The survival and dispersal of *Taenia* eggs in the environment: what are the implications for transmission? A systematic review

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**Abstract**

*Taenia* spp. are responsible for a substantial health and economic burden in affected populations. Knowledge of the fate of the eggs of *Taenia* spp. in the environment and of other factors facilitating the transmission of eggs to intermediate hosts is important for the control/elimination of infections caused by *Taenia* spp. The aim of this systematic review was to summarize current knowledge of the factors influencing the survival and dispersal of *Taenia* spp. eggs in the environment. Publications retrieved from international databases were systematically reviewed. Of the 1465 papers initially identified, data were ultimately extracted from 93 papers. The results of this systematic review indicate that survival is favoured at moderate temperatures (0–20 °C). Humidity seems to affect the survival of *Taenia* spp. eggs more than temperature. Under field circumstances, *Taenia* spp. eggs have been found to survive for up to 1 year. *Taenia* spp. eggs are commonly found on vegetables (0.9–30%) and in soil and water samples (0–43%), with their presence posing a risk to the consumer. Invertebrates may act as transport hosts, transferring the infection to an intermediate host, but the importance of this route of transmission is still open to question. Wastewater treatment systems are not capable of entirely eliminating *Taenia* spp. eggs. Access to surface water and the use of sewage sludge as fertilizer on pastures are important risk factors for bovine cysticercosis. Although information on the survival and spread of *Taenia* spp. eggs is available, in general the data retrieved and reviewed in this article were old, focused on very specific geographical regions and may not be relevant for other areas or not specific for different *Taenia* spp. Furthermore, it is unknown whether egg survival differs according to *Taenia* sp. Future studies are necessary to identify sustainable methods to identify and inactivate parasite eggs in the environment and reduce their spread.

**Keywords:** *Taenia*, Egg survival, Spread, Environment, Sewage treatment

**Background**

*Taenia* spp. are important tapeworm species in humans and domesticated animals that may lead to a substantial health and economic burden [1–3]. Humans are the sole definitive hosts of three zoonotic *Taenia* spp., namely *T. saginata*, *T. solium* and *T. asiatica* [4]. Other *Taenia* spp., such as *T. hydatigena*, *T. pisiformis*, *T. ovis*, *T. taeniaeformis* and *T. multiceps*, are mainly of veterinary importance. *Taenia saginata* is the most common and most widely distributed tapeworm in the human host [5]. *Taenia solium*, on the other hand, is endemic in large parts of Asia, Latin America and sub-Saharan Africa, while *T. asiatica* seems to be restricted to Asia [3]. Infections with *T. solium* and *T. asiatica* are considered to be neglected tropical diseases, and especially for infections caused by the former, the call for control and elimination is warranted as the parasite can also cause cysticercosis in humans. The establishment of cysticerci in the central nervous system may lead to
neurocysticercosis, which has been found to be associated with more than 30% of acquired epilepsy cases in endemic regions [6–9]. Humans become infected with *T. saginata*, *T. solium* and *T. asiatica* by consuming raw or undercooked infected beef, pork or pig organs containing cysticerci, the metacestode larvae of the tapeworm. Upon ingestion of a viable cysticercus, an adult tapeworm may develop that resides in the intestinal lumen of the human final host [3, 6]. Infection with a tapeworm (taeniosis) generally remains asymptomatic [10, 11] with some exceptions [12–14].

Gravid proglottids containing infective eggs are shed with the stool of the definitive host; in the case of *T. saginata* they may also be expelled independently of defecation [3]. In industrialized countries, inadequately treated sewage is generally considered to contribute to infections in cattle by *T. saginata*, as animals become infected by ingesting the eggs from contaminated pastures after flooding or from access to surface water [11]. On the other hand, in low-income countries, humans contaminate the environment (soil, crops and water) with *Taenia* spp. eggs present in faeces due to poor hygienic standards and the lack of latrines [15]. In general, contamination of food, soil and water can increase the risk of infection for humans (*T. solium*) and other intermediate hosts (all *Taenia* spp.) [16–18], as does possible spread *via* invertebrates and wind [19, 20].

Control and treatment options for *Taenia* spp. have generally been generated from a two-compartment approach, with the focus either on the definitive host or on the intermediate host. Interventions for *T. solium*, including education, meat inspection, sanitation, treatment of final and intermediate hosts and pig vaccination, have been implemented, either as single interventions or in combination [21]. However, focus on the third compartment, namely the egg stage in the environment, has often been neglected even though tapeworms have the ability to produce up to 300,000 eggs each day [22]. Therefore, egg survival and dispersal studies can lead to new insights on the survival capacity of eggs and to possible new control options to break the life-cycle of these parasites and prevent infection of cattle, pigs and humans. In general, egg survival experiments are conducted under *in vivo* or *in vitro* conditions. In *in vitro* experiments, eggs are checked for viability based on integrity (mostly morphological determination), hatching and activation (movement of the larva after hatching), the latter two approaches performed in designated media mimicking gastric juices [23–25]. These terms are often used interchangeably, so caution is necessary when interpreting study findings. In *in vivo* studies, egg infectivity is determined by feeding eggs to naïve intermediate host animals followed by dissecting the carcasses for cysticerci recovery [26].

The aim of the systematic review was to review current knowledge of the factors that influence the survival and dispersal of *Taenia* spp. eggs in the environment. More specifically, we aimed to summarize current knowledge on (i) the survival of *Taenia* spp. eggs under specific temperature and relative humidity (RH) conditions in laboratory and field experiments; (ii) the presence of eggs on vegetables, fruit, soil and water depending on the geographical area or climate zone of the study; (iii) the spread of eggs via different means, such as invertebrates and wind; and finally, (iv) the importance of sewage treatment systems in egg dispersal.

