Review article

Impacts of dams on freshwater turtles: a global review to identify conservation solutions

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Highlights

- Damming of rivers is an increasing global threat to natural resources and biodiversity, particularly for freshwater turtles, a culturally important but globally threatened group of vertebrates.
- A review of the scientific literature was conducted to understand threats, impacts and mitigation actions of dams for freshwater turtles.
- Studies were often short-term with geographic and taxonomic biases: most studies were from temperate regions of North America and none from Africa.
- Although several mitigation actions were proposed only four have been tested for freshwater turtles.
- There is an urgent need to generate robust effective mitigation actions, particularly in tropical regions experiencing rapid expansion in dams.

Abstract

Dams create many impacts on freshwater ecosystems and biodiversity. Freshwater turtles are at direct and indirect risk due to changes caused by damming including the loss of terrestrial and aquatic nesting and feeding habitats, changes to resource availability and reduced dispersal. We reviewed the global scientific literature that evaluated the impact of dams on freshwater turtles, and carried out additional searches of literature published in seventeen languages for studies evaluating actions to mitigate the impact of dams. The search produced 43 published articles documenting dam impacts on 29 freshwater turtle species from seven families (Chelidae, Chelydridae, Emydidae, Geoemydidae, Kinosternidae, Podocnemididae and Trionychidae) in 13 countries. More than a third of studies (41.9%, n = 18) focused on nine North American species of the Emydidae. Few studies were found from Europe and Asia and none from Africa. The number of studies, life-history stage studied and threat status differed significantly between temperate and tropical latitudes. Most studies were from temperate latitudes, where studies focused more on adults and less threatened species compared with tropical latitudes. Studies evaluated dam impacts as barriers and changes to water flow and quality, but no studies were found that assessed turtles and changes to land cover or mercury caused by dams. More than half of the studies (59%, n = 24) suggested actions to help mitigate dam impacts. Yet, only four studies on three temperate and one tropical species documented the effect of interventions (dam removal, flow management, artificial pond maintenance and community-based action). These findings demonstrate a lack of documented evidence evaluating dam impacts on freshwater turtles particularly in tropical regions. This lack of evidence reinforces the importance of strengthening and maintaining robust long-term studies of freshwater turtles needed to develop effective conservation actions for this group of vertebrates.

Keywords: Conservation evidence; Dams; Habitat transformation; Hydropower development; Mitigation actions; Turtles; Testudines.

1. INTRODUCTION

Anthropic change in land use by agriculture, urbanization and mining, as well as pollution and the construction of dams, contribute to the transformation of freshwater habitats and, as a consequence, to biodiversity loss (Bodie, 2001; Dudgeon, 2019). Biodiversity decline is generally related to modification and fragmentation of habitat and occurs in a more accelerated manner in fresh-water ecosystems compared to marine or terrestrial ecosystems (Harrison et al., 2018; He et al., 2018).

Rivers provide a wide variety of habitats and ecosystem services but are also a major source of electricity generation, with 16.4% of global production derived from hydropower dams (WBG, 2020). Planning and construction of hydropower dams is a development focus of national and international governments (Athayde et al., 2019; Gerlak et al., 2020) to satisfy the growing demand for electrical power and promote the use of sustainable energies (Almeida et al., 2016; Castello, 2021). In some cases, basins contain multiple dams with different uses including hydropower, water supply, flood control, for navigation by boats and/or as places used for recreational activities for human populations (Bennett et al., 2009; Clark et al., 2018; Hecht et al., 2019).

Currently, hydrological basins of high biodiversity importance, such as the Amazon basin (South America), the Congo (Africa), the Mekong (Asia), Ganges-Brahmaputra (Asia) and Yangtze (Asia), are a focus of rapid expansion in damming for hydropower development (Hecht et al., 2019; Winemiller et al., 2016; Zarfl et al., 2019). The construction and operation of hydropower dams can, however, trigger a cascade of effects across both the social and environmental sectors. In the social sector, indigenous and traditional riverside communities can lose resources essential for their subsistence, triggering changes to their cultures and ways of life and forcing evictions (Berkun, 2010; Fearnside, 2019; Santos et al., 2020). In the environmental sector, hydropower dams are considered primary threats to freshwater species, as well as the surrounding ecosystems including floodplains and wetlands (Berkun, 2010; Dudgeon, 2000; Vasconcelos et al., 2020).

Species that inhabit freshwater ecosystems are vulnerable to extinction due to dams impacts (Brum et al., 2021; Dudgeon, 2019; Tickner et al., 2020), as their life history and biological schedules often strongly depend on the hydrological regime (Zarfl et al., 2019). Although populations of freshwater vertebrate species have declined at more than twice the rate of terrestrial or marine vertebrates (Grooten and Almond, 2018; Tickner et al., 2020), relatively few studies have evaluated the impact of dams on vertebrates (dos Santos et al., 2021; He et al., 2018). Most of these studies focused on impacts to fish populations because fishes are often both an important source of protein for riverside communities as well as commercially important to national economies (Duponchelle et al., 2021). Indeed, impacts of dam developments could contribute to the extinction of vertebrate species [e.g. dolphins (Brownell Robert et al., 2017; Turvey et al., 2010)] or extirpation in impacted basins [e.g. turtles (Jian et al., 2013; Santoro et al., 2020)]. Despite the known impacts, there is little available evidence documenting dam mitigation interventions for aquatic fauna such as freshwater turtles (CEE, 2021; Sainsbury et al., 2021; Tickner et al., 2020).

Turtles are an ancient, widespread and instantly recognizable group that not only provide highly valued cultural, medicinal and economic resources across the globe (Haitao et al., 2008; Liu et al., 2020; Lovich et al., 2018; Mendiratta et al., 2017; Sigouin et al., 2017; TTWG et al., 2017) but also provide inspiration for the development of 21st century biomimetic robotics (Kim et al., 2012; Soliman et al., 2021). Of the currently recognized turtle species 79.4% (286) are species considered to be of aquatic or semiaquatic habits (Rhodin et al., 2018; Uetz et al., 2021). Freshwater turtles directly and indirectly provide benefits to human societies (Costanza et al., 1997; Lovich et al., 2018). The meat and eggs of freshwater turtles are used as food resources (Johns, 1987 ; Klemens and Thorbjarnarson, 1995; Nagel, 1979; Rebêlo and Pezzuti, 2000; Smith, 1979), while the fat, viscera and shell are used in traditional medicine (Dudgeon, 2019; Pezzuti et al., 2010). Freshwater turtles can also provide important ecological services for maintaining the functions and processes of aquatic and terrestrial ecosystems (Lovich et al., 2018).

The habitat requirements and life history of freshwater turtles vary among species and their habitats. Aquatic and semiaquatic turtles use diverse habitats including: river banks, flood plains, rapids, slow moving waters, shallow waters, large rivers, lakes and reservoirs (Moll and Moll, 2004). As primary consumers of vegetation freshwater turtles contribute to the transfer of energy, nutrients and matter (Lovich et al., 2018), contributing to cycling of minerals such as calcium and phosphorus (Lovich et al., 2018) and serving as seed dispersers. They also prey on small fish and invertebrates, and are themselves prey of larger vertebrates (Moll and Moll, 2004).

Although important to humans and aquatic ecosystem functioning, turtles are classified as the most threatened groups of freshwater vertebrates (Stanford et al., 2020; Tickner et al., 2020) with 61% of these species under some degree of threat (Rhodin et al., 2018; TTWG et al., 2017) mainly due to a combination of overexploitation and habitat loss (Stanford et al., 2020). The life history of freshwater turtles limits adaptive responses to rapid and devastating anthropic impacts, such as those caused by dams. Even protected areas are insufficient to buffer freshwater turtles from human impacts (Howell et al., 2019; Norris et al., 2019). Studies of population dynamics of freshwater turtles remain scarce, as there is a lack of robust information on the life history of many species particularly those found in the tropics (Rachmansah et al., 2020; Rhodin et al., 2018). As such, the ecological requirements and life history of at least 30% of turtle species are as yet unknown, making their conservation status difficult to evaluate (Rhodin et al., 2018).

In this paper we synthesize studies that have evaluated the state of conservation of freshwater turtles in areas around the world altered by dams. Our aim was to identify the research trends, mitigation actions both proposed and tested, gaps in the current knowledge about dam impacts, and solutions for freshwater turtles. The findings highlight the importance of better understanding dam impacts on freshwater turtles as a means for effective conservation actions for these among the most threatened groups of vertebrates.

2. METHODOLOGY

2.1. Literature search

A review of the scientific literature following the protocol of Preferred Reporting Items for Systematic Reviews and Meta-Analyses [PRISMA, (Page et al., 2021)] was conducted for articles published from 1945 to August 2021 in the ISI Web of Science (Core Collection) database. Searches were conducted in English using the following combination of terms: (turtle* OR terrapin* OR Chelon* OR Testudines OR Cryptodira OR Pleurodira) AND (hydropower OR dam* OR hydroelectric* OR reservoir*).

