

Salinity tolerances and use of saline environments by freshwater turtles: implications of sea level rise

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ABSTRACT

The projected rise in global mean sea levels places many freshwater turtle species at risk of saltwater intrusion into freshwater habitats. Freshwater turtles are disproportionately more threatened than other taxa; thus, understanding the role of salinity in determining their contemporary distribution and evolution should be a research priority. Freshwater turtles are a slowly evolving lineage; however, they can adapt physiologically or behaviourally to various levels of salinity and, therefore, temporarily occur in marine or brackish environments. Here, we provide the first comprehensive global review on freshwater turtle use and tolerance of brackish water ecosystems. We link together current knowledge of geographic occurrence, salinity tolerance, phylogenetic relationships, and physiological and behavioural mechanisms to generate a baseline understanding of the response of freshwater turtles to changing saline environments. We also review the potential origins of salinity tolerance in freshwater turtles. Finally, we integrate 2100 sea level rise (SLR) projections, species distribution maps, literature gathered on brackish water use, and a phylogeny to predict the exposure of freshwater turtles to projected SLR globally. From our synthesis of published literature and available data, we build a framework for spatial and phylogenetic conservation prioritization of coastal freshwater turtles. Based on our literature review, 70 species (~30% of coastal freshwater turtle species) from 10 of the 11 freshwater turtle families have been reported in brackish water ecosystems. Most anecdotal records, observations, and descriptions do not imply long-term salinity tolerance among freshwater turtles. Rather, experiments show that some species exhibit potential for adaptation and plasticity in physiological, behavioural, and life-history traits that enable them to endure varying periods (e.g. days or months) and levels of saltwater exposure. Species that specialize on brackish water habitats are likely to be vulnerable to SLR because of their exclusive coastal distributions and adaptations to a narrow range of salinities. Most species, however, have not been documented in brackish water habitats but may also be highly vulnerable to projected SLR. Our analysis suggests that approximately 90% of coastal freshwater turtle species assessed in our study will be affected by a 1-m increase in global mean SLR by 2100. Most at risk are freshwater turtles found in New Guinea, Southeast Asia, Australia, and North and South America that may lose more than 10% of their present geographic range. In addition, turtle species in the families Chelidae, Emydidae, and Trionychidae may experience the greatest exposure to projected SLR in their present geographic ranges. Better understanding of survival, growth, reproductive and population-level responses to SLR will improve region-specific population viability predictions of freshwater turtles that are increasingly exposed to SLR. Integrating phylogenetic, physiological, and spatial frameworks to assess the effects of projected SLR may improve identification of vulnerable species, guilds, and geographic regions in need of conservation prioritization. We conclude that the use of brackish and marine environments by freshwater turtles provides clues about the evolutionary processes that have prolonged their existence, shaped their unique coastal distributions, and may prove useful in predicting their response to a changing world.

Key words: salinization, salinity tolerance, sea level rise, brackish water ecosystems, freshwater turtles, climate change, reptiles.

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I. INTRODUCTION

Despite the physiological challenges that freshwater biota must overcome to maintain homeostasis in saline water, a remarkable array of mechanisms has enabled some organisms to exploit a broad range of salinities in their environment. While many freshwater species that evolved in isolated or constant, low-salinity environments, such as lakes, ponds, and stream headwaters, have no capacity to cope with salinity fluctuations (i.e. <0.5‰; Gray, 1988; Pokorný, 2009), others can tolerate exceptionally variable environmental conditions, thus enabling them to occupy a wider niche. Behavioural strategies allow some vertebrates to reduce the physiological impact of saline conditions (e.g. 0.5–35‰; Remane & Schlieper, 1971), and these can include moving along salinity gradients, drinking fresh water from surface sources, and reducing feeding (Greenberg *et al.*, 2006; Bower *et al.*, 2016). Other freshwater fauna have morphological and physiological adaptations (e.g. salt glands, regulation of blood, urea, and intercellular fluids) that enable them to tolerate, rather than avoid, saline conditions (Gray, 1988; Bower *et al.*, 2016).