**Methods**

A systematic review of literature published up to 31 July 2019 was conducted to collect information on the survival and dispersal of *Taenia* spp. eggs in the environment, using an approach that followed PRISMA guidelines [27]. No restriction was made on publication date. The protocol and the PRISMA checklist for this review can be found in Additional file 1 and Additional file 2, respectively. Two search engines, PubMed (http://www.ncbi.nlm.nih.gov/pubmed) and Web of Science (www.webofknowledge.com), were searched without the use of a specific time frame and using the following keywords and Boolean operators: *taeni*a AND egg* AND (surviv* OR viab* OR resist* OR longevi* OR activ* OR hatch* OR transmi* OR epi* OR infectiv* OR water OR wastewater OR sewage OR sludge OR river OR stream OR soil OR silt OR grass OR saline OR environment* OR medi*)

Outputs from the two search engines were first screened for the English language, and publications in languages other than English were excluded. The results were then compiled and screened for duplicates, after which titles and abstracts were screened for eligibility by two independent reviewers. Publications were excluded based on the following reasons: (i) studies on species other than *Taenia* spp.; (ii) studies outside the scope of this review (egg survival and dispersal), such as laboratory techniques for hatching; and (iii) reviews and editorial letters. Where possible, full texts were retrieved and evaluated according to the same criteria. The reference lists of each eligible article were also screened for relevant literature. Data were extracted from the records into predefined tables using Microsoft Excel (Microsoft Corp., Redmond, WA, USA).
Results
A total of 1460 publications were identified through the database searches, and an additional five articles were identified after screening the relevant literature. Ninety-three studies were included in the systematic review after careful elimination of the remaining papers based on the exclusion criteria (Fig. 1).

Egg survival
Twenty-four studies were identified that investigated Taenia spp. egg survival in the environment. The studies shown in Table 1 describe laboratory or field experiments aimed at determining the survival of eggs after exposure to a range of temperatures and relative humidities, to different light types and to various media. In general, humidity seems to affect Taenia spp. egg survival more than temperature, with low humidity (< 34%) hampering survival. Moderate temperatures (between 5 °C and 25 °C) favour survival, while warmer temperatures (> 25 °C) and freezing shorten survival times. Under field conditions, survival is dependent on the specific Taenia sp. studied and the specific outdoor conditions. In one study on Kenyan pastures, eggs were observed to survive up to 1 year [28].

Studies investigating the effect of heat treatment (> 40°C) were generally not directed at environmental factors affecting survival but more focussed on which factors were effective in destroying eggs (in this case, cooking or boiling of food and fluids). The ovicidal activity of several naturally occurring agents was investigated. A number of studies reported that the fungi Paecolimyces lilacinus and Pochonia chlamydosporia were able to colonize the egg contents of T. saginata and T. taeniaeformis eggs, which led to their destruction [29–33]. It was also reported that lime nitrogen had the most destructive effect on egg survival of all fertilizers tested, with the eggs only surviving for 2 days in this substance; survival in other fertilizers was 2 days in limestone, 10 days in ammonium nitrate with limestone, 3 days in superphosphate substance, 3–7 days in NPK3, 10 days in potash salt and 30–35 days in urea [34].

Environmental spread of eggs
A total of 43 papers, representing the majority of all publications retained in this review, described possible means of spreading of Taenia spp. eggs in the environment. Fifteen papers investigated the presence of helminth eggs on vegetables bought at markets, and a
| Test conditions | Species | Egg viability test | Result | Year of publication | Reference |
|----------------|---------|-------------------|--------|---------------------|-----------|
| − 4 °C for 45, 12.3 and 76.1 days | T. saginata | In vivo: 300,000 eggs fed to one calf per condition | Heavy infection after 4.5 days, moderate after 1.23 days and only 2 cysticerci after 76.1 days | 1960 | [77] |
| Between − 9 °C and 38 °C | T. hydatigena and T. ovis | In vivo: feeding to 8 lambs on days 90 and 273 (2000 T. hydatigena eggs each (eggs stored at − 9 °C and 7 °C fed to lambs on days 90 and 273). | Cysticerci formed after 90 days (279 at 7 °C and 14 at − 9 °C) and after 273 days at 7 °C (6 cysticerci), but not at − 9°C | 1977 | [74] |
| 4 °C in saline for 28 and 91 days | T. taeniaeformis | In vivo: intragastric application to mice | 36% cyst recovery after 28 days and 10% after 91 days | 1990 | [68] |
| 5-min-long heat treatment at 50 °C or 60 °C, with 22 °C as control | T. hydatigena | In vivo: 100–2000 eggs fed to lambs and cysticerci counted | The mean percentage of cysticerci recovered were 11.55, 1.22 and 0% for 22 °C, 50 °C and 60°C, respectively | 2013 | [95] |
| 4–5 °C in 1:10,000 merthiolate in normal saline | T. saginata | In vitro activation (Silverman’s hatching technique) and in vivo (calves) | Hatching (in vitro) and infectivity/survival (in vivo) for at least 168 days | 1962 | [73] |
| Between − 9 °C and 38 °C | T. hydatigena and T. ovis | In vitro hatching and activity: AGF and AIF | | |
| At 4 °C and at − 20 °C, − 9 °C, − 4 °C, 0 °C, 10 °C, 18–22 °C, 25 °C and 37 °C in saline with antibiotics and mycostatin (for up to 42 days) | T. multiceps | In vitro hatching, activation | 4°C: Activation levels increased up to 27 days (55%) but decreased afterwards (22% after 50 days). Eggs withstand freezing at − 20 °C for 42 days. Hatching ability lost after 7 days at 37 °C. Intermediate temperature shows no or negligible effects on activation | 1984 | [75] |
| 5-min-long heat treatment at 40 °C, 45 °C, 50 °C, 55 °C or 60 °C, 22 °C as control | T. hydatigena | In vitro: hatching | In vitro: Activation of 6.14% of 3.07% recovered eggs after treatment at 40 °C. 9947% reduction in activation or infectivity after treatment at 60 °C | 2013 | [95] |
| 5 °C and 20 °C in water and in silt for 2, 4 and 6 months and − 18°C for 1 week | T. saginata | In vitro: hatching with NaClO and activation with AIF | Activation after 6 months at 5 °C. Decreased activation at 20 °C. 4 months in water and 2 months in silt. Activation after 1 week at − 18°C | 2019 | [78] |
| Desiccation (on glass slides until water is evaporated), mild temperature (38 °C) | T. pisiformis, T. ovis, T. hydatigena, Echinococcus granulosus | In vitro: treatment with AIF or AGF (integrity, hatching and activation) | Desiccation most restrictive for survival, T. pisiformis and E. granulosus more susceptible | 1968 | [72] |
| RH of 31, 47 and 89% (19.5 °C) for up to 365 days | T. hydatigena | In vitro: vitality = ability to exclude 0.1% aqueous trypan blue | Vitality: 80–82% at 89% RH, 59.5–64.5% at 47% RH and 36–40% at 31% RH. Reduced vitality: 93.4% at 31% RH, 93.15% at 47% RH and 73.58% at 89% RH | 2017 | [96] |
Table 1 (continued)