2.2. Selection criteria and process

The search identified a total of 1001 articles (Supplemental material 1). Article titles and abstracts were screened to retain studies that potentially included freshwater turtles and dams [Fig.1 (Gough et al., 2020)]. The full text of 101 articles that passed screening was then read and articles were assessed based on two criteria: 1) the study had to include data on at least one freshwater turtle species; 2) the study evaluated current- or post-construction impacts and/or mitigation actions of dams (including removal). We included original research articles with primary and secondary data, including field based, modelling inference, interviews and laboratory (e.g. genetic) studies. Studies that included only summarized versions of compiled primary data (e.g. reviews and perspectives) were excluded.

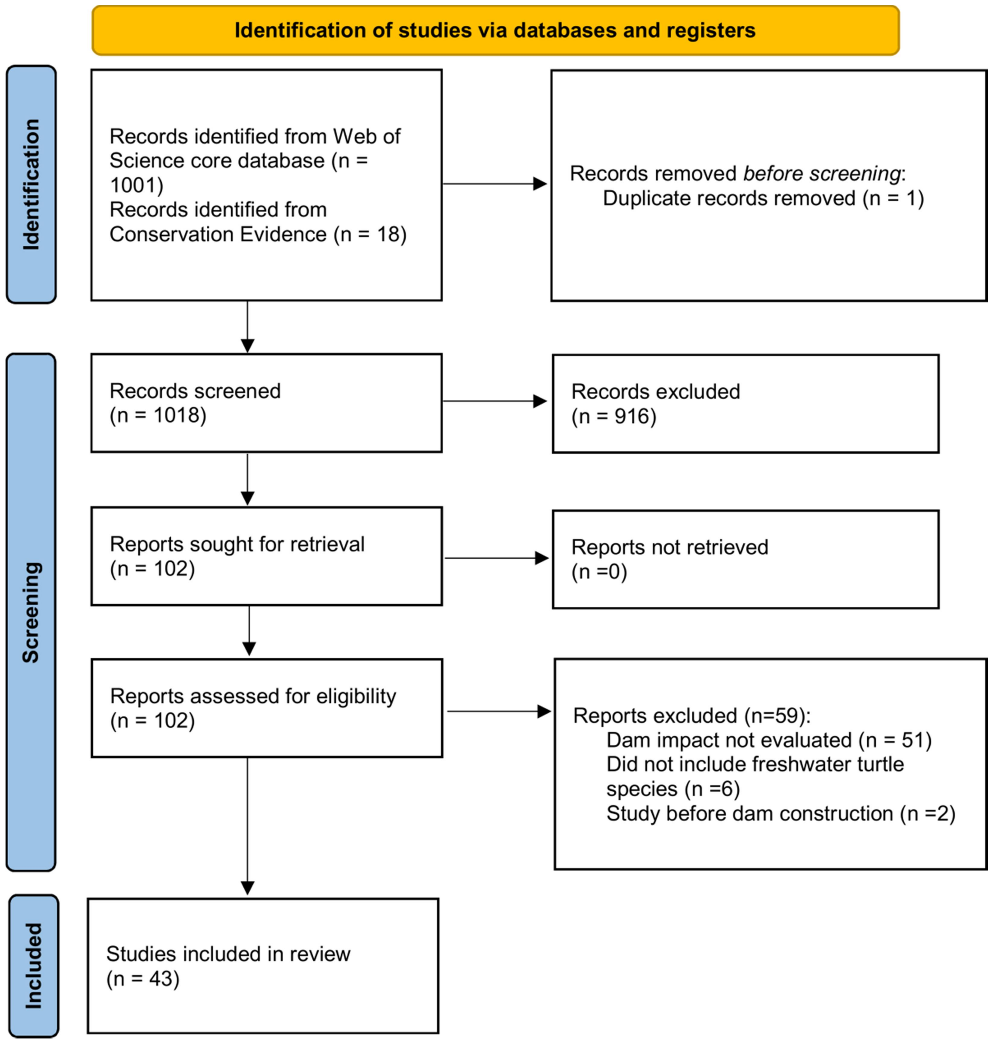

Figure 1. Literature search. Flow diagram with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) process steps and number of studies excluded and included.

2.3.Conservation Evidence literature database search for mitigation studies

The Conservation Evidence (https://www.conservationevidence.com/) discipline-wide literature database was also searched (Conservation Evidence, 2021). This is a database of publications that describe studies of conservation interventions, compiled using systematic searches of both English and non-English language journals (all titles and abstracts) and report series ('grey literature') (Sainsbury et al., 2021). To date, systematic searches of over 330 English language journals, over 300 non-English language journals (from 16 different languages) and 24 report series have been conducted (Supplementary material 2). At initial screening, all articles that measured the effect of an intervention that might be done to conserve biodiversity, or that might be done to change human behavior for the benefit of biodiversity were included. English language articles relevant to any reptile species were then read in full and reassessed based on whether the effectiveness of an action to mitigate the impact of dams on freshwater turtles was included. For non-English language articles that passed the initial screening, keyword searches for the terms 'turtle' and 'terrapin' were carried out, and the title and abstract of the resulting articles were read to check for any mention of freshwater turtles and dams.

2.4. Study data extraction

Data were extracted from a total of 43 selected articles (42 in English and one in Spanish). The following information was extracted from the text: study country, duration (in years), turtle species, and turtle life stage, which was grouped into three classes based on life history and management relevance (Lovich et al., 2018; Rachmansah et al., 2020; Shine and Iverson, 1995): early (nest/egg/hatchling), juvenile and/or adult turtle. Species' taxonomy and distribution (temperate or tropical latitude) was obtained from published data (TTWG et al., 2017). The threat status for each species was obtained from the most recently updated assessment (Rhodin et al., 2018).

All articles were classified in thematic areas based on the anthropic threats cited by the literature [Table 1, (Alho, 2011; Athayde et al., 2019; Lees et al., 2016; Winemiller et al., 2016)]. "Solutions" follow the six priority actions for the recovery of freshwater biodiversity identified by Tickner et al. (2020). For each article we identified the principal threats, impacts and solutions evaluated in the study: a) Threats, changes resulting from dams that generated direct or indirect impacts on freshwater turtles; b) Impacts, refers to consequences of these threats; c) Solutions, mitigation actions used or proposed to minimize dam development impacts on freshwater turtles (Table 1).

Table 1. Thematic areas. Thematic areas and typologies used to classify the 43 selected studies. Theme and associated descriptions based on previous reviews of dam impacts (Alho, 2011; Athayde et al., 2019; Lees et al., 2016; Winemiller et al., 2016). "Solutions" follow priority actions for the recovery of freshwater biodiversity (Tickner et al., 2020). "References" presents the list of studies from the literature search of dam impacts on freshwater turtles.

Theme	Description	References
Threat		
Physical barriers	Habitat fragmentation; change in species distribution and abundances; population isolation.	Bennett et al. (2009); Bennett et al. (2010); Bennett and Litzgus (2014); Berry et al. (2020);Gaillard et al. (2015); Ghaffari et al. (2014); Gonzalez-Zarate et al. (2011); Ihlow et al. (2014); Kiesow and Warcken (2017); Melancon et al. (2013); Reese and Welsh Jr (1998a); Reinertsen et al. (2016); Ward et al. (2013).
Land cover change	Feeding/nesting/refuge habitat loss.	-
River flow	Changes to river flow alter seasonal availability of habitat.	Bayrakcý et al. (2016);Bondi and Marks (2013); Clark et al. (2018); Fagundes et al. (2021); Gallego-García and Castaño-Mora (2008); Jian et al. (2013);Le Duc et al. (2020);McDougall et al. (2015) ;Norris et al. (2018a); Pitt et al. (2021); Richards-Dimitrie et al. (2013); Tornabene et al. (2019); Tucker et al. (2012).
Water quality	Dams change physical and chemical properties (e.g., oxygen levels, water temperature and sediment flow).	Clark et al. (2009); Reese and Welsh Jr (1998b); Selman and Jones (2017); Snover et al. (2015).
Mercury	Mercury bioaccumulation effects (mercury levels change due to changes in water quality).	-
Impact		
Movement	Home range, migration, density and abundance.	Berry et al. (2020); Bondi and Marks (2013); Clark et al. (2018); Ghaffari et al. (2014); Reese and Welsh Jr (1998a); Tornabene et al. (2019); (Ficheux et al., 2014);
Reproduction	Behavior, nest-site selection, embryonic development, hatchling success, sex ratio.	Fagundes et al. (2021); Gallego-García and Castaño-Mora (2008); Jian et al. (2013); McDougall et al. (2015); Norris et al. (2018a);
Nutrition	Feeding behavior.	Melancon et al. (2013); Richards-Dimitrie et al. (2013); Tucker et al. (2012).
Growth rate		Bennett et al. (2009); Snover et al. (2015).
Survival	Disease, predation risk, injuries.	Bennett and Litzgus (2014); (Ficheux et al., 2014)
Sensitivity	Abiotic factors that influence the presence/absence of species, i.e. dissolved oxygen, temperature, water depth.	Bayrakcý et al. (2016); Clark et al. (2009); Gonzalez-Zarate et al. (2011); Le Duc et al. (2020); Pitt et al. (2021); Reese and Welsh Jr (1998b); Selman and Jones (2017).

