayfish, shrimp)	3	0.26 (0.03–0.73)	57.1	4.35	–	–
<i>Mollusca</i> (oysters, mussels, shellfish)	10	7.45 (2.06–15.81)	99.1	962.83	7.56	0.067

significant health danger due to their ability to infect a wide variety of hosts such as other marine animals and humans. However, they are particularly at risk for *T. gondii* infection, and therefore, they can be considered a bioindicator for monitoring waterborne pathogens [37, 38]. The high prevalence rate of *T. gondii* in the examined marine species may indicate that the nearby terrestrial environment in the studied area was heavily contaminated by *T. gondii*, and consequently, contamination was transferred to the aquatic environment. Furthermore, marine hosts may associate with *T. gondii* infection as paratenic hosts in some area [39]. Hence, contamination of marine animal species is an important bioindicator for contamination of aquatic environments.

Each cat, as final host for *T. gondii*, shed over 3–810 million oocysts. The sporulation of the oocysts takes 1–5 days, and they can remain infective in the soil for up to 18 months [40]. Furthermore, experiments showed that oocysts of *T. gondii* can sporulate in sea water and survive at 4 °C for 24 months and then infect mice [12]. One important factor in infected hosts is the strain of the parasite, which plays a major role in the toxoplasmosis prognosis. So far, the genotypes *T. gondii* were classified as classical types I, II, III, mix/recombinant atypical, and African lineages [41]. Comparison between *T. gondii* genotypes from the marine and terrestrial environments would help clarify routes and mechanisms of land-sea transmission. Type I strains, which are highly virulent and pathogenic, can lead to acquired ocular toxoplasmosis in individuals with disseminated congenital form of *T. gondii* [42, 43]. Aksoy et al. [37] reported *T. gondii* type 1 infection in *Mytilus galloprovincialis* (Mediterranean mussel), one of the most consumed shellfish in Turkey. The authors suggested that these types of contaminated seafood may be involved in the transmission of the parasite to humans and other hosts. Type II *T. gondii* strains are the vast majority of human infections and have a worldwide distribution. Type II strains are causative agents for numerous asymptomatic toxoplasmosis cases in Europe, it can be pathogenic for two important categories of subjects, namely immature fetuses and immunocompromised individuals [43]. On the basis of a previous study, Dubey et al. [44] showed Type II *T. gondii* from a striped dolphin (*Stenella coeruleoalba*) in Costa Rica. It is noteworthy that Type III *T. gondii* in mice are classified as avirulent strain. Study carried out by Hancock et al. [45] showed the first report of type III *T. gondii* in a Hawaiian monk seal. This genotype was determined to be restriction fragment length polymorphisms (RFLP) of the SAG2 gene. On the other hand, it has previously been shown that Type X strains of *T. gondii* are virulent for southern sea otters from coastal California [27]. Additionally, one interesting study has demonstrated Type X strains of *T. gondii* in canids, coastal-dwelling felids, nearshore-dwelling sea otters, and marine bivalve. It is assumed that contaminated runoff to feline faecal rapidly reaches sea from lands, and

otters could be infected with *T. gondii* via the consumption of filter-feeding marine invertebrates [46].

The prevalence rate of marine *T. gondii* infection in various regions of the world was very different, and ranged from 0 to 100%. These differences may originate from different types of marine animals, sample sizes, and diagnostic approaches in the reviewed studies. Regarding continents, North America showed the highest *T. gondii* infection in marine animals that may suggest the level of fecal contamination of the soil and water reservoirs. Our analysis also showed that there is either no available data (Africa) or very limited literature (Antarctica, Oceania, and South America) on the prevalence of *T. gondii* infection in significant parts of the globe. Therefore, it is essential to conduct more studies to determine the putative role of *T. gondii* on marine species. The main limitation expressed in the included studies regarding prevalence of *T. gondii* infection in marine animal species was related to the use of different diagnostic methods with varying sensitivity and specificity due to their great impact on the results. The use of an accurate and reliable technique can help to correctly interpret the results of *T. gondii* prevalence in marine species in different parts of the world.

Conclusion

The results of current study indicated that the global prevalence rate of *T. gondii* infection was high in marine animals. It is well demonstrated that *T. gondii* parasite has a very successful adaptation in aquatic environments. Despite the worldwide range and broad marine animals host record of *T. gondii* infection, there was no evidence regarding toxoplasmosis in these animals in most parts of the world. Therefore, it is necessary to develop surveillance for detection of *T. gondii* in aquatic animals in different regions with appropriate molecular and serological techniques. It is also important to know the ecology of this parasite in aquatic environment to design appropriate strategies for monitoring, controlling, and prevention of the transmission of toxoplasmosis to humans or other hosts.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11686-021-00507-z>.