Although fish have radiated to occupy a variety of niches in almost every aquatic habitat, reptiles are comparatively more restricted. Interestingly, water salinity is a key parameter that limits the geographic distribution of most coastal reptiles (Dunson & Mazzotti, 1989; Jackson, Butler, & Brooks, 1996; Brischoux *et al.*, 2012). In contrast to fish, most extant aquatic and semi-aquatic reptiles lack physiological adaptations to maintain blood solutes within a tolerable range (e.g. ionic and osmotic regulation; Shoemaker & Nagy, 1977). Although the skin of many reptiles is mostly impermeable to sodium and limits uptake (Hart *et al.*, 1991), an excess amount of sodium is still gained through feeding and other activities. Nevertheless, adaptation to life in high-salinity environments has evolved independently several times in turtles, squamates, and crocodiles (e.g. Schmidt-Nielsen & Fänge, 1958). Four evolutionary steps have been identified for progressive adaptation to marine life: (i) behavioural osmoregulation such as identifying and avoiding high salinities; (ii) reduction in salt uptake, water loss, and incidental drinking;

(iii) development of rudimentary salt glands; and (iv) development of highly functioning salt glands and morphological adaptations (Dunson & Mazzotti, 1989). The presence of adaptations to marine habitats, even in predominantly freshwater turtle species, may be evidence for a possible marine or estuarine phase in the evolution of some coastal freshwater species.

Turtles (Testudines) constitute a reptilian order that is frequently reported as using brackish water systems, and approximately 70% of turtle species have a geographic range extending along a coastline. Understanding how significant these brackish water habitats are to turtles is important because 59% of turtle species are threatened with extinction. The projected 1 m or more rise in global mean sea levels (GMSL) by 2100 (Jevrejeva, Moore, & Grinsted, 2012; Horton *et al.*, 2014) implies that many extant coastal turtle species (~90%, see Section III) are likely to be affected to some degree by saltwater intrusion into freshwater habitats. Despite the perilous conservation status of many turtles, (e.g. Todd, Wilson, & Gibbons, 2010), the extent to which they tolerate brackish or marine environments and thus, our ability to predict the future impact of salt incursion, is not well known (Neill, 1958; Rasmussen *et al.*, 2011). The distribution, fossil record, and phylogeny of turtles, however, are well documented (Rödder *et al.*, 2013), making them useful resources for comparative analyses. Here, we provide the first comprehensive review of freshwater and estuarine turtles that occur exclusively, seasonally, and occasionally in brackish water ecosystems. We synthesize the literature on freshwater turtles that use brackish and saline environments, their physiological, morphological, and behavioural mechanisms, and suggested evolutionary origins of salinity tolerance. In addition, we use an unmitigated warming scenario for 2100 sea level rise (SLR) to overlay estimates of projected SLR on georeferenced coastal species distributions around the world. Furthermore, we use a large-scale turtle phylogeny accompanied by records from our literature review to interpret phylogenetic relatedness of coastal freshwater turtle species found in brackish water and examine their potential exposure to projected SLR.