Genetic diversity	Adaptive potential.	Bennett et al. (2010); Gaillard et al. (2015); Ihlow et al. (2014); Kiesow and Warcken (2017); Reinertsen et al. (2016); Ward et al. (2013).
Solutions		
Accelerate implementation of environmental flows	River basin planning, water allocation, infrastructure design and operation.	(Tornabene et al., 2019); (Norris et al., 2018a); (Ward et al., 2013); (Tucker et al., 2012); (Reese and Welsh Jr, 1998b); (McDougall et al., 2015); (Ficheux et al., 2014); (Espinoza et al., 2021); (Tornabene et al., 2018)
Improve water quality	Waste water treatment, regulation of polluting industries, market instruments, improved agricultural practices, nature-based solutions.	
Protect, create and restore critical habitats	Protected areas, land-use planning, markets for ecosystem services, habitat restoration.	(Fagundes et al., 2021); (Pitt et al., 2021); (Norris et al., 2018a); (Ghaffari et al., 2014); (Bennett and Litzgus, 2014); (Reese and Welsh Jr, 1998b); (Gonzalez-Zarate et al., 2011); (Stone et al., 2014); (Tornabene et al., 2018); (Tornabene et al., 2019); (Chelazzi et al., 2007)
Manage exploitation of freshwater species.	Science-based management, community management, bycatch reduction.	(Fagundes et al., 2021); (Pitt et al., 2021); (Le Duc et al., 2020); (Ihlow et al., 2014); (Jian et al., 2013); (Gonzalez-Zarate et al., 2011); (Selman and Jones, 2017);
Prevent and control nonnative species invasions in freshwater habitats	Identification and control of introduction pathways, control and eradication of established invasive nonnative species.	(Berry et al., 2020); (Koizumi et al., 2016); (Koizumi et al., 2017)
Safeguard and restore freshwater connectivity	System-scale infrastructure planning, dam reoperation and removal, levee repositioning, passes.	Pitt et al. (2021); (Ghaffari et al., 2014); (Ihlow et al., 2014); (Tucker et al., 2012); (Gaillard et al., 2015); (Ward et al., 2013)

2.5 Data analysis

Patterns in the geographic distribution of publications were evaluated using maps and descriptive analysis. Taxonomic representativeness was assessed using non-parametric tests to compare frequency distributions of studied species with that of extant species per Family (TTWG et al., 2017; Uetz et al., 2021). Similarly, to understand if studied species could be considered as reflecting 21st century threats, the threat status of studied species was compared against the distribution of extant species (Rhodin et al., 2018). Non-parametric tests were preferred as they are robust and widely adopted for cases with discrete data and small group sizes (Agresti, 2012) and to avoid increased probability of type I errors with parametric frequentist or Bayesian options (Kelter, 2021). Finally, based on the literature reviewed we qualitatively synthesized the effect level on each turtle life stage as positive (with an ecological or biological benefit); neutral (no relevant ecological and biological impacts); negative (harms the turtle life stage); and unstudied (if we did not find literature to support it). All analyses were performed in R (R Development Core Team, 2020) with functions available in base R and "tidyverse" collection of packages (Wickham et al., 2019).

3. RESULTS

3.1. Geographic and taxonomic bias in the literature

The 43 articles selected included studies based on field surveys (76.7%, n = 33), laboratory research (14.0%, n = 6), interviews (5.7%, n = 2) and modelling inference (5.7%, n = 2). Several studies (16.3%, n = 7) were conducted along waterways with dams providing multiple functions (e.g., a mix of hydropower, water supply, flood control, and navigation). Most studies evaluated more localized impacts of dams with single functions, with hydropower dams evaluated in 37.2% (n = 16) of selected articles, whereas 44.2% (n = 19) involved water supply/irrigation dams and 2.0% (n = 1) was a predominantly navigational water way with locks and dams.

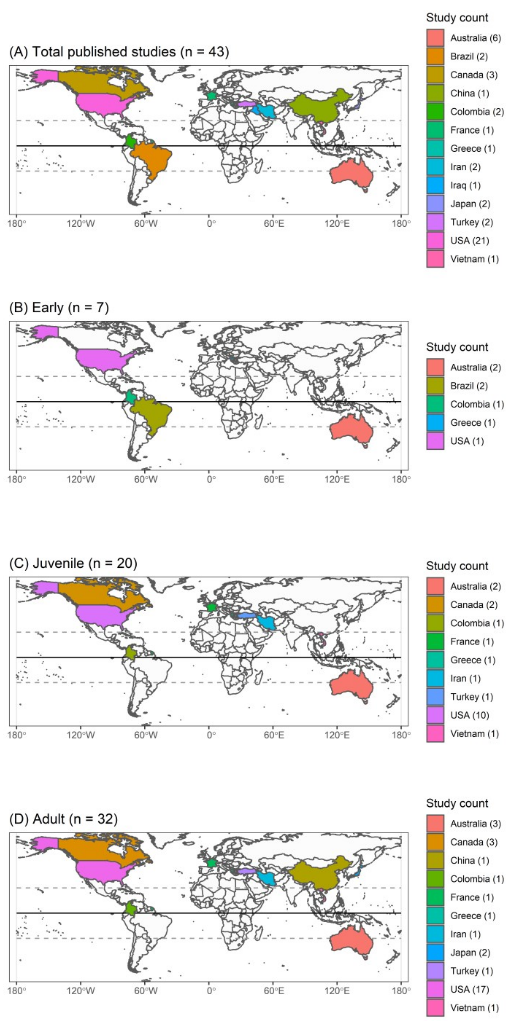

Figure 2. Geographic distribution of articles. Maps showing the geographic distribution of countries where studies were conducted. Showing (A) overall distribution of studies, and countries with studies examining (B) early (nest/egg/hatchling), (C) juvenile or (D) adult life-stages for measures of dam impacts.

There were clear geographic differences in the number of studies (Fig. 2), with more than half of studies from North America (n = 24), followed by Australia (n = 6). No studies were found from Africa (Fig. 2). Adult turtles were the main focus for studies, with 32 articles from 11 countries examining adults (Fig. 2). Additionally, 20 articles from nine countries examined juveniles and seven articles from five countries studied early stages (nests, eggs or hatchling, Fig. 2). Three studies focusing on genetics did not specify the life-stage from which tissue samples were collected (Gaillard et al., 2015; Ihlow et al., 2014; Kiesow and Warcken, 2017). One study evaluated turtle presence and absence at different sites without specifying life-stage (Gonzalez-Zarate et al., 2011) and two studies did not specify the life stage of captured turtles (Clark et al., 2018; Stone et al., 2014).

Freshwater turtles are found in 11 Testudine families (species counts in parentheses): Chelydridae (5), Dermatemydidae (1), Kinosternidae (31), Emydidae (51), Platysternidae (1), Geoemydidae (71), Carettochelyidae (1), Trionychidae (32), Chelidae (58), Pelomedusidae (27) and Podocnemididae (8) (Rhodin et al., 2018; Uetz et al., 2021). Studies examined dam impacts on 29 freshwater turtle species from seven of 11 families (Table 2). Although there was a weak positive relationship, the number of studies was not significantly correlated to the number of extant species in each family (Spearman's Rho = 0.40, p = 0.379, Fig. 3). More than a third of studies (41.9%, n = 18) focused on nine North American species of the Emydidae. The Chelydridae (2.3%, n = 1) was the least studied family and Geoemydidae most underrepresented of the studied families (Fig. 3) relative to extant aquatic turtle diversity (Rhodin et al., 2018; Uetz et al., 2021). The number of species studied in each family was also not significantly correlated to the number of extant species in each family (Spearman's Rho = 0.36, p = 0.379) and followed a similar pattern to number of studies, with Emydidae species most frequently studied and Chelydridae the most understudied (Fig.3). Of the four unstudied families three included few (5 or fewer) species, but with 27 extant species

Pelomedusidae (expected range of 4 to 7 studies, Fig. 3) was the most underrepresented of all families.