| Test conditions | Species | Egg viability test | Result | Year of publication |
|-----------------|---------|--------------------|--------|---------------------|
| High T (37 - 39°C) or low T (3 - 5°C) AND high RH (89-94%) or low RH (32-33%) | *T. pisiformis* | *In vivo* | 2000 eggs fed to 7–10 rabbits in each group (control group received fresh sample of eggs at the beginning of the experiment) | 1975 [76] |
| Between 7 °C and 65 °C plus desiccation (water removed) (up to 300 days) | *T. hydatigena, T. ovis* and *T. multiceps* | *In vitro* | Hatching: AGF and AIF | 1977 [74] |
| High temperature (30–80 °C), different RH (10, 80, 90 and 95%) and different contact times | *T. solium* (and other helminth genera) | *In vitro* | Hatching with NaClO solution | 2010 [97] |
| Pastures contaminated with egg suspensions (2000–4000 eggs/sq yard): high rainfall vs dry (Kenya) | *T. saginata* | *In vivo* | 14 calves allowed to graze for 3 to 143 days (13–413 days after infection pasture) | 1948 [28] |
| Outdoor on patch of 2.0m² (Australia): winter (0–20 °C) and summer (8–30 °C) | *T. pisiformis* | *In vivo* | Rabbits grazing on patch (maximum 126 days) | 1975 [76] |
| Batches of 11,500 eggs deposited outdoors on natural soil surface (starting from May and September for up to 9.5 months) | *T. saginata* | *In vivo* | Batches fed to calves | 1990 [80] |
| Outdoor storage (May–June) in UK | *T. multiceps* | *In vitro* | Hatching, activation | 1984 [75] |
| In freshwater stream in Denmark from December to February (fluctuating temperature: 10 to 17°C) and outdoors for 1 week in February (−6–5 °C) | *T. saginata* | *In vitro* | Hatching with NaClO and activation with AIF | 2019 [78] |
| Ensilation of eggs with minced potato (up to 28 days) | *T. hydatigena* | *In vivo* | 2000 eggs fed to lambs and cysticerci counted | 2013 [98] |
| Gravid segments fixed in 70% EtOH or FA or frozen for 1 week | *T. taeniaeformis* | *In vitro* | Hatching (0.5% NaClO method) | 1994 [99] |
Table 1 (continued)

| Test conditions | Species | Egg viability test | Result | Year of publication | Reference |
|-----------------|---------|--------------------|--------|---------------------|-----------|
| Exposure to UV radiation (eggs and eggs freed of the embryophore): 254 nm, dose rate of 0.6 mJ/cm²/s for 600 to 9600 s or 60 mJ/cm²/s for 6 to 192 s | T. taeniaeformis | In vivo: oral inoculation of 5000 eggs in rats | Number of cysticerci decreased dose dependently and no cysticerci were recovered after exposure to a total dose of 2880 mJ/cm². After removal of embryophore, no cysticercus development after a total dose of 30 mJ/m² | 1997 | [100] |
| Exposure to UV radiation: UVA (near UV wavelength of 320–400 nm), UVB (mid UV, 290–320 nm) and UVC (far UV, 200–290 nm) for 30, 90, 270, 810, 2430 and 7290 s | T. taeniaeformis | In vivo: oral inoculation of 3,000 eggs in rats | UVC exposure significant effect on number of cysticerci from 90 s of exposure onwards (and smaller cysts), 100% reduction from 2430 s of exposure onwards. UVA reduction was 31.9 and 28.3% and UVB reduction was 51.8 and 54.8% at 2430 and 7290 s, respectively | 2001 | [101] |
| Sunlight (0 °C; 24 h) and UV light (20 °C; 24 h, 8 days) | T. pisiformis | In vitro: treatment with AIF or AGF (integrity, hatching and activation) | No difference in integrity, hatching and activation between control and treated eggs | 1968 | [72] |
| Exposure to UV radiation (250 nm), up to 48 h | T. multiceps | In vitro hatching, activation | Hatching reduced to 3% after 24 h | 1984 | [75] |
| Lime dose of 15 and 20% CaO w/v dry basis with 80 or 90% humidity | T. solium (and other helminth genera) | In vitro: hatching with NaClO solution | For complete inactivation: 20% CaO dose (pH 12.5) and 80% humidity for 5 months | 2010 | [97] |
| High temperature (25–80 °C), different RH (10, 80, 90 and 95% RH), pH (neutral, 15–20% quicklime), contact times | T. solium (and other helminth genera) | In vitro: hatching with NaClO solution | For complete inactivation: combination of temperature > 70 °C and 80% humidity for 120 min OR pH 5.3, 45 °C, 90% RH for 6 days OR pH 12.7, 45 °C, 90% RH for 19 days | 2012 | [102] |