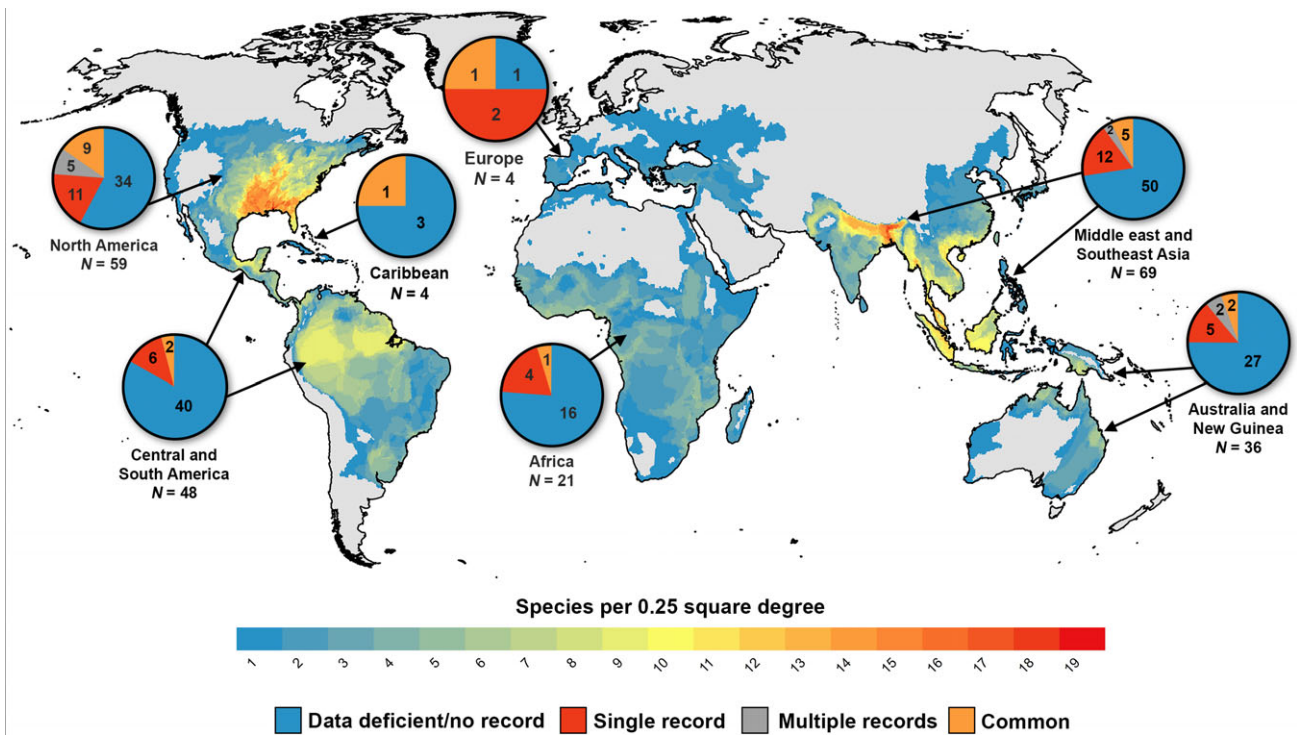


Fig. 1. Global geographic distribution of freshwater turtle species that have a geographic range extending along or overlapping a coastline or estuary ($N = 241$), and the number of species previously detected in brackish water from each continent or region. The pie charts represent the number of species that are data deficient or lacking a record, species that have a single record, multiple records, or are common in brackish water, as defined in the key.

II. METHODS

We defined distributions for turtle species using georeferenced maps generated by the Turtle Taxonomy Working Group (TTWG, 2014). To our knowledge, TTWG (2014) represents the most up to date, accurate, and comprehensive study of turtle distributions available. We define freshwater turtles as those species represented by 11 families (Cheloniidae, Pelomedusidae, Podocnemididae, Carettochelyidae, Chelydridae, Dermatemydidae, Emydidae, Geoemydidae, Kinosternidae, Platysternidae, and Trionychidae) — thus excluding only the two sea turtle families (Cheloniidae, Dermochelyidae) and single family of terrestrial tortoises (Testudinidae). The 11 families of freshwater turtles include some species often characterized in the literature or even colloquially described as ‘estuarine’ turtles (Bour, 2008), but exclude solely marine turtles.

We searched the scientific literature for records, reports, and investigations of freshwater turtles that have been recorded in brackish water environments. As a baseline for literature collection, we used reviews conducted by Neill (1958) and Rasmussen *et al.* (2011). Neill (1958) provided references from the 1940s and 1950s, whereas Rasmussen *et al.* (2011) provided references from the 1960s to the early 2000s. In addition, we used *Google Scholar*, *Web of Science*, *Wiley InterScience* and *WorldCat* to search the literature. We searched for the following words and phrases: ‘turtle salinity

tolerance’, ‘turtles; salinity’, ‘turtles; brackish water’, ‘turtle; osmoregulation’, ‘reptiles; salinity’, and ‘reptiles; brackish water’. To be included, each study or record had to report the species name, general location of the observation, life-history stage (adult, juvenile, hatchling), and specify whether the study was conducted experimentally with captive individuals or in the wild. Many studies did not record the specific habitat type (e.g. mangrove, tidal marsh, coastal estuary, etc.) or salinity (‰), thus we did not make habitat type or salinity measurement a selection criterion.