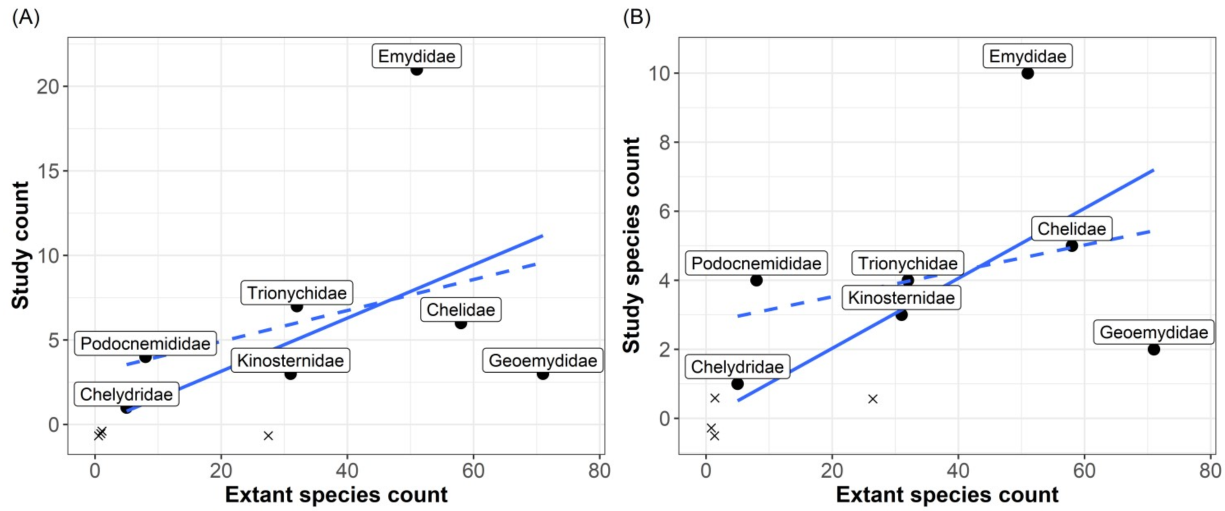

Figure 3. Taxonomic representativeness of articles. Comparison of the number studies (A) and studied species (B) and extant turtle species per Family [from TTWG et al. (2017)]. Solid lines from a linear model of the expected number in proportion to extant species count, dashed lines from linear model of values obtained from the literature review (lines added to aid visual interpretation). Crosses show the number of extant species in families with no studies (not included in the linear models, crosses are dodged to avoid overlapping).

According to the updated classifications, of the studied species 48% (n = 14) were classified as threatened (CR, EN or VU, Table 2). Whereas 41% (n = 12) of all studied species were classified as Least Concern (LC) and 10% (n = 3) as Near Threatened. The distribution of threatened and nonthreatened species was not significantly different from 50:50 (χ^2= 0.03, df = 1, p = 0.853) and follows the expected distribution (χ^2 = 1.001, df = 1, p = 0.578) of the threat status from 360 Testudine species [n = 187 and 138 threatened and unthreatened species respectively, (Rhodin et al., 2018)]. The number of temperate and tropical species studied did differ between threat status categories (Fisher's Exact Test, p = 0.009), with studies of temperate species having a greater proportion of LC (50 and 22% of studied species, temperate and tropical respectively) and tropical a greater proportion of CR species studied (5 and 44% of studied species, temperate and tropical respectively).

Table 2. Turtle species. Number of studies examining threats of dams to freshwater turtles obtained from the published literature. Mean values for age at first reproduction ("AFR", in years) and maximum longevity ("ML", in years).

Family (study count)	Species[a]	Region[b]	Study count[c]				AFR[d]	ML[e]
			No.	Early	Juvenile	Adult		
Chelidae (6)								
	Chelodina longicollis (LC)	Temperate	1	0	1	1	10.5	
	Elseya albagula (EN)	Tropical	2	1	1	1		
	Elusor macrurus (CR)	Tropical	2	1	0	1	15.0	
	Emydura macquarii (LC)	Tropical	2	0	1	1	8.0	
	Myuchelys latisternum (LC)	Tropical	2	0	1	1		
Chelydridae (1)								
	Chelydra serpentina (LC)	Temperate	1	0	1	1	10.8	47.0
Emydidae (21)								
	Actinemys marmorata (VU)	Temperate	6	1	4	5	6.0	
	Emys orbicularis (NT)	Temperate	1	0	1	1	17.1	
	Graptemys caglei (EN)	Temperate	1	0	0	1		14.5
	Graptemys geographica (LC)	Temperate	5	0	3	5	10.8	19.2
	Graptemys oculifera (VU)	Temperate	2	0	0	1	8.5	36.9
	Graptemys ouachitensis (LC)	Temperate	1	0	1	1	6.3	34.9
	Graptemys pearlensis (EN)	Temperate	1	0	0	1		
	Graptemys pseudogeographica (LC)	Temperate	1	0	0	0	6.0	35.4
	Graptemys pulchra (NT)	Temperate	1	0	1	1	12.0	20.0
	Trachemys scripta (LC)	Temperate	4	0	2	4	6.7	50.2
Geoemydidae (3)								
	Mauremys reevesii (EN)	Temperate	1	0	0	1	10.5	24.2
	Mauremys rivulata (LC)	Temperate	2	1	2	2		
Kinosternidae (3)								
	Kinosternon sonoriense (NT)	Temperate	1	0	0	0	6.0	
	Sternotherus depressus (CR)	Temperate	1	0	1	1	7.0	
	Sternotherus odoratus (LC)	Temperate	1	0	1	1	4.0	
Podocnemididae (4)								
	Podocnemis expansa (CR)	Tropical	1	1	0	0	12.3	40.2
	Podocnemis lewyana (CR)	Tropical	2	1	1	1	5.5	
	Podocnemis sextuberculata (VU)	Tropical	1	1	0	0	5.0	50.0
	Podocnemis unifilis (EN)	Tropical	2	2	0	0	9.3	50.8
Trionychidae (7)								
	Apalone mutica (LC)	Temperate	1	0	0	1	7.8	
	Apalone spinifera (LC)	Temperate	3	0	0	3	8.5	50.0
	Rafetus euphraticus (EN)	Temperate	2	0	1	1		
	Rafetus swinhoei (CR)	Tropical	2	0	1	2		

[a] Text in parenthesis represents the revised IUCN Red List classification for each species (Rhodin et al., 2018).
[b] Latitudinal distribution based on maps and descriptions in TTWG et al. (2017).
[c] When the same article studied multiple species the same article is included multiple times in the species study counts presented.
[d] Age at first reproduction ("AFR", years) from data in Rachmansah et al. (2020) and Species360 (https://www.species360.org/serving-conservation/turtles-tortoises-cites/, accessed 10 September 2021).
[e] Maximum longevity ("ML", years) from Species360 (https://www.species360.org/serving-conservation/turtles-tortoises-cites/, accessed 10 September 2021).

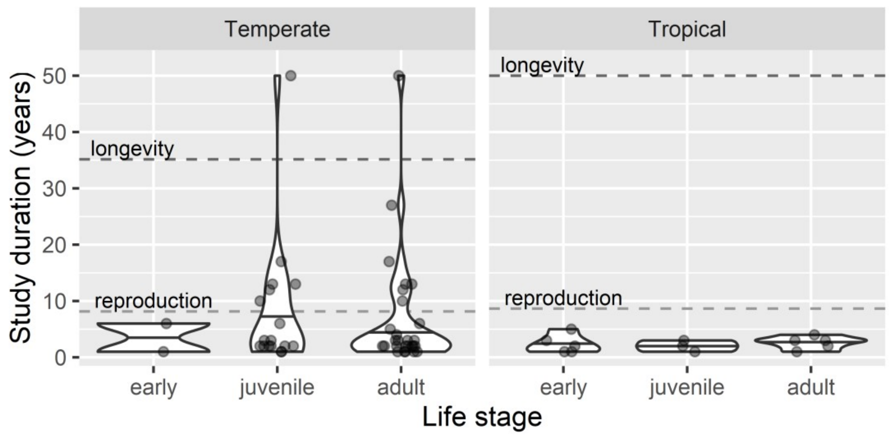

Figure 4. Study duration. Comparison of the years of study examining dam impacts on freshwater turtles in temperate and tropical regions. Distribution of values compared across three life-stage classes (early, juvenile and/or adult, n = 37 studies). Solid horizontal lines are 50% quantile of values per life-stage class. Dashed horizontal lines are median values for age at first reproduction (n = 16 and 6 species, temperate and tropical respectively) and maximum longevity (n = 10 and 3 species, temperate and tropical respectively).