Studies are ordered by test conditions (temperature, RH, season, UV radiation, combination of conditions) and within this order by in vivo vs. in vitro studies, and then by publication year (oldest to most recent). In vitro studies focus on integrity (morphological), hatching and activation (movement of the larvae), and in vivo studies focus on infectivity and survival determined by recovery of cysticerci.

AGF, Artificial gastric fluid; AIF, artificial intestinal fluid; CaO, calcium oxide; EtOH, ethanol; FA, formaldehyde; NaClO, sodium hypochlorite; RH, relative humidity; UV ultraviolet.
number also examined the effect of washing of vegetables on the number of eggs (Table 2). In general, prevalence of *Taenia* spp. eggs found on fruits and vegetables is high, ranging from 0.9 to 33%.

Research on the contamination of fruits and vegetables has been conducted in only few countries and consequently in only a few climate zones. Although all five major climate zones are represented in the studies reviewed, many of the climate subdivisions are not. Survival of eggs was found to be very dependent on temperature and RH and, therefore, also on climate zone. The authors of most studies agreed that leafy vegetables had a higher prevalence of parasites than smooth vegetables, such as tomatoes and cucumbers [35–43]. Parasite egg prevalence in general, and the prevalence of *Taenia* spp. eggs specifically, was higher in the summer and spring compared to the winter and autumn [37, 44, 45].

Federer et al. [17] studied the presence of taeniid DNA by multiplex-PCR in the water used to wash the fruit and vegetable mixes fed to zoo animals in Switzerland. The vegetables and fruits in the mix originated from all over Europe. In the autumn, 18% of the water samples contained taeniid DNA, compared to 28% in the spring.

### Table 2 Overview of results on *Taenia* spp. egg prevalence on vegetables and fruit

| Country      | Climate zone                                      | *Taenia* spp. egg prevalence before washing, no species specified (N = sample size) | *Taenia* spp. egg prevalence after washing (N = sample size) | Year of publication | Reference |
|--------------|---------------------------------------------------|------------------------------------------------------------------------------------|-------------------------------------------------------------|-------------------|-----------|
| Iran         | Hot desert with Mediterranean and continental hot summer climate in the north | 0.9% (N = 772)                                                                   | 0 (N = 772)                                                  | 2016              | [41]      |
| Iran         | Hot desert with Mediterranean and continental hot summer climate in the north | 9.2% (N = 304)                                                                   | 1.3% (N = 304) (traditional washing)c | 2012              | [45]      |
| Iran         | Hot desert with Mediterranean and continental hot summer climate in the north | 1.8% (N = 218) (Taenia/Echinococcus)                                             | 0 (N = 436)                                                  | 2010              | [42]      |
| Iran         | Hot desert with Mediterranean and continental hot summer climate in the north | 4.86% (N = 453)                                                                  | NA^d                                                          | 2016              | [37]      |
| Nigeria      | Tropical Savanna climate with hot semi-arid climate in the north | 10.6% (N = 199)                                                                  | NA                                                           | 2012              | [40]      |
| Nigeria      | Tropical Savanna climate with hot semi-arid climate in the north | 1.25% (N = 960)                                                                  | NA                                                           | 2015              | [36]      |
| Nigeria      | Tropical Savanna climate with hot semi-arid climate in the north | 2% (N = 1130) (Taenia/Echinococcus)                                              | NA                                                           | 2012              | [35]      |
| Pakistan     | Hot desert with hot semi-arid climate in the north | 2.7% (N = 520)                                                                   | NA                                                           | 2017              | [39]      |
| Turkey       | Mixed cold semi-arid, Mediterranean and continental hot summer climate | 3.5% (N = 203)                                                                   | 0 (N = 406)                                                  | 2005              | [84]      |
| Turkey       | Mixed cold semi-arid, Mediterranean and continental hot summer climate | 2.7% (N = 111) (Taenia/Echinococcus)                                              | NA                                                           | 2013              | [103]     |
| Jordan       | Hot desert                                        | 6% (N = 133)                                                                      | NA                                                           | 2016              | [38]      |
| Saudi Arabia | Hot desert                                        | 3.2% (N = 470) (Taenia/Echinococcus)                                             | NA                                                           | 2010              | [44]      |
| Vietnam      | Tropical savanna climate                          | <1% (N = 317)                                                                     | NA                                                           | 2009              | [43]      |
| Libya        | Hot desert                                        | *Taenia/Echinococcus* spp.: in 6% of tomato (N = 36), 25% of cucumber (N = 36), 33% of lettuce (N = 27) and 30% of cress samples (N = 27) | NA                                                           | 2010              | [83]      |

^a Köppen climate classification  
^b Immersed in tap water in sink for 6–7 min, then, rinsed for 1.5–2 mins  
^c Washed, immersed in solution containing 200 ppm active calcium hypochlorite for 30 mins, rinsed in automated fruit-vegetable washer.  
^d Not applicable, not investigated in the study.
Eleven papers reported on egg presence in soil and water samples (Table 3). Again, most articles focussed on all parasitic material found, and the results for *Taenia* spp. eggs were only a small part of the total results. In general, prevalence ranged from 0 to 43%.