In addition to our inclusion criteria above, we also determined whether species were common or not in brackish water environments. Specifically, we created a categorical saline habitat occurrence index, noting whether there was no record (0), a single observational record (1), multiple individual citations or observations (>1 record by a separate study and investigator) across the species’ range (2), or whether the study suggested or described the species as commonly captured in saline environments (3). We considered species with only a single record or no record to be uncommon or understudied in saline environments (i.e. data deficient).

To address the broad potential effects of projected SLR on turtles of the world, we used an unmitigated warming scenario for 2100 (Representative Concentration Pathways; RCP 8.5; Horton *et al.*, 2014). These models project a 0.5–1.5 m range (~ 1 m) of SLR by 2100 (Horton *et al.*, 2014). Due to the wide range in SLR predictions (Jevrejeva

Table 1. Freshwater turtle species recorded from brackish and ocean environments classified by family, species name, common name, and region. Species are also categorized based on saline habitat occurrence index: 1 indicates a single brackish water record or single publication; 2 indicates that there are multiple records or publications; and 3 indicates that the species is common in brackish water environments within and among publications

Family	Species name	Common name	Saline habitat occurrence index	Region	Reference
Carettochelyidae	<i>Carettochelys insculpta</i>	Pig-nosed turtle	3	Australia, East Asia	Eisemberg <i>et al.</i> (2015); Cann (1978); Georges <i>et al.</i> (2008)
Chelidae	<i>Chelodina expansa</i>	Broad-shelled long-necked turtle	2	Australia	Bower <i>et al.</i> (2012)
	<i>Chelodina longicollis</i>	Eastern long-necked turtle	2	Australia	Bower <i>et al.</i> (2013)
	<i>Chelodina oblonga</i>	Northern snake-necked turtle	1	New Guinea	Rhodin & Mittermeier (1976)
	<i>Chelus fimbriata</i>	Matamata turtle	1	South America	Pritchard & Trebbau (1984)
	<i>Elseya albagula</i>	White-throated snapping turtle	1	Australia	Hamann <i>et al.</i> (2004)
	<i>Emydura macquarii</i>	Murray river turtle	1	Australia	Bower <i>et al.</i> (2012)
	<i>Emydura subglobosa</i>	Red-bellied short-necked turtle	1	Australia, East Asia	Liem (1983)
Chelydridae	<i>Emydura victoriae</i>	Victoria river red-faced turtle	1	Australia	VertNet (2016)
	<i>Chelydra serpentina</i>	Common snapping turtle	3	North America	Albers, Sileo, & Mulhern (1986); Kinneary (1993); Neill (1958); Dunson (1986); Vogt & Guzman (1988)
	<i>Macrochelys temminckii</i>	Alligator snapping turtle	3	North America	Neill (1958); Jackson Jr. & Ross (1971); J.C.G. (pers. comm.)
Dermatemydidae	<i>Dermatemys mawii</i>	Central American river turtle	1	Central America	Moll (1986)
Emydidae	<i>Actinemys marmorata</i>	Western pond turtle	2	North America	Neill (1958), M.A. (pers. obs.)
	<i>Emys orbicularis</i>	European pond turtle	3	Europe	Kami <i>et al.</i> (2006)
	<i>Chrysemys picta</i>	Painted turtle	1	North America	Neill (1958)
	<i>Clemmys guttata</i>	Spotted turtle	3	North America	Neill (1958); Schwartz (1961)
	<i>Deirochelys reticularia</i>	Chicken turtle	1	North America	Neill (1958)
	<i>Graptemys kohni</i>	Mississippi map turtle	1	North America	Schwartz & Dutcher (1961)
	<i>Graptemys flavimaculata</i>	Yellow-blotched map turtle	1	North America	Selman & Jones (2011)
	<i>Graptemys nigrinoda</i>	Black-knobbed map turtle	1	North America	J.C. Godwin (pers. comm.)
	<i>Malaclemys terrapin</i>	Diamondback terrapin	3	North America	Burger & Montevecchi (1975); Montevecchi & Burger (1975)
	<i>Pseudemys alabamensis</i>	Alabama red-bellied cooter	3	North America	Leary <i>et al.</i> (2008); Pritchard (1979); Jackson Jr. & Ross (1974); Carr (1952)
	<i>Pseudemys concinna</i>	River cooter	3	North America	Carr (1952); Neill (1958)
	<i>Pseudemys floridana</i>	Coastal plain cooter	1	North America	Neill (1958)
	<i>Pseudemys nelsoni</i>	Florida red-bellied turtle	3	North America	Neill (1958); Dunson & Seidel (1986)
	<i>Pseudemys rubriventris</i>	Northern red-bellied cooter	2	North America	Carr (1952); Arndt (1975)
	<i>Terrapene carolina</i>	Common box turtle	1	North America	Neill (1958); Jones, Willey, & Charney (2016)
<i>Trachemys decussata</i>	Cuban slider	3	North America	Dunson & Seidel (1986)	
<i>Trachemys nebulosa</i>	Baja California slider	1	North America	Carr (1952)	