Most (74.4%, n = 32) studies were conducted in temperate latitudes (Table 2, Fig. 2). Many more studies in temperate regions focused on older age classes (4.4, 37.0 and 58.7% for early, juvenile and adults stages respectively) than in tropical regions (38.5, 23.1, and 38.5% for early, juvenile and adults, respectively, Fisher's Exact Test p = 0.00904, Fig. 4). Most studies were of short survey duration, with 79.1% (n = 34) of studies five or fewer years. The vast majority of studies were much shorter than either mean maximum longevity or age at first reproduction of the studied species. Indeed, there were only eight (18.6%) long-term studies (studies of more than 10 years), all from temperate regions (Fig. 4), with only one study (Pitt et al., 2021) continuing for longer than the maximum longevity of the studied species. There were no long-term studies in tropical regions with the majority of tropical studies focusing on early life stages, whereas studies in temperate regions focused more on juvenile and adult stages (Fig. 4).

3.2. Threats and impacts

Relative to thematic areas, the principal focus of research was evaluating the impacts of river flow and physical barriers (n = 21 and 13 respectively) and to a lesser degree water quality, with nine studies (Fig. 5). No studies were found that addressed changes in land cover or mercury levels in turtles caused by dams. The principal biological impacts on freshwater turtles measured were movement (n = 12), sensitivity (n = 9), genetics and reproduction with six articles each, and nutrition with five studies. The areas with least studies were growth rate (n = 4) and just one study examined the threats of injuries for turtle survival (Fig. 5).

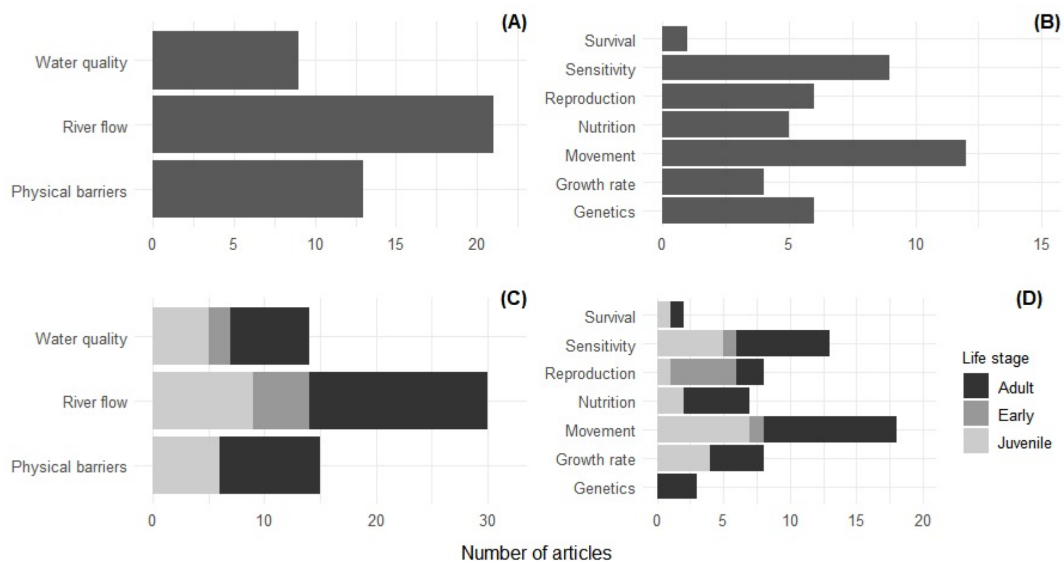

Figure 5. Thematic areas. Total of studies by threats (**A**) and impacts (**B**) and the turtle life stage (**C** and **D**) according to the thematic areas identified in the review of selected articles. When the same article studied multiple life-stages the same article is included multiple times in the counts presented (C and D).

Based on the literature reviewed a qualitative synthesis about the effects on turtle life stage (Table 3) revealed that threats and impacts differed across life stages and between species. In the early stages, river flow and water quality were identified as negative threats. In the juvenile stage, river flow and physical barriers were negative threats, while water quality was negative and positive in the same time, but this varies between turtle species studied. In the adult stage river flow was a negative threat, water quality and physical barriers was positive and negative for some species. The land cover change and mercury remain unstudied as threats in all life stage evaluated. In the case of impacts, in the early life stage movement was positive and negative, while nutrition was neutral, and impacts on reproduction, growth rate, survival and sensitivity were negative. In the juvenile stage, four impacts was negative (movement, reproduction, nutrition and survival), growth rate was positive and sensitivity was considered as positive [i.e. new environmental conditions create refuge habitat for juveniles (Ryan et al., 2015)] and negative [i.e. reduction of oxygen levels limits the presence of turtle species (Clark et al., 2009)]. In the adult stage four impacts were negative (reproduction, nutrition, survival, sensitivity), movement was positive [i.e. favors introduction of alien species (Berry et al., 2020)] and negative [i.e. affecting turtle movement (Bennett et al., 2010)].The impacts on genetic diversity were unknown in all three life stages.

Table 3. Impact level (negative, neutral, positive, unknown or unstudied) from each threat identified and associated dam impacts on freshwater river turtles.

Theme	Turtle life stage		
	Early	Juvenile	Adult
Threat			
Land cover change	Unstudied	Unstudied	Unstudied
River flow	Negative	Negative	Negative
Water quality	Negative	Positive/Negative	Positive/Negative
Mercury	Unstudied	Unstudied	Unstudied
Physical barriers	Unstudied	Negative	Positive/Negative
Impact			
Movement	Positive/Negative	Negative	Positive/Negative
Reproduction	Negative	Negative	Negative
Nutrition	Neutral	Negative	Negative
Growth rate	Negative	Positive	Positive/Negative
Survival	Negative	Negative	Negative
Sensitivity	Negative	Positive/Negative	Negative
Genetic diversity	Unknown	Unknown	Unknown

3.3. Mitigation actions

A total of four studies tested the effect of four mitigation actions (Espinoza et al., 2021; Ficheux et al., 2014; Pitt et al., 2021; Stone et al., 2014). Of these studies, three were from temperate regions with long-term data collection spanning 50 (Pitt et al., 2021), 20 (Stone et al., 2014) and 17 years (Ficheux et al., 2014) and one was a relatively short term (3 year) study from sub-tropical Australia (Espinoza et al., 2021). One article (Pitt et al., 2021) documented the effect of dam removal on the northern map turtle (*Graptemys geographica*). A study from the USA (Stone et al., 2014) demonstrated the potential of volunteers to help implement actions (dam repair and silt removal) to maintain artificial impoundments for the Sonora mud turtle (*Kinosternon sonoriense*). Another from southern France (Ficheux et al., 2014) showed how earlier flooding across wetland areas improved hibernation success for the European pond turtle (*Emys orbicularis*); whilst the study from Australia (Espinoza et al., 2021) demonstrated how environmental flow management could facilitate movements of adult Mary River turtles (*Elusor macrurus*).

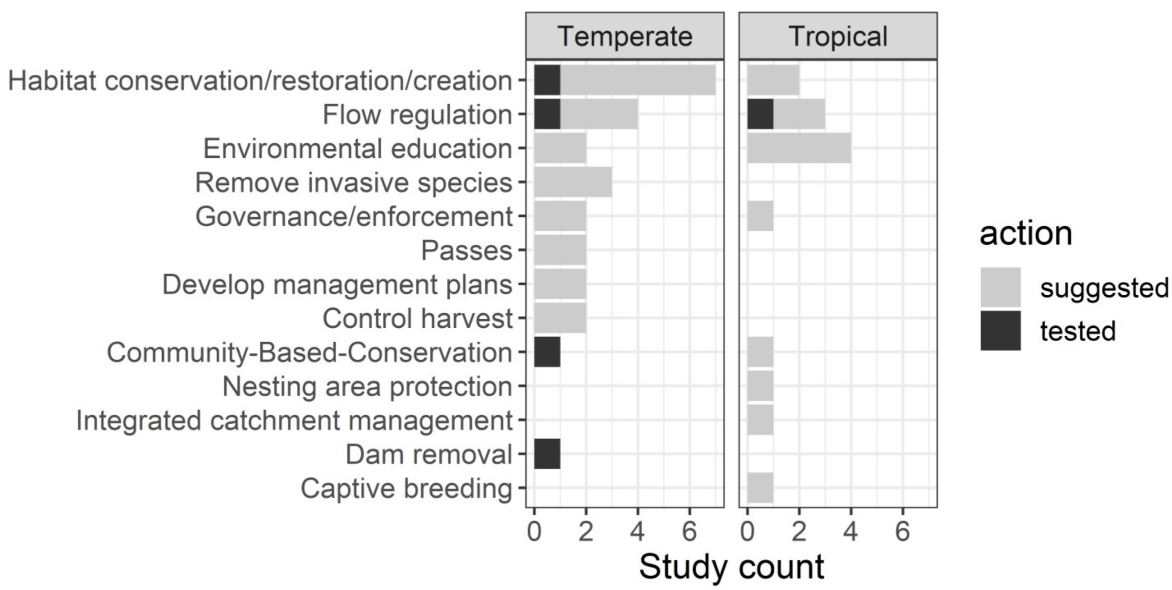

Figure 6. Mitigation actions. Actions presented in 24 of 43 selected articles compared between studies of freshwater turtle species in temperate and tropical regions.