Invertebrates are considered to be possible vectors for the spread of parasitic eggs. In Thailand, one of 820 cockroaches collected in open-air shopping markets in Thailand carried a *Taenia* spp. egg [46], while in Peru, out of 54 pools of 309 wild-caught *Aphodius* spp. beetles, two were positive for *T. solium*, three were positive for *T. hydatigena* and two were positive for other taeniid eggs [47]. In two studies carried out in Mexico, on the other hand, none of the 600 [48] and 1187 [49] flies caught in kitchens carried *Taenia* spp. eggs in their gut.

To confirm the possibility that an invertebrate species might carry and disseminate eggs in the environment, eggs have been fed to selected species in laboratory experiments. Beetles (*Pterostichus vulgaris*, *Aphodius fimetarius*, *A. luridus*, *Ammophorus rubripes*), flies (*Calliphora quadramaculata*, *C. hortona*, *C. stygia*) and earthworms (*Eisenia fetida*, *Lumbricus terrestris* and *Allolobophora caliginosa*) fed with *Taenia* spp. eggs were found to contain eggs in the digestive tract after dissection [19, 50–52]. When beetles (*Ammophorus rubripes*) and blowflies (*Hybopygia varia*, *Calliphora quadramaculata*, *C. hortona* and *C. stygia*) infected in the laboratory with *Taenia* spp. eggs were fed to pigs and lambs, respectively, 94.4% of pigs presented with cysticercosis and all blowflies had transferred the infection [19, 53].

Lawson and Gemmell [19, 20, 54–56] performed several experiments to determine the possible infection route via invertebrates and dispersal in the field. Lambs that were allowed to graze downwind of dog kennels or in close proximity to a plot where infected dogs had been previously kept contained a much higher level of cysticerci, detected during autopsy, than those grazing elsewhere. Dead blowflies containing eggs of *T. hydatigena* spread on a pasture were able to transmit infection if ingested by lambs (70% of 14 lambs infected). In another experiment, blowflies were first exposed to *T. pisiformis* eggs by contact with faeces from infected dogs and then afterwards given access to pasture. Five of eight rabbits subsequently allowed to graze on this pasture became infected. In a similar experiment, blowflies were allowed to come into contact with dog faeces contaminated with *T. hydatigena* eggs before they had access to meat. This meat was subsequently fed to pigs, and 100% of the pigs became infected. On the other hand, in experiments where human faeces containing *T. saginata* eggs were deposited 1.5 m from a pasture where calves were grazing, none of the calves contained cysticerci after 8 to 10 weeks [57]. On the Scottish island of St. Kilda, sheep were found to be commonly infected with *T. hydatigena* despite the absence of definitive hosts for this species. Torgerson et al. [58, 59] concluded that eggs had been transported by insects or birds from the nearest inhabited land mass 60 km further away. Lawson and Gemmell [19] also investigated the role of wind in the dispersal of eggs. Faecal samples contaminated with *T. pisiformis* eggs were placed in front of a fan and trays were placed to capture whatever was moved by the draft. The sediment was fed to rabbits, but none became infected.

Evidence for transmission between intermediate hosts does exist. In one experiment, pigs fed with proglottids of *T. solium* were placed among naïve pigs [60]. In each of the four trials, at least one of the naïve pigs became infected, but with much lower cyst intensities compared to the primarily infected pigs. Whether secondary infection was attributable to coprophagic habits is yet to be demonstrated.

**Sewage treatment and surface water**

A number of authors have linked access to surface water with a higher risk for cysticercosis, suggesting that eggs either end up in the surface water directly or as they pass through water treatment systems. Kyvsgaard et al. [61] found that allowing cattle access to drink from streams in Denmark was a major risk factor for bovine cysticercosis. Boone et al. [62] reported that the flooding of pastures, free access of cattle to surface water and proximity of wastewater effluent were explanatory variables for bovine cysticercosis in Belgium. In Brazil, the water source from rivers or streams was determined to be the main risk factor for bovine cysticercosis in multiple farms [63]. The flooding of agricultural land and grassland has also been associated with human and porcine cysticercosis in Kenya [64].

Several studies have shown that wastewater treatment plants are not fully capable of removing helminth eggs, including those of *Taenia* spp., from water (Table 4).

Newton et al. [65] laboratory tested different treatment processes for their ability to remove *T. saginata* eggs from wastewater. A sedimentation test showed that removal varied from 51 to 98% after 15 and 120 min, respectively. Sand filtration was able to remove 99.6% of eggs from the wastewater and a trickling filter could removed 62–70%.

Eggs that are removed from wastewater in wastewater treatment systems are deposited in the sewage sludge that is formed during the process. Using untreated sludge to fertilize crops and pasture will therefore lead to a higher risk. Several studies have reported that some types of sludge treatment are inadequate in terms of inactivating taeniid eggs (Table 5).