Table 1. Continued

Family	Species name	Common name	Saline habitat occurrence index	Region	Reference
	<i>Trachemys ornata</i>	Ornate slider	1	North America	Neill (1958)
	<i>Trachemys scripta</i>	Red-eared slider	3	North America	Neill (1958); DeGregorio, Grosse, & Gibbons (2012)
	<i>Trachemys venusta</i>	Meso-american slider	3	Central America	Pritchard & Trebbau (1984); Vogt & Guzman (1988)
Geoemydidae	<i>Trachemys callirostris</i>	Colombian slider	1	South America	Pritchard & Trebbau (1984)
	<i>Batagur affinis</i>	Southern river terrapin	1	East Asia	Rasmussen <i>et al.</i> (2011)
	<i>Batagur baska</i>	Northern river terrapin	3	East Asia	Rasmussen <i>et al.</i> (2011); Davenport & Wong (1986); Sharma & Tisen (2000)
	<i>Batagur borneoensis</i>	Painted terrapin	2	East Asia	Rasmussen <i>et al.</i> (2011); Davenport & Wong (1986); Dunson & Moll (1980); Pritchard (1979); Sharma & Tisen (2000)
	<i>Cuora amboinensis</i>	Southeast Asian box turtle	1	East Asia	Sharma & Tisen (2000)
	<i>Cyclemys dentata</i>	Asian leaf turtle	1	East Asia	Sharma & Tisen (2000)
	<i>Mauremys sinensis</i>	Chinese stripe-necked turtle	1	East Asia	Chen & Lue (2010)
	<i>Mauremys rivulata</i>	Balkan terrapin	1	Europe	Broggi (2012)
	<i>Mauremys leprosa</i>	Mediterranean pond turtle	1	Europe	Malkmus (2004)
	<i>Orlitia borneensis</i>	Malaysian giant turtle	3	East Asia	Sharma & Tisen (2000)
	<i>Pangshura tecta</i>	Indian roofed turtle	1	East Asia	Sharma & Tisen (2000)
	<i>Pangshura tentoria</i>	Indian tent turtle	1	East Asia	Sharma & Tisen (2000)
	<i>Siebenrockiella crassicollis</i>	Black marsh turtle	1	East Asia	Sharma & Tisen (2000)
Kinosternidae	<i>Kinostemon baurii</i>	Striped mud turtle	3	North America	Neill (1958); Dunson (1981)
	<i>Kinostemon leucostomum</i>	White-lipped mud turtle	1	Central America	Vogt & Guzman (1988)
	<i>Kinostemon herrerae</i>	Herrera's mud turtle	1	North America	Legler & Vogt (2013)
	<i>Kinostemon scorpioides</i>	Scorpion mud turtle	3	Central America, South America	Acuña-Mesen, Castaing, & Flores (1983); Forero-Medina, Castaño-Mora, & Montenegro (2007)
	<i>Kinostemon subrubrum</i>	Eastern mud turtle	3	North America	Neill (1958); Schwartz (1961)
	<i>Staurotypus triporcatus</i>	Northern giant musk turtle	1	Central America	Vogt & Guzman (1988)
	<i>Sternotherus odoratus</i>	Common musk turtle	1	North America	Neill (1958)
Pelomedusidae	<i>Pelomedusa subrufa</i>	African helmeted terrapin	1	Africa	Luiselli (2009)
	<i>Pelusios castaneus</i>	West African mud turtle	1	Africa	Barnett & Emms (2005)
	<i>Pelusios niger</i>	West African black mud Turtle	1	Africa	Luiselli (2009)
Podocnemididae	<i>Podocnemis expansa</i>	Giant South American turtle	1	South America	Portal, Luz, & Medonça (2005)
Trionychidae	<i>Amyda cartilaginea</i>	Asiatic softshell turtle	2	East Asia	Neill, 1958); Sharma & Tisen (2000); Eisenberg <i>et al.</i> (2015)
	<i>Apalone ferox</i>	Florida softshell turtle	2	North America	Neill (1958); Pritchard (1979); Eisenberg <i>et al.</i> (2015)
	<i>Apalone spinifera</i>	Spiny softshell turtle	2	North America	Seidel (1975); Cagle & Chaney (1950); Neill (1958)
	<i>Chitra indica</i>	Indian narrow-headed softshell turtle	1	East Asia	Sharma & Tisen (2000)