Far more studies (79%, n = 34) presented suggestions for possible actions and/or directions for future advances. From these 34, the need for more research (including suggestions such as: more studies, long-term studies, further investigation, monitoring programs, more detailed investigation, additional research) was most often cited (71%, n = 24). The same number of studies (n = 24) also suggested future actions to help mitigate dam impacts. Although tropical regions had fewer studies, there was an insignificant ($\chi^2 = 0.9168$, df = 1, p = 0.3383) tendency for proportionally more studies to suggest actions from tropical regions 73% (8/11 studies) than temperate regions (50%, 16/32 studies). The principal suggestions to mitigate dam impacts (Fig. 6) were habitat conservation/restoration/creation (8 studies), environmental education (6 studies) and flow regulation (5 studies). While improving governance and enforcement was suggested three times [improved regulation of recreational boating (Bennett and Litzgus, 2014), more rigorous environmental impact assessments (Norris et al., 2018a) and additional state/federal protections for declining species (Selman and Jones, 2017)].

4. DISCUSSION

This review assessed research studies on dam impacts on freshwater turtles to describe the trends and identify the thematic fields and gaps in current research. Studies were primarily focused on the study of river flow changes, however, there were few studies in some regions, principally in the tropics, and gaps on important themes like bioaccumulation of mercury linked to hydropower dams. Based on the information analyzed, we first discuss the descriptive dimensions. Secondly, to ensure the objectivity of content analysis, we applied a structured and systematic approach to integrate the information reviewed (Wu et al., 2019). Finally, we describe the impacts of dams on freshwater turtle populations and the mitigation actions proposed and implemented for turtle recovery and conservation.

4.1. Descriptive dimensions

In general, few studies focused on dam impacts on freshwater turtles, additionally there were marked differences in the scientific production between temperate and tropical latitudes. Differences were found between studies evaluating the life history of turtles from these two latitudes. Our finding that 62.5% of studies were from USA and 66% of the total studies were from temperate latitudes confirms results from a previous study that showed most scientific knowledge came from temperate regions (Rachmansah et al., 2020). This geographic bias was particularly surprising as tropical regions have a high potential for hydropower development (Athayde et al., 2019; Grill et al., 2019; Lees et al., 2016; Tundisi et al., 2014), with high biodiversity index [High-Biodiversity Wilderness Area, (Mittermeier et al., 1998)] and are also considered turtle priority areas, as is the case of river basins in tropical Asia, South America and Africa (Buhlmann et al., 2009; Ennen et al., 2021; Mittermeier et al., 2015).

It is possible that the lack of studies on impacts from Asia and Africa could be a result of the English language searches. Based on evidence from recent studies it does however appear likely that there are indeed very few studies documenting impacts on freshwater turtles across Asian and African basins impacted by dams. A recent special issue regarding the Lower Mekong basin (with 20 published articles, https://www.mdpi.com/journal/water/special_issues/Mekong_River#published, accessed 8 September 2021) includes no articles examining freshwater turtles. Indeed an assessment of the Lower Mekong basin used IUCN species range polygons and included only one threatened reptile species (species name unreported) in a simulation exercise to assess the freshwater health across the basin (Souter et al., 2020). Another English language based meta-analysis assessed primary and secondary literature (e.g. reports) included only a single fisher report with unconfirmed impacts on two unidentified soft-shell turtle species weighing 1 and 4 kg (Null et al., 2021).

4.2. Threats and impacts of dams on freshwater turtles.

The installation, construction and operation of dams generate changes in river systems and in their ecological interactions (Lees et al., 2016; Reid et al., 2019; Winemiller et al., 2016). Based on our results, the principal ecosystem changes that impact freshwater turtles were river flow modification, physical barriers and water quality. Land cover change was not assessed as a direct impact of dams on freshwater turtles in the articles reviewed.

4.2.1 Changes in water quality

A lack of oxygen may limit the presence and establishment of diving species in transformed reservoir environments. Reservoir installation requires the filling and permanent flooding of great surfaces, spanning part of the land ecosystems and destroying the Aquatic terrestrial transition zone (Bodie, 2001; Fearnside, 2019; Melack and Coe, 2020). In consequence the lotic system is transformed into a lentic system (Forsberg et al., 2017; Reid et al., 2019) and the natural flood pulse becomes artificially regulated (Timpe and Kaplan, 2017). In the area of the reservoir, where the environment is lentic, the production of oxygen decreases as the turbidity of the water increases, which in turn limits the penetration of sunlight and affects primary productivity (Forsberg et al., 2017; Santos et al., 2020). Lack of oxygen in reservoirs has implications for turtle physiology as it limits the capacity to obtain oxygen from the water, which can reduce diving ability by 51% (Clark et al., 2018). The impact of changing oxygen levels was recorded in Australia for *Elusor macrurus* hatchlings, a species with bimodal respiration which, nevertheless, cannot withstand hypoxia conditions for long periods of time (Clark et al., 2009). However, the eutrophication in water supply dams caused by agricultural runoff, may benefit some turtle species, for example an increase in emergent vegetation could be potential refuge habitat for the juvenile stages of *Chelodina longicollis* [Table 3, (Ryan et al., 2015)]. Additionally, adults of *Actinemys marmorata* and *Pseudemys scripta* are benefited by the higher water temperatures in reservoirs that increased the time available for foraging and growth rates [Table 3, (Gibbons, 1970; Snover et al., 2015)].

The new physical-chemical environment (e.g. lower pH) and the elevated rates of decomposition of submerged organic matter increases mercury methylation by bacteria (Regnell and Watras, 2019). Methylmercury (methylHg) is an extremely toxic contaminant that can be highly damaging to people (Budnik and Casteleyn, 2019; Ceccatelli et al., 2010) and aquatic organisms including turtles (Barraza et al., 2021; Di Marzio et al., 2019; Green et al., 2010; Hopkins et al., 2013; Schneider and Vogt, 2018; Slimani et al., 2018). Patterns of mercury contamination have been intensely studied around dams (Budnik and Casteleyn, 2019; Millera Ferriz et al., 2021; Pestana et al., 2019; Wang et al., 2004). Few ecotoxicological studies focused on freshwater turtles exist [(Thompson et al., 2018) but see (Lu et al., 2019; Tada et al., 2007)], with most focusing on fish due to their economic importance and use as a food resource (Duponchelle et al., 2021; Moran et al., 2018). Despite this, the presence of mercury has been documented in turtles from temperate (Burger and Gibbons, 1998; Meyer et al., 2014; Slimani et al., 2018) and tropical regions (Eggins et al., 2015; Schneider et al., 2009; Schneider et al., 2010). As freshwater turtles are often consumed by riverside populations there is a strong potential for freshwater turtles to represent a source of dietary methylmercury (Green et al., 2010). The lack of studies assessing bioaccumulation of mercury in freshwater turtles in and around dams was therefore surprising.

In various regions around the world many communities have the tradition of consuming turtle eggs and meat as a source of protein or for medicinal use (Dudgeon, 2019; Green et al., 2010; Pezzuti et al., 2010; Winemiller et al., 2016). Freshwater turtles absorb methylmercury through their digestive system as the organic forms of mercury are soluble in fats, oils, lipids and remain bound to proteins in all the tissues of the organism (Green et al., 2010; Schneider and Vogt, 2018). This was shown in the lower Xingu river basin in Brazil where concentrations of 0.06 mg/kg of Hg were found, mostly in the livers of the yellow-spotted river turtle [*Podocnemis unifilis* (Souza-Araujo et al., 2015)]. This can be explained because the principal detoxification processes are located in that organ (Green et al., 2010; Souza-Araujo et al., 2015). The bioaccumulation of mercury also threatens embryonic development as contaminants are transferred from breeding females to their eggs (Green et al., 2010; Thompson et al., 2018). Thus, mercury can affect the determination of sex, causing abnormal androgen synthesis and impacting the regulation of enzymes involved in steroidogenesis (Bodie, 2001; Thompson et al., 2018).

4.2.2 Changes in river flow

4.2.2.1 Loss of feeding habitat

As a consequence of dam reservoir the flood plain vegetation disappears, as it becomes permanently submerged (Guo et al., 2021; Schöngart et al., 2021). Additionally, wetland (Dudgeon, 2000; Santoro et al., 2020) and terrestrial (Resende et al., 2019; Schöngart et al., 2021; Zhang et al., 2021) environments are also adversely impacted (Schöngart et al., 2021). As a consequence, the habitat and food resources used by freshwater turtles changes, which may directly harm nutrition (Pezzuti et al., 2016; Tucker et al., 2012), growth (Bondi and Marks, 2013) and survival (Bennett et al., 2009; Bennett and Litzgus, 2014).