In a study by Ilsøe et al. [66] that was carried out following several outbreaks of bovine cysticercosis in
| Country          | Climate zone                        | Medium                                                                 | Identification method                              | Result (N = sample size)                                                                 | Year of publication | Reference |
|------------------|-------------------------------------|------------------------------------------------------------------------|---------------------------------------------------|------------------------------------------------------------------------------------------|---------------------|-----------|
| Cameroon         | Tropical monsoon and tropical savanna climate | Water: Marshy areas                                                    | Formalin–ether concentration and Kato-Katz technique | Taenia spp. eggs detected with a maximum of 118 eggs/l in short rainy season (N = 96)     | 2019                | [109]     |
| Canada           | Subarctic and tundra climate        | Sediment: Water supply for cattle                                      | Sedimentation and Sheather’s flotation technique  | 9 eggs in total (N = 482)                                                                  | 2004                | [86]      |
| Iraq             | Hot desert, hot semi-arid and Mediterranean hot summer climate | Soil: Public squares and parks                                        | Zinc sulphate flotation                            | 6.2% (Taenia spp.) (N = 48)                                                              | 2015                | [104]     |
| Mexico           | Tropical, arid and semi-arid climate | Soil: In village with porcine cysticercosis                            | Modified Faust’s technique                         | No eggs of Taenia spp. (N = 400)                                                          | 1989                | [48]      |
| Mexico           | Tropical, arid and semi-arid climate | Soil: in and around houses                                            | Centrifugation/flotation                           | 6% (N = 15) (T. solium)                                                                   | 1991                | [105]     |
| Mexico           | Tropical, arid and semi-arid climate | Drinking water                                                        | Light microscopy of sediment after centrifugation  | 8% (N = 12) (T. solium)                                                                   | 1991                | [105]     |
| Mexico           | Tropical, arid and semi-arid climate | Objects: Houses of tapeworm carriers (T. solium)                      | Method of Graham: microscopy after collecting eggs with cellulose tape | 0% (N = 35)                                                                              | 1991                | [105]     |
| Mexico           | Tropical, arid and semi-arid climate | Soil: In and around houses (toilet, backyard, kitchen, washboard, water containers, corrals) | Centrifugation/flotation                            | 43% of samples positive for Taenia spp. eggs in spring (N = 109), 7.8% in summer (N = 116), 29.2% in autumn (N = 113) and 17% in winter (N = 53). Highest prevalence in kitchen soil samples     | 2008                | [85]      |
| Nigeria          | Tropical savanna climate with hot semi-arid climate in the North         | Soil: Playgrounds                                                      | Sieving, sedimentation, flotation                  | 36.9% (N = 608) (Taenia spp./Echinococcus spp.) Higher prevalence in dry period            | 2008                | [106]     |
| Peru             | Hot desert, tundra and tropical rainforest climate                        | Soil: Village                                                          | Sugar–Percoll sedimentation                        | 2.9% (N = 336) (Taenia spp.)                                                             | 2018                | [108]     |
| Slovakia         | Humid continental climate          | Soil: Sandpits                                                         | Sheather’s flotation technique                     | 0.7% (N = 285) (Taenia spp.)                                                             | 2014                | [18]      |
| Turkey           | Mixed cold semi-arid, Mediterranean and Continental hot summer climate    | Soil: Playgrounds                                                      | Zinc sulphate flotation                            | 1% (N = 480) (Taenia spp.)                                                               | 2006                | [107]     |
| Zimbabwe         | Hot semi-arid and dry-winter subtropical highland climate                 | Drinking water: Boreholes, bowsers, lakes, rivers, springs, taps and wells | Filtration/centrifugation                          | Taenia spp. eggs found in rivers and lakes (sample size and prevalence not indicated)   | 2011                | [16]      |

* Köppen climate classification
Table 4 Overview of results on *Taenia* spp. egg presence in the influent/effluent of wastewater treatment systems.

| Country                  | Wastewater treatment system          | Egg recovery                                                                 | Influent                      | Effluent                         | Year of publication | Reference |
|--------------------------|--------------------------------------|------------------------------------------------------------------------------|-------------------------------|----------------------------------|---------------------|-----------|
| Morocco                  | Activated sludge and natural lagoon  | Modified Bailenger method (sedimentation, centrifugation, flotation and McMaster) | 5.28 eggs/l (N = 6) and 0 eggs/L (N = 6) | 0 eggs/l (N = 6) and 0 eggs/L (N = 6) | 2018 [110]          |           |
| Colombia                 | Series of anaerobic, facultative and maturation ponds | Modified Bailenger method                                                   | 63 helmith eggs/l (N = 8)     | 0 eggs/l (N = 8)                 | 2002 [111]          |           |
| Iran                     | Activated sludge Natural lagoons     | Modified Bailenger method                                                   | Low number present in 2 of 8 plants (3 and 1.25 eggs/l) (N = 16/plant) | < 1 egg/l (N = 16/plant)         | 2006 [112]          |           |
| Morocco                  | Stabilization ponds                  | Bailenger method                                                            | 0.1 eggs/l (N = 48)           | 0 eggs/l (N = 48)                | 2000 [113]          |           |
| Tunisia                  | Activated sludge Stabilization ponds  | Bailenger method                                                            | From 28 to 208 eggs/l (N = 174) | From 17 to 52 eggs/l (N = 174)    | 2009 [88]           |           |
| Colombia                 | Anaerobic biodigestors               | Filtration, sedimentation, centrifugation and recovery by Sheather and McMaster method | Eggs in 10% of samples (N = 80) | Eggs in 10% of samples (N = 80) | 2012 [114]          |           |
| South Africa and Lesotho | Centralized plant                    | Sieving, sedimentation and flotation                                        | 6.4–29.6 eggs/l to 2.3 eggs/l (N = 55) | 1.4 to 84 eggs/L – 0.25 eggs/L (N = 55) | 2018 [87]          |           |
| Bolivia                  | Facultative pond followed by maturation pond | Centrifugation, flotation and biphasic separation                           | 306–3006 eggs/l (N = 3)       | 45 eggs/L (N = 3)                | 2013 [115]          |           |
| Tunisia                  | Activated sludge Natural lagoons     | Modified Bailenger method                                                   | *Taeniid eggs in 85% of samples (N = 117) | *Taeniid eggs in 30% of samples (N = 117) | 2018 [89]          |           |