Table 1. Continued

Family	Species name	Common name	Saline habitat occurrence index	Region	Reference
	<i>Chitra chitra</i>	Asian narrow-headed softshell turtle	1	East Asia	Eisemberg <i>et al.</i> (2015)
	<i>Dogania subplana</i>	Malayan soft-shelled turtle	1	East Asia	Eisemberg <i>et al.</i> (2015)
	<i>Palea steindachneri</i>	Wattle-necked softshell turtle	1	East Asia	Eisemberg <i>et al.</i> (2015)
	<i>Nilssonina hurum</i>	Indian peacock softshell turtle	1	East Asia	Sharma & Tisen (2000)
	<i>Pelochelys bibroni</i>	New Guinea giant softshell	3	East Asia	Rhodin <i>et al.</i> (1993); Neill (1958)
	<i>Pelochelys cantorii</i>	Asian giant softshell turtle	3	East Asia	Sharma & Tisen (2000); Rasmussen <i>et al.</i> (2011)
	<i>Pelodiscus sinensis</i>	Chinese softshell turtle	1	East Asia	Lim & Das (1999)
	<i>Trionyx triunguis</i>	Nile softshell turtle	3	Africa	Pritchard (1979); Venizelos & Kasperek (2006); Taskavak <i>et al.</i> (1999); Taskavak & Akcinar (2009)
	<i>Lissemys punctata</i>	Indian flapshell turtle	3	East Asia	Sethy, Samantasinghar, & Pramanik (2015); Eisemberg <i>et al.</i> (2015)
	<i>Rafetus euphraticus</i>	Euphrates softshell turtle	1	Middle East	Eisemberg <i>et al.</i> (2015)

et al., 2012; Horton *et al.*, 2014), we selected a 1 m increase SLR scenario to overlay with our georeferenced turtle distributions. Using ArcGIS 10.5, we used the mosaic function to merge a 1-km resolution global digital elevation model (DEM; GTOPO30) including total pixel area 1 m or less with all georeferenced coastal freshwater turtle species distributions ($N = 241$). Subsequently, % overlap was extracted using the Extract by Attributes tool in the Spatial Analyst toolbox for our SLR scenario by pixel (0.008333×0.008333 decimal degrees) for each turtle distribution.

To account for broad phylogenetic associations among species, we used a large-scale turtle phylogeny that includes 288 species from all extant families (R.C. Thomson, P.Q. Spinks & H.B. Shaffer, in preparation). Although 15% of species in the present review were missing from the phylogeny, we added these species by randomly placing branches within the subtree corresponding to the genus of each missing species. We trimmed this phylogeny to 240 species with range distributions overlapping a coastline or estuary, and seven sea turtles. We then mapped the saline habitat occurrence index for each species and per cent overlap of each species' range with projected SLR onto the phylogeny.