The loss of feeding habitat, together with the changes in the flood pulse, can strongly impact the availability of food resources (Bennett et al., 2009; Schöngart et al., 2021). This was shown in Australia where the diet of three freshwater turtle species was evaluated, comparing places with and without damming impact (Tucker et al., 2012). In places where dams were built, reduced ingestion of subaquatic plants and fruits by *Emydura kreffti* and *Elseya albagula* was found. Likewise, *Myuchelys latisternum* showed a diminished ingestion of aquatic invertebrates in comparison to river habitats that were not impacted (Tucker et al., 2012). As such, the adaptive response of turtles to dams, as a function of the availability of prey and fruits, may ultimately depend on their capacity to change their foraging strategies (Petrov et al., 2018; Richards-Dimitrie et al., 2013).

The lateral and vertical connectivity between aquatic and terrestrial zones is related to spatial and temporal variation in flow rates and flooding regimes, which form diverse and dynamic habitats that sustain high indices of aquatic and nonaquatic biodiversity (Latrubesse et al., 2021). There are species of plants that are adapted to the temporal and spatial variation in flooding dynamic. Seasonally flooded forests are used as feeding and breeding habitats for various organisms like turtles (Andrade et al., 2015; Schöngart et al., 2021). During the rainy season, flooded Amazonian vegetation is used as a feeding area due to the availability and accessibility of fruits, seeds, leaves, stems and periphyton (Félix-Silva, 2009). The food resources used by aquatic and semiaquatic turtles, however, vary between species. For example, there are species with more specialized diets based on consuming different parts of the plants and their fruits as is the case of *Dermatemys mawiii* in northern California (Snover et al., 2015); or carnivores like *Myuchelys latisternum* in southeastern Queensland (Tucker et al., 2012). Some species, like the genus *Podocnemis*, might be preferentially herbivores but, as a function of food availability, may consume insects or small fish in central Amazonia (Cunha et al., 2020). In comparison, other species may not be able to switch to alternative sources, as for example the Murray River short-necked turtle (*Emydura macquarii*) that may be limited by the availability of filamentous algae (Petrov et al., 2018). The flood pulse also plays a role in the access to food. For example, insect larvae may depend on shallow waters for their development, and macrophytes are also reduced when water levels fluctuate (Tucker et al., 2012).

4.2.2.2 Loss of nesting habitat

The modification of the flood pulse directly affects aquatic and semiaquatic turtles, because their life history is often synchronized with river dynamics (Moll and Moll, 2004). As an example, reproduction can be tied to the seasonal availability of nesting habitats; nesting behavior in some tropical South American species begins during the dry season, when sand banks and beaches along rivers are exposed and subsequent hatchling emergence occurs prior to flooding by rising river levels (Alho, 2011; Eisemberg et al., 2016; Moll and Moll, 2004). Therefore, an alteration in a river's annual flooding cycle caused by a dam can reduce the availability of nesting areas (Norris et al., 2018a), as well as the duration of the dry period, which may affect the reproduction behavior and success of these species (Alho, 2011; Eisemberg et al., 2016; Tornabene et al., 2018).

Nests of turtle species that use terrestrial habitats (e.g. river banks) as nesting areas may be at greater risk from flooding (Bodie, 2001), as is the case of species of the genus *Podocnemis* (Norris et al., 2018a; Norris et al., 2020) and species of the North American Emydidae and Trionychidae [e.g. *Graptemys geographica* and *Apalone spinifera* (Pitt et al., 2021)]. Eggs of species adapted to laying nests on land may withstand brief flooding [e.g. up to two days for *Podocnemis unifilis* eggs (Norris et al., 2020)] but permanent immersion during the early stages of incubation diminishes the survival of the embryos (Bodie, 2001). Indeed, a study found that eggs of the Chelidae *Emydura krefftii* may not tolerate being under water for more than half an hour (Hollier, 2012).

The artificial regulation of dammed river levels can result in permanent flooding or a reduction in nesting areas used by females. This was recorded in the Araguari River basin, eastern Amazonia, where the filling of a new hydropower dam reservoir in 2016, resulted in the flooding and total loss of 3.9 hectares of potential habitats and areas previously used by the yellow-spotted river turtle *Podocnemis unifilis* (Norris et al., 2018a). The same study also demonstrated a drastic reduction of monitored nesting areas (Norris et al., 2018a). Additionally, nest site overlap may also occur as a consequence of intra- and interspecies competition for the available nesting space (Alho, 2011).

Besides Norris et al. (2018a), no other study evaluated freshwater turtle nesting patterns with baseline monitoring previous to dam installation. Research in China in the Red River region, estimated that the construction of 11 planned hydropower dams may permanently flood 73% (27 km of the river) of potential nesting habitat for the species *Rafetus swinhoei* (Jian et al., 2013). This loss of habitat, coupled with the historic exploitation of *R. swinhoei* throughout its range, will contribute to increasing the risk of extinction of the rarest freshwater turtle in the world (Jian et al., 2013; Stanford et al., 2020).

In the absence of adequate nesting habitat, nest-site selection by females may be compromised as nests may be placed in the spaces available, even if they may not represent a good choice for females, eggs or hatchlings (Boyer, 1965; Kolbe and Janzen, 2002; Refsnider and Janzen, 2010; Schlaepfer et al., 2002). Changes in the microclimate of nests, for example an increase in substrate humidity, can also affect hatching rates, sex ratio, embryonic development, hatchling body size, locomotion ability, and hatching success (Refsnider et al., 2013). Nest-site selection can affect the nest's vulnerability to predation by wildlife (Spencer, 2002) and humans (Michalski et al., 2020) and may even render nests susceptible to submersion by flash floods that can occur due to hard-to-predict events, resulting from climate change (Eisemberg et al., 2016) or inflow impoundment by dams (McDougall et al., 2015; Norris et al., 2020). The release of water by dams can also generate negative impacts, with the release of water by the Kota hydropower dam in India causing the Chambal River to rise 1.2 m, which in turn caused the flooding of nesting areas and a loss of 7.7% and 9.6% of the nests of *Batagur kachuga* and *Batagur dhongoka* respectively (Rao and Singh, 1987).

4.2.3 Physical barriers

The physical barrier created by dams limits transportation and downstream availability of nutrients and sediments, (Lees et al., 2016; Timpe and Kaplan, 2017; Tundisi et al., 2014). In addition, the artificial regulation of flooding pulse and the physical barrier, created by the dam itself, causes the retention of sediments in the reservoir. This change drastically reduces the volume of sand that can be transported downstream leading to the progressive disappearance of potential nesting areas for freshwater river turtles (Le Duc et al., 2020; Lenhart et al., 2013). Furthermore, the decrease in sediment recharge can worsen in basins with more than one dam on one fluvial system, due to the cumulative effects of multiple dams (Forsberg et al., 2017).

Within the natural environment, the dam itself becomes an artificial physical barrier that breaks the connectivity of the river (Bodie, 2001; Castello and Macedo, 2015; Chelazzi et al., 2007; Grill et al., 2019). One potential impact of dams is in modifying the habitats required among specialized species (Buchanan et al., 2019; Clark et al., 2018). It is common for freshwater turtles to be displaced or disappear when they cannot find the necessary conditions for their survival. This reduces the population abundance in their places of occurrence (Félix-Silva et al., 2019) and favors the establishment of more generalist species if, and when, they find the adequate ecological requirements (Chelazzi et al., 2007).

In Australia, the changes in the relative abundance of the generalist species *E. macquarii* and the more specialist *M. laisternum* were studied over a period of five years after the construction of the Wyaralong water supply dam. It was found that the abundance of both species was lower in locations near the dam (Clark et al., 2018). Similarly, in the basin system of the Da, Chu and Ma rivers in the province of Thanh Hoa in Vietnam, a decrease in the abundance of fish and absence of the Yangtze giant softshell turtle *R. swinhoei* was recorded after the installation of the Hoa Binh hydropower dam, according to interviews with fishermen (Le Duc et al., 2020). Similarly in China, once the sand banks were flooded by the Nansha hydropower dam in 2006, it was no longer possible to detect the presence of *R. swinhoei* (Jian et al., 2013).

The abundance of turtles can also be reduced by an increase in human predation, as a result of the migration of people to the construction sites of hydropower dams in search of job opportunities (Pezzuti et al., 2016). This, in consequence, leads to long-term changes in population recruitment, as selective capture, as well as the availability of Chelonians as food impacts the size of the population, its biomass and sex-ratio (Félix-Silva et al., 2019). Furthermore, increased disturbance by ships navigating the river to transport building materials may interrupt the dispersal movement of breeding females (Alho, 2011), and turtles can be accidentally injured by the propeller blades of boats and ships (Bennett and Litzgus, 2014).