Discussion

The results summarized in the review show that as a general rule humidity seems to affect *Taenia* spp. egg survival more than temperature, with low humidity hampering survival (< 34%) [72]. Moderate temperatures (5–25 °C) favour survival [73, 75], while warmer temperatures (> 25°C) shorten survival time [74, 76], as does freezing [77]. Under field conditions, *Taenia* spp. eggs can survive for at least 1 year, as demonstrated by Duthy et al. [28] on Kenyan pastures (*T. saginata*). Other *Taenia* spp. have been shown to survive outdoors for a shorter
Table 5  Overview of results on *Taenia* spp. egg presence in the sludge of wastewater treatment systems

| Country       | Sludge type and/or treatment                                                                 | Egg recovery                                                                 | Presence (N = sample size)                                                                 | Year of publication | Reference |
|---------------|---------------------------------------------------------------------------------------------|------------------------------------------------------------------------------|------------------------------------------------------------------------------------------|---------------------|-----------|
| South Africa  | Treatment: sludge drying beds for 2 months                                                   | Flotation, sedimentation                                                     | 54 *Taenia* spp. eggs/g with 20 eggs/g viable (N = 60)                                   | 2018                | [90]      |
| Senegal       | Treatment: sludge drying beds for 2 months                                                   | Flotation, sedimentation                                                     | 0 eggs (N = 3)                                                                           | 2018                | [90]      |
| Brazil        | Dry matter sludge biosolids                                                                  | Filtration, sedimentation, centrifugation and flotation                      | 4.85 helminth eggs/g; of which 0.3% *Taenia* spp. (N = 22)                               | 1997                | [116]     |
| Slovakia      | Raw sludge, activated sludge and drained stabilised sludge                                   | Sedimentation, centrifugation, flotation                                      | 2.27% raw sludge, 1.14% activated sludge and 2% drained stabilised sludge (N = 276)     | 2015                | [117]     |
| France        | Anaerobically digested sludge                                                                | Modified Faust technique (flotation)                                         | Between 2200 and 2400 *Taenia* spp. eggs/kg* sludge (N = 21)                           | 1990                | [118]     |
| England/Wales | /                                                                                           | /                                                                            | Taenid eggs in at least one sample/water authority (N = 162)                           | 1984                | [119]     |
| Morocco       | 3 systems: Natural lagooning, infiltration–percolation sludge followed by sand filtration, and activated sludge plant | Applied flotation method for the analyses of biowastes                     | *Taenia* spp. eggs in natural lagooning: 2 eggs/g; in infiltration–percolation sludge: 8 eggs/g; in sand filtration: 2 eggs/g; in activated sludge: 4 eggs/g (N not indicated) | 2019                | [120]     |
| Mexico        | Sludge from 3 systems: Conventional APT* with parallel plates; sludge blanket APT; and sand-assisted sedimentation | US EPA technique                                                            | 90% of helminth eggs destroyed (N not indicated)                                          | 2000                | [91]      |
| Australia     | Treatment: Chlorine, copper sulphate, slaked lime, ferric sulphate, UV light, drying, moist heat and cold | *In vivo* feeding to calves                                                  | Only drying, keeping dry for 1 day in the presence of a small amount of common salt and boiling for 5 min killed the eggs (N not indicated) | 1937                | [92]      |

*APT, Advanced primary treatment (coagulation/flocculation/sedimentation); US EPA, United States Environmental Protection Agency*
time period (T. multiceps, Wales, [75]), suggesting that survival is dependent on the Taenia spp. studied and the outdoor conditions. Since most of the studies included in this review covered only a limited time period and given current knowledge that eggs are able to survive for at least 1 year, the fact that many studies still found eggs to survive at the end of the study period does not allow a solid conclusion to be made on when survival will have decreased to a minimum [73, 76, 78]. The long survival time, certainly under optimal conditions, inevitably increases the chance for an egg to infect a new host and transmit the infection.

The studies retrieved during the literature search mostly describe experiments on egg survival in Taenia spp. other than T. saginata, T. asiatica and T. solium. The eggs of these other Taenia spp. might be affected in a similar way when put under stress although this is not a certainty; for example, eggs of Echinococcus granulosus, which are morphologically identical to those of Taenia spp. were still infective after freezing to –30°C [79].

Several in vivo experiments included in this review reported questionable results due to the unknown prior infection status of the experimental animals (e.g. [28]), unknown prior infectivity status of the pasture or the absence of a control for natural infection occurring during the experiment (e.g. [28]). In other experiments, a small sample size was often reported (e.g. [80]). Experiments using in vivo techniques, detecting cysticerci in test animals, may be biased because the establishment of cysticerci is highly variable among individual animals [81]. Coman and Rickard [26] found that in vitro techniques for assessing the hatching and viability of T. pisiformis eggs did not reliably agree with their infectivity in rabbits, indicating that it may not be possible to compare results from studies using in vitro and in vivo techniques.

There is a lack of recent, structured research on the environmental factors affecting egg survival of the zoonotic Taenia spp. Studies on this topic can be complicated by the accessibility of Taenia spp. eggs for experimental work. To be able to compare results, homogenous batches of eggs are necessary, but developmental stages and egg infectivity are highly variable between individual tapeworms, between proglottids from the same tapeworm and even within one proglottid [82]. In addition, laboratory extraction and preparation processes may affect the viability of eggs. It should also be noted that working with eggs of T. solium is highly hazardous. As a proxy for studies on the survival of eggs of zoonotic Taenia spp., eggs of non-zoonotic Taenia spp. may be used, which are easier to obtain and do not pose a health hazard in the laboratory. However, although eggs of Taenia spp. are morphologically indistinguishable, their resistance to environmental conditions may differ. It is important to obtain species-specific data which may help inform dynamic transmission models for the zoonotic Taenia spp. An understanding of the distribution of egg survival times under different conditions would help setting-specific parameterization and greatly facilitate modelling.