III. RESULTS AND DISCUSSION

Of the 335 currently recognized extant turtle species, only seven are exclusively marine sea turtles and approximately 50 are terrestrial tortoises (TTWG, 2014). The majority of the remaining 278 species are either semi-aquatic or aquatic freshwater turtles, of which, approximately 241 (excluding

sub-species) have a geographic range that extends along a coastline or estuary (TTWG, 2014; Fig. 1). Only a handful of freshwater species – 6 according to Rasmussen *et al.* (2011) and 21 according to Neill (1958) – have previously been described using brackish water environments. However, we found several additions to these records. We identified that 70 coastal freshwater turtle species from 10 of the 11 extant families use or inhabit estuarine or brackish water environments (Table 1). Of these 70 species, 21 were commonly observed or documented in different brackish water environments. Turtles of the most speciose family Emydidae had the most species documented once, twice, or commonly in marine and brackish water (21 species; Fig. 2), followed by 14 species in the family Trionychidae (Lee *et al.*, 2006; Fig. 2). Data deficiency or non-use of brackish water environments was common (173 species) across all coastal freshwater turtle families, especially in the families Geoemydidae, Emydidae, and Chelidae (Fig. 2).

Freshwater turtles using brackish water habitats have been reported on every continent where turtles occur (Fig. 1). The majority of species observed in brackish water occur in the southeastern USA and Southeast Asia, which also coincides with areas of highest turtle species richness globally (Fig. 1), as well as regions with the most scientific publications in English (Lovich & Ennen, 2013). Among all regions, turtles were reported inhabiting estuaries, salt marshes, and mangroves for varying periods of time (e.g. Dunson & Moll, 1980; Dunson & Seidel, 1986; Kinneary, 1993; Rhodin, Mittermeier, & Hall, 1993; Taskavak, Reimann, & Polder, 1999; Rasmussen *et al.*, 2011; see Table 1). Populations of four species (*Batagur baska*, *B. affinis*, *Malaclemys terrapin*, and

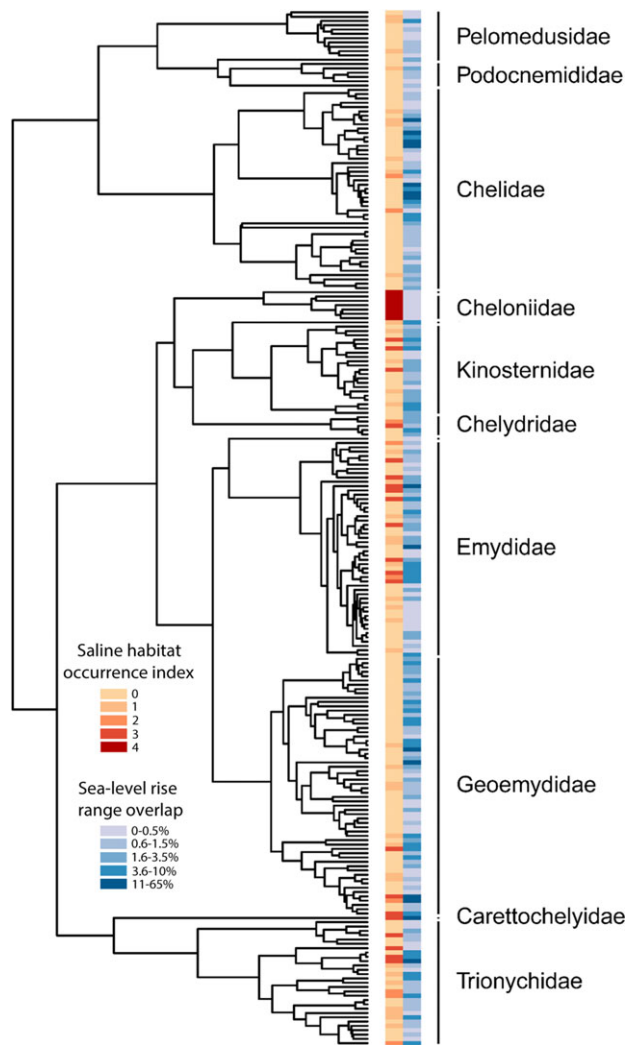


Fig. 2. Phylogeny of 240 freshwater turtle species and sea turtles with range distributions that overlap a coastline/estuary. Saline habitat occurrence index denoted by red colour scale: 0 indicates no current records or non-use of brackish water; 1 is one record; 2 is multiple records; 3 indicates species is common in brackish water environments; and 4 is sea turtles. The per cent overlap between sea-level rise and geographic range is shown by the blue scale. Note that the monotypic families Dermochelyidae, Platysternidae, and Dermatemydidae are not labeled due to space constraints.