Acknowledgements Maria de Lourdes Pereira acknowledge project CICECO-Aveiro Institute of Materials, UIDB/50011/2020 and UIDP/50011/2020.

Author Contributions Conceptualization, ASP and EA; methodology, ASP, FR, and MTR; formal analysis, EA, AG and SMO; investigation, HM, AS, and MLP; data curation, EA and MLP; writing original draft preparation, ASP, MTR, HM; writing-review and editing, EA, MLP,

and ASP; all authors have read and agreed to the published version of the manuscript.

Declarations

Conflict of Interest The authors declare that there is no conflict of interest regarding the publication of this article.

Availability of Data and Material Data supporting the conclusions of this article are included within the article.

References

- Mikaelian I, Boisclair J, Dubey J, Kennedy S, Martineau D (2000) Toxoplasmosis in beluga whales (*Delphinapterus leucas*) from the St Lawrence estuary: two case reports and a serological survey. *J Comp Pathol* 122(1):73–76. <https://doi.org/10.1053/jcpa.1999.0341>
- Bossart GD (2006) Marine mammals as sentinel species for oceans and human health. *Oceanography* 19(2):134–137. <https://doi.org/10.1177/0300985810388525>
- Aguirre AA, Longcore T, Barbieri M, Dabritz H, Hill D, Klein PN et al (2019) The one health approach to toxoplasmosis: epidemiology, control, and prevention strategies. *Eco Health* 16(2):378–390. <https://doi.org/10.1007/s10393-019-01405-7>
- Dubey J (2004) Toxoplasmosis—a waterborne zoonosis. *Vet Parasitol* 126(1–2):57–72. <https://doi.org/10.1016/j.vetpar.2004.09.005>
- Hoseini SA, Dehgani SM, Daryani A, Gholami S, Ebrahimi F, Pagheh AS, Arefkhan N (2014) Serological survey of toxoplasmosis in pregnant women. *J Maz Univ Med Sci* 24(114):146–150
- Safarpour H, Cevik M, Zarean M, Barac A, Hatam-Nahavandi K, Rahimi MT et al (2020) Global status of *Toxoplasma gondii* infection and associated risk factors in people living with HIV. *AIDS* 34(3):469–474. <https://doi.org/10.1097/QAD.0000000000002424>
- Anvari D, Sharif M, Sarvi S, Aghayan SA, Gholami S, Pagheh AS, Hosseini SA, Saberi R et al (2019) Seroprevalence of *Toxoplasma gondii* infection in cancer patients: a systematic review and meta-analysis. *Microb Pathog* 129:30–42. <https://doi.org/10.1016/j.micpath.2019.01.040>
- Djurkovic-Djakovic O, Dupouy-Camet J, Van der Giessen J, Dubey JP (2019) Toxoplasmosis: overview from a one health perspective. *Food Waterborne Parasitol* 15:e00054. <https://doi.org/10.1016/j.fawpar.2019.e00054>
- Fujii K, Kakumoto C, Kobayashi M, Saito S, Kariya T, Watanabe Y et al (2007) Seroepidemiology of *Toxoplasma gondii* and *Neospora caninum* in seals around Hokkaido, Japan. *J Vet Med Sci* 69(4):393–398. <https://doi.org/10.1292/jvms.69.393>
- Fayer R, Dubey JP, Lindsay DS (2004) Zoonotic protozoa: from land to sea. *Trends Parasitol* 20(11):531–536. <https://doi.org/10.1016/j.pt.2004.08.008>
- Lindsay DS, Collins MV, Mitchell SM, Cole RA, Flick GJ, Wetch CN et al (2003) Sporulation and survival of *Toxoplasma gondii* oocysts in seawater. *J Eukaryot Microbiol* 50:687–688. <https://doi.org/10.1111/j.1550-7408.2003.tb00688.x>
- Lindsay DS, Dubey J (2009) Long-term survival of *Toxoplasma gondii* sporulated oocysts in seawater. *J Parasitol* 95(4):1019–1020. <https://doi.org/10.1645/GE-1919.1>
- Cole RA, Lindsay D, Howe D, Roderick CL, Dubey J, Thomas N et al (2000) Biological and molecular characterizations of *Toxoplasma gondii* strains obtained from southern sea otters (*Enhydra*