The prevalence of Taenia spp. eggs found on fruits and vegetables is high, ranging from 0.9 to 33% [41, 83]. These studies were mostly conducted in developing countries where environmental contamination is expected to be higher due to inadequate sanitary practices. The risk for infection in these countries is therefore most likely higher than in Europe, although in Europe Taenia spp. DNA was found on up to 28% of samples (purchased from fields, greenhouses and wholesalers) in the spring [17]. After industrial washing, the prevalence is greatly reduced, although little information is available on this subject [41, 45, 84]. Overall, there is a risk for infection for the consumer. Industrial washing is performed using active calcium hypochlorite; regular washing with water might not sufficiently reduce the risk.

In soil and water samples, prevalence ranges from 0 to 43% [48, 85]. Studies analysing soil and water samples were performed in a more varied selection of countries. However, similar to the literature regarding parasite egg prevalence on fruits and vegetables, these articles generally focussed on parasite eggs other than those of Taenia spp.; as such, the information available is limited. It has also been shown that egg recovery from vegetables, fruits and the environment (soil and water) was low [86], which may have resulted in underestimation of the data. Variable survival and initial parasite loads on fruit and vegetables and in the soil and water might be found in other climate zones that are not represented in our review. Hygienic standards could vary significantly among regions, and results may not be relevant for other regions. Contamination of fruits and vegetables could happen at any stage during the transit from the field (where the crop was fertilized) to the processing. Poor personal hygiene and general unsanitary conditions could lead to post-washing contamination and hence transmission [36].

Although there is a good body of information showing that eggs can spread and even infect animals through invertebrates in experimental settings, it remains unclear how likely and how important these scenarios could be in real-life settings. Only four articles considered the parasite egg load of insects caught in the wild, and prevalence in these studies was low.

An important factor in the spread and survival of parasitic eggs is the wastewater treatment system. As seen from the results shown here, egg removal efficiency is very variable in the different systems used in different
countries, and many systems were found to be unable to fully remove *Taenia* spp. eggs from the treatment water [87–89], allowing the eggs to spread over larger distances *via* waterways. As egg survival is determined by humidity, eggs are able to survive in water for a long time. Furthermore, several articles pinpointed access to surface water or the proximity of a wastewater treatment plant as risk factors for cysticercosis [61–63].

The inability to remove *Taenia* spp. eggs from the wastewater may be due to the type of wastewater treatment system and its quality. The variability between systems and between parasite egg load in the influent make it difficult to project these results to other regions and wastewater management systems. The papers also focussed on total parasite egg load and provided only limited information on *Taenia* spp.

Most of the eggs end up in the sewage sludge produced during the processing of wastewater [90–92], and experiments have proven that eggs can remain viable for a long time, retaining their infectivity for hosts and thus potentially leading to outbreaks [66–69]. Therefore, using sludge from wastewater treatment plants to fertilize fields on which crops used for animal fodder and human food are subsequently grown could lead to a very high risk of infection. In the EU, the use of sewage sludge in agriculture on land grazed by cattle is restricted and regulated under Council Directive 86/278/EEC [93]. In general, the Directive states that sludge can be used, albeit under conditions in which harmful effects are prevented to soil, vegetation, animals and humans. Sludge must be treated prior to its application on fields by either injecting or working into the soil. In terms of the risk of *Taenia* spp. eggs, there needs to be a minimum of 3 weeks of no grazing or harvesting of crops after treatment with sludge. As it has been demonstrated that eggs remain viable up to 1 year, this period is clearly too short. Some EU countries, however, have a more stringent national legislation compared to the EU directive (Austria, Belgium, Denmark, France, Germany, Netherlands, Sweden) [94].

**Conclusions**

In conclusion, the results of this systematic review show that our knowledge of the survival and transmission of *Taenia* spp. eggs in the environment is limited. Indeed, in terms of factors determining egg survival, the results were often doubtful, and in terms of contamination of food, soil, water and the water and sludge from the sewage treatment process, the information was focussed on specific regions (climate zones) or was not specific for *Taenia* spp. Current results indicate that egg survival at moderate temperatures (5–25°C), combined with other conditions favourable for survival (e.g. RH > 80%), together with the large number of factors facilitating egg dispersal (ineffective sewage treatment, contamination of food, possible dispersal in water and soil and to some extent transmission by invertebrates) are making future control/elimination of *Taenia* spp. challenging. Future studies are necessary to identify applicable and sustainable methods to identify and inactivate parasite eggs in the environment and to reduce the spread thereof. Molecular techniques, such as the use of microsatellite markers, to examine genetic variability at the farm or regional level may help unravel specific knowledge gaps. Understanding the epidemiology and the transmission dynamics of *Taenia* spp., and thus approaching egg survival and the dispersal problem from a different angle, might result in new insights and lead to other, possibly more efficient control options.

**Supplementary Information**

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Additional file 1: The protocol used for this review.

Additional file 2: PRISMA checklist.

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Author’s contributions

All authors (FJ, PD, SG, VO, MVJ, CT) contributed to the conception and design of the review. The systematic review was performed by FJ and CT, and development of the manuscript was mainly the responsibility of FJ, with the help of CT. All authors contributed to the changes made to subsequent versions from the first version onwards. All authors read and approved the final manuscript.

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