The fragmentation of free flowing river habitat limits migrations, causes isolation and diminishes the genetic flow between populations of freshwater turtles (Gallego-García et al., 2018). In Canada, on the Trent-Severn Waterway, it was found that the dispersal and area of occurrence of females of *Graptemys geographica* were less in the areas fragmented by locks, dikes and hydropower dams (1.53 ± 0.31 km), compared to females found in contiguous areas [8.51 ± 1.59 km, (Bennett et al., 2010)]. Dams divide populations, making mating more difficult among the survivors (Jian et al., 2013) and decreasing the adaptive capacity of impacted populations as genetic diversity is lost. This could result in increased inbreeding, with potential consequences for reproductive fitness and survival in the disturbed environment. These are factors that, together, have implications on population recruitment (Bennett et al., 2010; Buchanan et al., 2019; Gallego-García et al., 2018; Ihlow et al., 2014). The physical barriers and permanently inundated lotic environment created by dams can also favor certain species including non-native turtle species (Berry et al., 2020). Additionally, the dams could provide new potential habitat for freshwater turtles, like permanent impoundments of otherwise ephemeral streams (Stone et al., 2014), and dams providing water supply for cattle can also be used as permanent habitat by the generalist species like *Actinemys marmorata*

[Table 3, (Germano, 2016)]. But, such cases depend on active management to maintain healthy populations, as highlighted by an example from Europe showing the importance of managing cattle to avoid trampling and appropriate management of flow regimes for the impacted turtle species (Ficheux et al., 2014). Additionally, evaluating these impacts of dams as barriers at a genetic level can take several generations and depending on the species can require many decades if not centuries for the changes to manifest (Bennett et al., 2010; Gaillard et al., 2015; Kiesow and Warcken, 2017; Reinertsen et al., 2016; Ward et al., 2013).

4.3. Mitigation actions

To our knowledge, the present study constitutes the most extensive search of the literature for assessing the impact of dams on freshwater turtles and mitigation measures that have been carried out to date, and the inclusion of over 300 non-English language journals increases confidence that important sources of evidence for actions to mitigate impacts have not been missed (Amano et al., 2021). Among the measures to mitigate / minimize dam impacts on freshwater turtles the most frequently suggested were habitat conservation/restoration/creation (Ghaffari et al., 2014; Gonzalez-Zarate et al., 2011; Norris et al., 2018a; Pitt et al., 2021; Reese and Welsh Jr, 1998b; Tornabene et al., 2019) and environmental education (Ghaffari et al., 2014; Gonzalez-Zarate et al., 2011; Ihlow et al., 2014; Jian et al., 2013; Le Duc et al., 2020; Norris et al., 2018a). Promoting habitat creation and restoration would likely contribute to long-term conservation of breeding and nesting areas, as well as potential foraging areas for turtles. Restored vegetation can also help reduce erosion, improve water quality, and promote the reestablishment of a variety of aquatic and terrestrial species (Santoro et al., 2020). However, no published studies were found that evaluated the implementation of these suggested measures for freshwater turtle species impacted by dams.

Studies also suggested that the companies in charge of dam development and operation should adopt a holistic vision of catchment management, including measures such as the regulation of water flows for the specific freshwater turtles impacted and adapting inlets to favor turtle dispersal between rivers and the available flood plains (Howard et al., 2017; McDougall et al., 2015). Indeed an example from Australia showed that such changes to flow rate could also benefit other species without negatively affecting energy generation (McDougall et al., 2015).

Although more than half of studies suggested mitigation actions, only four evaluated interventions. This pattern follows global trends where for most threatened species, only a small proportion of available budgets are implemented (Gerber, 2016), with an example from the US demonstrating that only a small fraction of proposed management tasks for species recovery are achieved (Gibbs and Currie, 2012). Although the majority of studies suggested the need for additional research including long-term monitoring, monitoring is not sufficient to solve conservation problems (Buxton et al., 2020; Legg and Nagy, 2006) and/or support the achievement of sustainable development goals (Brownson and Fowler, 2020; Fisher et al., 2020; Martinez-Harms et al., 2018). It is worth noting that a number of other studies were highlighted within the Conservation Evidence database that evaluated a range of interventions with potential relevance to the threat of dams on freshwater turtles. For example, studies evaluating habitat restoration/creation (e.g. “Create or restore ponds”) or education and awareness raising (e.g. “Engage local communities in conservation activities”) may provide evidence that could be applicable for a wide range of taxa and be implemented in response to a large number of threats, including those arising from dams. While interventions and actions developed and implemented within local contexts may well have the most relevant results, it remains an open question the extent to which relevant evidence can be shared across different species groups, habitats and contexts. Such sharing of evidence could go some way to filling gaps in the literature and increase the collective capacity for using evidence to inform conservation decision making.

Community Based Conservation encourages social organization and the creation of initiatives to conserve natural capital. In addition to that, it significantly reduces the extraction of eggs and the levels of conflict of interest between the members of the society (Norris et al., 2018b). Several studies have already shown that the survival of turtle hatchlings and adults increases through conservation by community management (Norris et al., 2020; Norris et al., 2019). Community Based Conservation also encourages participation to monitor, protect, and reduce predation of freshwater turtles within communities (Campos-Silva et al., 2018; Rivera et al., 2021; Vallejo-Betancur et al., 2018). Actions may also include rescue activities such as that which occurred in the eastern Brazilian Amazon, where community based actions contributed to the rescue of 926 eggs, 65 premature hatchlings and the release of 599 hatchlings of *P. unifilis* during the flooding of nests by rising water levels (Norris et al., 2020). However, community participation in any conservation project requires that the communities be taken into consideration when creating plans or management projects (Campos-Silva et al., 2018; Rivera et al., 2021), procuring sources of economic income, as well as providing the necessary inputs for project development so that they are not abandoned due to lack of resources (Norris et al., 2018b; Stone et al., 2014).

It is necessary to strengthen the protection and monitoring of existing nesting areas (Forero-Medina et al., 2019), and of juvenile and adult turtles (Hance, 2020). Such actions should be supported by additional research to establish if population recruitment is occurring and provide more robust estimates of turtle population dynamics particularly in the tropics (Norris et al., 2019; Rachmansah et al., 2020). This could be achieved with the promotion of social, governmental, business and research center participation (Guo et al., 2021). It may also be possible to complement this with environmental education actions at different levels of society (including children), to revalue the importance of freshwater turtles as components of the ecosystem and diverse cultures (Ghaffari et al., 2014; Gonzalez-Zarate et al., 2011; Le Duc et al., 2020). Another strategy would be to implement community management to regain the cultural, economic, ecological, political and social values of the communities over their natural resources (Brownson and Fowler, 2020; Campos-Silva et al., 2018; Harper et al., 2021; Lopes et al., 2021).

In addition, it is necessary to demand that the corresponding environmental authorities conduct more robust and rigorous Environmental Impact Assessments (Norris et al., 2018a), as well as provide support to supervise compliance with mitigation actions and monitoring their effectiveness by the companies that operate dams to mitigate the impacts and prevent the loss of species and ecological functions (Guo et al., 2021; Valiente-Banuet et al., 2015).

5. CONCLUSIONS

Our literature review showed that many relevant topics still have a few studies for freshwater turtles, particularly in tropical regions. Although changes in the river flow caused by dams on freshwater turtles were the principal focus of studies, there were important information gaps regarding the effects of changes in water quality, mercury bioaccumulation and changes in land cover. With only a four studies testing interventions, much more evidence is required to evaluate mitigation actions across different life-stages and geographic regions. Integrated monitoring programs that provide evidence at relevant spatial and temporal scales for the different life-stages are needed to promote the conservation of these threatened species. Actions that mitigate known negative impacts are urgently required to prevent the collapse of populations of critically endangered freshwater turtle species.

6. ACKNOWLEDGEMENTS

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7. DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

8. AUTHORS' CONTRIBUTION STATEMENT (CREDIT):

AB: Conceptualization (equal); Data Curation (equal); Formal Analysis (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal)

FM: Conceptualization (equal); Writing – review and editing (equal)

WHM: Writing – review and editing; contributed to development and creation of Conservation Evidence database

RKS: Writing – review and editing; contributed to development and creation of Conservation Evidence database

WJS: Writing – review and editing; created concept of Conservation Evidence database and contributed to its development and creation

JPG: Conceptualization (equal); Writing – review and editing (equal)

DN: Conceptualization (equal); Methodology (equal); Data Curation (equal); Formal Analysis (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal)

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