- lutris nereis*). J Parasitol 86(3):526–530. [https://doi.org/10.1645/0022-3395\(2000\)086\[0526:BAMCOT\]2.0.CO;2](https://doi.org/10.1645/0022-3395(2000)086[0526:BAMCOT]2.0.CO;2)
14. Ubey JP, Murata FH, Cerqueira-Cézar CK, Kwok OC, Grigg ME (2020) Recent epidemiologic and clinical importance of *Toxoplasma gondii* infections in marine mammals: 2009–2020. Vet Parasitol. <https://doi.org/10.1016/j.vetpar.2020.109296>
 15. Mathews PD, Da Silva VM, Rosas FC, Neto JAdA, Lazzarini SM, Ribeiro DC et al (2012) Occurrence of antibodies to *Toxoplasma gondii* and *Lepstospira* spp. in manatees (*Trichechus inunguis*) of the Brazilian Amazon. J Zoo Wildl Med 43(1):85–88. <https://doi.org/10.1638/2011-0178.1>
 16. Oksanen A, Åsbakk K, Prestrud K, Aars J, Derocher A, Tryland M et al (2009) Prevalence of antibodies against *Toxoplasma gondii* in polar bears (*Ursus maritimus*) from Svalbard and East Greenland. J Parasitol 95(1):89–94. <https://doi.org/10.1645/GE-1590.1>
 17. Dubey J, Zarnke R, Thomas N, Wong S, Van Bonn W, Briggs M et al (2003) *Toxoplasma gondii*, *Neospora caninum*, *Sarcocystis neurona*, and *Sarcocystis canis*-like infections in marine mammals. Vet Parasitol 116(4):275–296. [https://doi.org/10.1016/s0304-4017\(03\)00263-2](https://doi.org/10.1016/s0304-4017(03)00263-2)
 18. Dubey J, Mergl J, Gehring E, Sundar N, Velmurugan G, Kwok O et al (2009) Toxoplasmosis in captive dolphins (*Tursiops truncatus*) and walrus (*Odobenus rosmarus*). J Parasitol 95(1):82–85. <https://doi.org/10.1645/GE-1764.1>
 19. Miller M, Conrad P, James E, Packham A, Toy-Choutka S, Murray MJ et al (2008) Transplacental toxoplasmosis in a wild southern sea otter (*Enhydra lutris nereis*). Vet Parasitol 153(1–2):12–18. <https://doi.org/10.1016/j.vetpar.2008.01.015>
 20. Kreuder C, Miller M, Jessup D, Lowenstine LJ, Harris M, Ames J et al (2003) Patterns of mortality in southern sea otters (*Enhydra lutris nereis*) from 1998–2001. J Wildl Dis 39(3):495–509. <https://doi.org/10.7589/0090-3558-39.3.495>
 21. Thomas N, Dubey J, Lindsay D, Cole RA, Meteyer C (2007) Protozoal meningoencephalitis in sea otters (*Enhydra lutris*): a histopathological and immunohistochemical study of naturally occurring cases. J Comp Pathol 137(2–3):102–121. <https://doi.org/10.1016/j.jcpa.2007.05.001>
 22. Miller MA, Sverlow K, Crosbie PR, Barr BC, Lowenstine LJ, Gulland FM et al (2001) Isolation and characterization of two parasitic protozoa from a Pacific harbor seal (*Phoca vitulina richardsi*) with mening oencephalomyelitis. J Parasitol 87(4):816–822. [https://doi.org/10.1645/0022-3395\(2001\)087\[0816:IACOTP\]2.0.CO;2](https://doi.org/10.1645/0022-3395(2001)087[0816:IACOTP]2.0.CO;2)
 23. Pelt RV, Dieterich R (1973) Staphylococcal infection and toxoplasmosis in a young harbor seal. J Wildl Dis 9(3):258–261. <https://doi.org/10.7589/0090-3558-9.3.258>
 24. Van Wormer E, Fritz H, Shapiro K, Mazet JAK, Conrad PA (2013) Molecules to modeling: *Toxoplasma gondii* oocysts at the human–animal–environment interface. Comp Immunol Microbiol Infect Dis 36(3):217–231. <https://doi.org/10.1016/j.cimid.2012.10.006>
 25. Mazzariol S, Marcer F, Mignone W, Serracca L, Gorla M, Marsili L et al (2012) Dolphin *Morbillivirus* and *Toxoplasma gondii* coinfection in a Mediterranean fin whale (*Balaenoptera physalus*). BMC Vet Res 8(1):1–5. <https://doi.org/10.1186/1746-6148-8-20>
 26. van de Velde N, Devleeschauwer B, Leopold M, Begeman L, Ijs-seldijk L, Hiemstra S et al (2016) *Toxoplasma gondii* in stranded marine mammals from the North Sea and Eastern Atlantic Ocean: findings and diagnostic difficulties. Vet Parasitol 230:25–32. <https://doi.org/10.1016/j.vetpar.2016.10.021>
 27. Conrad PA, Miller M, Kreuder C, James E, Mazet J, Dabritz H et al (2005) Transmission of *Toxoplasma*: clues from the study of sea otters as sentinels of *Toxoplasma gondii* flow into the marine environment. Int J Parasitol 35(11–12):1155–1168. <https://doi.org/10.1016/j.ijpara.2005.07.002>
 28. Jessup DA, Miller M, Ames J, Harris M, Kreuder C, Conrad PA et al (2004) Southern sea otter as a sentinel of marine ecosystem health. EcoHealth 1(3):239–245. <https://doi.org/10.1007/s10393-004-0093-7>
 29. Stewart JR, Gast RJ, Fujioka RS, Solo-Gabriele HM, Meschke JS, Amaral-Zettler LA et al (2008) The coastal environment and human health: microbial indicators, pathogens, sentinels and reservoirs. J Environ Health 7(2):1–14. <https://doi.org/10.1186/1476-069X-7-S2-S3>
 30. Moher D, Liberati A, Tetzlaff J, Altman DG (2010) Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. Int J Surg 8(5):336–341. <https://doi.org/10.1016/j.ijsu.2010.02.007>
 31. Moosazadeh M, Nekoei-Moghadam M, Emrani Z, Amiresmaili M (2014) Prevalence of unwanted pregnancy in Iran: a systematic review and meta-analysis. Int J Health Plan Manag 29(3):e277–e290. <https://doi.org/10.1002/hpm.2184>
 32. Von Elm E, Altman DG, Egger M, Pocock SJ, Gøtzsche PC, Vandenbroucke JP (2007) The Strengthening the Reporting of Observational Studies in Epidemiology (STROBE) statement: guidelines for reporting observational studies. Bull World Health Organ 85:867–872. <https://doi.org/10.1016/j.ijju.2014.07.013>
 33. Miller M, Gardner I, Kreuder C, Paradies D, Worcester K, Jessup D et al (2002) Coastal freshwater runoff is a risk factor for *Toxoplasma gondii* infection of southern sea otters (*Enhydra lutris nereis*). Int J Parasitol 32(8):997–1006. [https://doi.org/10.1016/s0020-7519\(02\)00069-3](https://doi.org/10.1016/s0020-7519(02)00069-3)
 34. Johnson CK, Tinker MT, Estes JA, Conrad PA, Staedler M, Miller MA et al (2009) Prey choice and habitat use drive sea otter pathogen exposure in a resource-limited coastal system. Proc Natl Acad Sci 106(7):2242–2247. <https://doi.org/10.1073/pnas.0806449106>
 35. Shapiro K, Miller M, Mazet J (2012) Temporal association between land-based runoff events and California sea otter (*Enhydra lutris nereis*) protozoal mortalities. J Wildl Dis 48(2):394–404. <https://doi.org/10.7589/0090-3558-48.2.394>
 36. Packham AE, Sverlow KW, Conrad PA, Loomis EF, Rowe JD, Anderson ML et al (1998) A modified agglutination test for *Neospora caninum*: development, optimization, and comparison to the indirect fluorescent-antibody test and enzyme-linked immunosorbent assay. Clin Diagn Lab Immunol 5(4):467–473. <https://doi.org/10.1128/CDLI.5.4.467-473.1998>
 37. Aksoy U, Marangi M, Papini R, Ozkoc S, Delibas SB, Giangaspero A (2014) Detection of *Toxoplasma gondii* and *Cyclospora cayatanensis* in *Mytilus galloprovincialis* from Izmir Province coast (Turkey) by real time PCR/high-resolution melting analysis (HRM). Food Microbiol 44:128–135. <https://doi.org/10.1016/j.fm.2014.05.012>
 38. Arkush KD, Miller MA, Leutenegger CM, Gardner IA, Packham AE, Heckerroth AR et al (2003) Molecular and bioassay-based detection of *Toxoplasma gondii* oocyst uptake by mussels (*Mytilus galloprovincialis*). Int J Parasitol 33(10):1087–1097. [https://doi.org/10.1016/s0020-7519\(03\)00181-4](https://doi.org/10.1016/s0020-7519(03)00181-4)
 39. Shapiro K, Bahia-Oliveira L, Dixon B, Dumètre A, de Wit LA, VanWormer E et al (2019) Environmental transmission of *Toxoplasma gondii*: oocysts in water, soil and food. Food Waterborne Parasitol 15:e00049. <https://doi.org/10.1016/j.fawpar.2019.e00049>
 40. Dubey J, Jones J (2008) *Toxoplasma gondii* infection in humans and animals in the United States. Int J Parasitol 38(11):1257–1278. <https://doi.org/10.1016/j.ijpara.2008.03.007>
 41. Hosseini S, Amouei A, Sharif M, Sarvi S, Galal L, Javidnia J et al (2019) Human toxoplasmosis: a systematic review for genetic diversity of *Toxoplasma gondii* in clinical samples. Epidemiol Infect 147:e36. <https://doi.org/10.1017/S0950268818002947>
 42. Ahmadpour E, Sarvi S, Soteh MBH, Sharif M, Rahimi MT, Valad R et al (2017) Enhancing immune responses to a DNA vaccine encoding *Toxoplasma gondii* GRA14 by calcium phosphate nanoparticles as an adjuvant. Immunol Lett 185:40–47. <https://doi.org/10.1016/j.imlet.2017.03.006>

43. Dardé M (2008) *Toxoplasma gondii*, “new” genotypes and virulence. *Parasite* 15(3):366–371. <https://doi.org/10.1051/parasite/2008153366>
44. Dubey J, Fair P, Sundar N, Velmurugan G, Kwok OCH, McFee W et al (2008) Isolation of *Toxoplasma gondii* from bottlenose dolphins (*Tursiops truncatus*). *J Parasitol* 94(4):821–823. <https://doi.org/10.1645/GE-1444.1>
45. Hancock K, Thiele LA, Zajac AM, Elvinger F, Lindsay DS (2005) Prevalence of antibodies to *Toxoplasma gondii* in raccoons (*Procyon lotor*) from an urban area of Northern Virginia. *J Parasitol* 91(3):694–695. <https://doi.org/10.1645/GE-443R>
46. Miller M, Miller W, Conrad PA, James E, Melli A, Leutenegger C et al (2008) Type X *Toxoplasma gondii* in a wild mussel and terrestrial carnivores from coastal California: new linkages between terrestrial mammals, runoff and toxoplasmosis of sea otters. *Int J Parasitol* 38(11):1319–1328. <https://doi.org/10.1016/j.ijpara.2008.02.005>
47. Bowater RO, Norton J, Johnson S, Hill B, Odonoghue P, Prior H (2003) Toxoplasmosis in Indo-Pacific humpbacked dolphins (*Sousa chinensis*), from Queensland. *Aust Vet J* 81(10):627–632. <https://doi.org/10.1111/j.1751-0813.2003.tb12509.x>
48. Cabezón O, Resendes A, Domingo M, Raga J, Agustí C, Alegre F et al (2004) Seroprevalence of *Toxoplasma gondii* antibodies in wild dolphins from the Spanish Mediterranean coast. *J Parasitol* 90(3):643–644. <https://doi.org/10.1645/GE-257R>
49. Omata Y, Hammond T, Itoh K, Murata K (2005) Antibodies against *Toxoplasma gondii* in the Pacific bottlenose dolphin (*Tursiops aduncus*) from the Solomon Islands. *J Parasitol* 91(4):965–967. <https://doi.org/10.1645/GE-3457RN.1>
50. Alekseev AY, Rozanova E, Ustinova E, Tumanov YI, Kuvshinova I, Shestopalov A (2007) The prevalence of antibodies to morbilliviruses, *Brucella*, and *Toxoplasma* in the Black Sea bottlenose dolphin *Tursiops truncatus ponticus* maintained in captivity. *Russ J Mar Biol* 33(6):425–428
51. Alekseev AY, Reguzova AY, Rozanova E, Abramov A, Tumanov YV, Kuvshinova I et al (2009) Detection of specific antibodies to morbilliviruses, *Brucella* and *Toxoplasma* in the Black Sea dolphin *Tursiops truncatus ponticus* and the beluga whale *Delphinapterus leucas* from the Sea of Okhotsk in 2002–2007. *Russ J Mar Biol* 35(6):494–497. <https://doi.org/10.1134/S1063074009060078>
52. Forman D, West N, Francis J, Guy E (2009) The sero-prevalence of *Toxoplasma gondii* in British marine mammals. *Mem Inst Oswaldo Cruz* 104(2):296–298. <https://doi.org/10.1590/S0074-02762009000200024>
53. Di Guardo G, Proietto U, Di Francesco CE, Marsilio F, Zaccaroni A, Scaravelli D et al (2010) Cerebral toxoplasmosis in striped dolphins (*Stenella coeruleoalba*) stranded along the Ligurian Sea coast of Italy. *Vet Pathol* 47(2):245–253. <https://doi.org/10.1177/0300985809358036>
54. Pretti C, Mancianti F, Nardoni S, Ariti G, Monni G, Bello Dd et al (2010) Detection of *Toxoplasma gondii* infection in dolphins stranded along the Tuscan coast, Italy. *Rev Med Vet* 161(10):428–431
55. Santos PS, Albuquerque GR, Da Silva V, Martin AR, Marvulo MFV, Souza S et al (2011) Seroprevalence of *Toxoplasma gondii* in free-living Amazon River dolphins (*Inia geoffrensis*) from central Amazon, Brazil. *Vet Parasitol* 183(1–2):171–173. <https://doi.org/10.1016/j.vetpar.2011.06.007>
56. Alvarado-Esquivel C, Sánchez-Okrucky R, Dubey J (2012) Serological evidence of *Toxoplasma gondii* infection in captive marine mammals in Mexico. *Vet Parasitol* 184(2–4):321–324. <https://doi.org/10.1016/j.vetpar.2011.08.036>
57. Roe WD, Howe L, Baker EJ, Burrows L, Hunter SA (2013) An atypical genotype of *Toxoplasma gondii* as a cause of mortality in Hector’s dolphins (*Cephalorhynchus hectori*). *Vet Parasitol* 192(1–3):67–74. <https://doi.org/10.1016/j.vetpar.2012.11.001>
58. Bernal-Guadarrama MJ, Salichs J, Almunia J, García-Parraga D, Fernández-Gallardo N, Santana-Morales MÁ et al (2014) Development of an indirect immunofluorescence technique for the diagnosis of toxoplasmosis in bottlenose dolphins. *Parasitol Res* 113(2):451–455. <https://doi.org/10.1007/s00436-013-3674-y>
59. Profeta F, Di Francesco CE, Marsilio F, Mignone W, Di Nocera F, De Carlo E et al (2015) Retrospective seroepidemiological investigations against *Morbillivirus*, *Toxoplasma gondii* and *Brucella* spp. in cetaceans stranded along the Italian coastline (1998–2014). *Res Vet Sci* 101:89–92. <https://doi.org/10.1016/j.rvsc.2015.06.008>
60. Pintore MD, Mignone W, Di Guardo G, Mazzariol S, Ballardini M, Florio CL et al (2018) Neuropathologic findings in cetaceans stranded in Italy (2002–14). *J Wildl Dis* 54(2):295–303. <https://doi.org/10.7589/2017-02-035>
61. Costa-Silva S, Sacristán C, Gonzales-Viera O, Díaz-Delgado J, Sánchez-Sarmiento AM, Marigo J et al (2019) *Toxoplasma gondii* in cetaceans of Brazil: a histopathological and immunohistochemical survey. *Rev Bras Parasitol Vet* 28:395–402
62. Oksanen A, Tryland M, Johnsen K, Dubey J (1998) Serosurvey of *Toxoplasma gondii* in North Atlantic marine mammals by the use of agglutination test employing whole tachyzoites and dithiothreitol. *Comp Immunol Microbiol Infect Dis* 21(2):107–114. [https://doi.org/10.1016/s0147-9571\(97\)00028-3](https://doi.org/10.1016/s0147-9571(97)00028-3)
63. Hermosilla C, Silva LM, Kleinertz S, Prieto R, Silva MA, Taubert A (2016) Endoparasite survey of free-swimming baleen whales (*Balaenoptera musculus*, *B. physalus*, *B. borealis*) and sperm whales (*Physeter macrocephalus*) using non/minimally invasive methods. *Parasitol Res* 115(2):889–896. <https://doi.org/10.1007/s00436-015-4835-y>
64. Alekseev AY, Shpak O, Adamenko L, Glazov D, Galkina I, Schelkanov MY et al (2017) Serological detection of causative agents of infectious and invasive diseases in the beluga whale *Delphinapterus leucas* (Pallas, 1776) (Cetacea: *Monodontidae*) from Sakhalinsky Bay. *Russ J Mar Biol* 43(6):485–490. <https://doi.org/10.1134/S1063074017060037>
65. Iqbal A, Lair S, Dixon B (2018) *Toxoplasma gondii* infection in stranded St. Lawrence Estuary beluga *Delphinapterus leucas* in Quebec, Canada. *Dis Aquat Org* 130(3):165–175. <https://doi.org/10.3354/dao03262>
66. Marcer F, Marchiori E, Centelleghé C, Ajzenberg D, Gustinelli A, Meroni V et al (2019) Parasitological and pathological findings in fin whales *Balaenoptera physalus* stranded along Italian coastlines. *Dis Aquat Organ* 133(1):25–37. <https://doi.org/10.3354/dao03327>
67. Lambourn D, Jeffries S, Dubey J (2001) Seroprevalence of *Toxoplasma gondii* in harbor seals (*Phoca vitulina*) in southern Puget Sound, Washington. *J Parasitol* 87(5):1196–1197. [https://doi.org/10.1645/0022-3395\(2001\)087\[1196:SOTGIH\]2.0.CO;2](https://doi.org/10.1645/0022-3395(2001)087[1196:SOTGIH]2.0.CO;2)
68. Measures LN, Dubey J, Labelle P, Martineau D (2004) Seroprevalence of *Toxoplasma gondii* in Canadian pinnipeds. *J Wildl Dis* 40(2):294–300. <https://doi.org/10.7589/0090-3558-40.2.294>
69. Simon A, Chambellant M, Ward BJ, Simard M, Proulx J-F, Lévesque B et al (2011) Spatio-temporal variations and age effect on *Toxoplasma gondii* seroprevalence in seals from the Canadian Arctic. *Parasitology* 138(11):1362–1368. <https://doi.org/10.1017/S0031182011001260>
70. Rengifo-Herrera C, Ortega-Mora LM, Álvarez-García G, Gómez-Bautista M, García-Párraga D, García-Peña FJ et al (2012) Detection of *Toxoplasma gondii* antibodies in Antarctic pinnipeds. *Vet Parasitol* 190(1–2):259–262. <https://doi.org/10.1016/j.vetpar.2012.05.020>
71. Jensen S, Nymo I, Forcada J, Godfroid J, Hall A (2012) Prevalence of *Toxoplasma gondii* antibodies in pinnipeds from Antarctica. *Ecol Manag Restor* 2:129–138

72. Jankowski G, Adkesson MJ, Saliki JT, Cárdenas-Alayza S, Majluf P (2015) Survey for infectious disease in the South American fur seal (*Arctocephalus australis*) population at Punta San Juan, Peru. *J Zoo Wildl Med* 46:246–254. <https://doi.org/10.1638/2014-0120.1>
73. Bauer KL, Goertz CE, Belovarac JA, Walton RW, Dunn JL, Tuomi P (2016) Infectious disease and toxicological monitoring of stranded pacific harbor seals (*Phoca vitulina richardsi*) in cook inlet as surrogates for monitoring endangered belugas (*Delphinapterus leucas*). *J Zoo Wildl Med* 47(3):770–780. <https://doi.org/10.1638/2015-0147.1>
74. Namroodi S, Shirazi AS, Khaleghi SR, Mills JN, Kheirabady V (2018) Frequency of exposure of endangered Caspian seals to canine distemper virus, *Leptospira interrogans*, and *Toxoplasma gondii*. *PLoS ONE* 13(4):e0196070. <https://doi.org/10.1371/journal.pone.0196070>
75. Carlson-Bremer D, Colegrove KM, Gulland FM, Conrad PA, Mazet JA, Johnson CK (2015) Epidemiology and pathology of *Toxoplasma gondii* in free-ranging California sea lions (*Zalophus californianus*). *J Wildl Dis* 51(2):362–373. <https://doi.org/10.7589/2014-08-205>
76. Michael S, Howe L, Chilvers B, Morel P, Roe W (2016) Seroprevalence of *Toxoplasma gondii* in mainland and sub-Antarctic New Zealand sea lion (*Phocarcos hookeri*) populations. *N Z Vet J* 64(5):293–297. <https://doi.org/10.1080/00480169.2016.1191974>
77. Tociłowski ME, Lappin MR, Sumner PW, Stoskopf MK (1997) Serologic survey for toxoplasmosis in river otters. *J Wildl Dis* 33(3):649–652. <https://doi.org/10.7589/0090-3558-33.3.649>
78. Miller M, Gardner I, Packham A, Mazet J, Hanni K, Jessup D et al (2002) Evaluation of an indirect fluorescent antibody test (IFAT) for demonstration of antibodies to *Toxoplasma gondii* in the sea otter (*Enhydra lutris*). *J Parasitol* 88(3):594–599. [https://doi.org/10.1645/0022-3395\(2002\)088\[0594:EOAIFA\]2.0.CO;2](https://doi.org/10.1645/0022-3395(2002)088[0594:EOAIFA]2.0.CO;2)
79. Miller MA, Grigg ME, Kreuder C, James E, Melli A, Crosbie P et al (2004) An unusual genotype of *Toxoplasma gondii* is common in California sea otters (*Enhydra lutris nereis*) and is a cause of mortality. *Int J Parasitol* 34(3):275–284. <https://doi.org/10.1016/j.ijpara.2003.12.008>
80. Gaydos JK, Conrad PA, Gilardi KV, Blundell GM, Ben-David M (2007) Does human proximity affect antibody prevalence in marine-foraging river otters (*Lontra canadensis*)? *J Wildl Dis* 43(1):116–123. <https://doi.org/10.7589/0090-3558-43.1.116>
81. Verma SK, Knowles S, Cerqueira-Cézar CK, Kwok OC, Jiang T, Su C et al (2018) An update on *Toxoplasma gondii* infections in northern sea otters (*Enhydra lutris kenyoni*) from Washington State, USA. *Vet Parasitol* 258(133):7. <https://doi.org/10.1016/j.vetpar.2018.05.011>
82. Esmerini PO, Gennari SM, Pena HF (2010) Analysis of marine bivalve shellfish from the fish market in Santos city, São Paulo state, Brazil, for *Toxoplasma gondii*. *Vet Parasitol* 170(1–2):8–13. <https://doi.org/10.1016/j.vetpar.2010.01.036>
83. Zhang M, Yang Z, Wang S, Tao L, Xu L, Yan R et al (2014) Detection of *Toxoplasma gondii* in shellfish and fish in parts of China. *Vet Parasitol* 200(1–2):85–89. <https://doi.org/10.1016/j.vetpar.2013.10.022>
84. Marangi M, Giangaspero A, Lacasella V, Lonigro A, Gasser RB (2015) Multiplex PCR for the detection and quantification of zoonotic taxa of *Giardia*, *Cryptosporidium* and *Toxoplasma* in wastewater and mussels. *Mol Cell Probes* 29(2):122–125. <https://doi.org/10.1016/j.mcp.2015.01.001>
85. Marquis ND, Record NR, Robledo JAF (2015) Survey for protozoan parasites in Eastern oysters (*Crassostrea virginica*) from the Gulf of Maine using PCR-based assays. *Parasitol Int* 64(5):299–302. <https://doi.org/10.1016/j.parint.2015.04.001>
86. Ribeiro L, Santos L, Brito P Jr, Maciel B, Da Silva A, Albuquerque G (2015) Detection of *Toxoplasma gondii* DNA in Brazilian oysters (*Crassostrea rhizophorae*). *Genet Mol Res* 14(2):4658–4665. <https://doi.org/10.4238/2015.May.4.25>
87. Cong W, Zhang N-Z, Hou J-L, Wang X-C, Ma J-G, Zhu X-Q et al (2017) First detection and genetic characterization of *Toxoplasma gondii* in market-sold oysters in China. *Infect Genet Evol* 54:276–278. <https://doi.org/10.1016/j.meegid.2017.07.014>
88. Coupe A, Howe L, Burrows E, Sine A, Pita A, Velathanthiri N et al (2018) First report of *Toxoplasma gondii* sporulated oocysts and *Giardia duodenalis* in commercial green-lipped mussels (*Perna canaliculus*) in New Zealand. *Parasitol Res* 117(5):1453–1463. <https://doi.org/10.1007/s00436-018-5832-8>
89. Cong W, Zhang N-Z, Yuan D-Q, Zou Y, Li S, Liang Z-L (2019) Detection and genetic characterization of *Toxoplasma gondii* in market-sold mussels (*Mytilus edulis*) in certain provinces of China. *Microb Pathogen* 136:103687. <https://doi.org/10.1016/j.micpath.2019.103687>
90. Marquis ND, Bishop TJ, Record NR, Countway PD, Fernández Robledo JA (2019) Molecular Epizootiology of *Toxoplasma gondii* and *Cryptosporidium parvum* in the Eastern Oyster (*Crassostrea virginica*) from Maine (USA). *Pathogens* 8(3):125. <https://doi.org/10.3390/pathogens8030125>
91. Marino AMF, Giunta RP, Salvaggio A, Castello A, Alfonzetti T, Barbagallo A et al (2019) (2019) *Toxoplasma gondii* in edible fishes captured in the Mediterranean basin. *Zoonoses Public Health* 66(7):826–834. <https://doi.org/10.1111/zph.12630>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.