Orlitia borneensis) were restricted to or exclusive to brackish water (Sharma & Tisen, 2000; Weissenbacher *et al.*, 2015). Furthermore, multiple species restricted their use of brackish water to short periods (days to months) or specific life-history stages (typically as adults). For example, several species like *B. borneensis*, *B. baska*, *B. affinis*, *Carettochelys insculpta*, *Trachemys venusta*, *Podocnemis expansa*, *Pelochelys bibroni*, and *Trionyx triunguis* migrate into brackish and sea water to nest on oceanfront beaches (Georges *et al.*, 2008; Eisemberg *et al.*, 2015). It is suspected that these turtles use tidal currents to enter and retreat from coastal estuarine areas on their nesting forays (Eisemberg *et al.*, 2015).

Table 2. Mean and range of per cent overlap of global mean sea level on freshwater turtle species ranges (*N*), arranged by family. Predicted overlap values are based on an unmitigated 2100 sea level rise prediction of 1 m increase in global mean sea level

Turtle family	N	Mean % overlap	Range of % overlap
Carettochelyidae	1	19.7	19.7
Chelidae	49	6.3	0.0–65
Chelydridae	5	2.3	0.9–3.8
Dermatemydidae	1	4.7	4.7
Emydidae	51	3.1	0.0–31.2
Geoemydidae	60	3.2	0.0–17.4
Kinosternidae	21	2.4	0.04–6.2
Pelomedusidae	17	1.1	0.02–5.2
Platysternidae	1	0.1	0.1
Podocnemididae	6	0.8	0.2–1.7
Trionychidae	29	2.9	0.04–30.5

Under an unmitigated upper SLR scenario (~1 m by 2100), approximately 90% of coastal freshwater turtle species would be affected by SLR. The predicted per cent overlap of SLR on geographic coastal species ranges averaged 3.6%, but ranged from 0 to 65% across 241 species in the 11 families (Table 2). Regions predicted to be most at risk from SLR were New Guinea, Southeast Asia, Australia, and North and South America where upwards of 15 species may lose greater than 10% of their present geographic range to increases in GMSL (Table 3). Specifically, freshwater turtles in low-lying areas of New Guinea may experience the greatest range inundation by projected SLR, with an average overlap of 20.8% between coastal distributions and SLR by 2100 (Table 3, Fig. 3). Species in the families Carettochelyidae, Chelidae, Emydidae, and Trionychidae may experience the greatest impact of projected SLR in their present geographic ranges. For example, projected SLR in 2100 is expected to affect 65% of the range of the snake-necked turtle (*Chelodina reimanni*), and 19.7% of the range of the pig-nosed turtle (*Carettochelys insculpta*) from Oceania (Fig. 3). Furthermore, *Malaclemys terrapin*, *Pelochelys bibroni*, and *Trachemys adiutrix* are predicted to experience an average of 30.3% overlap (31.2%, 30.5%, 29.2%, respectively) with projected SLR.

(1) Observational and experimental evidence of salinity tolerance

Many freshwater turtles are highly sensitive to saline conditions (Dunson, 1981), and multiple species lose mass or die when exposed to increased salinity (Bentley, Bretz, & Schmidt-Nielsen, 1967; Dunson & Seidel, 1986). However, there are exceptions where freshwater aquatic species tolerate brackish water habitats or otherwise use saline environments (Rasmussen *et al.*, 2011). Experimental studies on salinity tolerance in freshwater turtles commonly gauge salinity tolerance by measuring mass loss following prolonged submersion in water of known salinities measured in parts per thousand (‰). Studies assessing salinity tolerance for freshwater turtles *via* mass loss have been conducted on adult

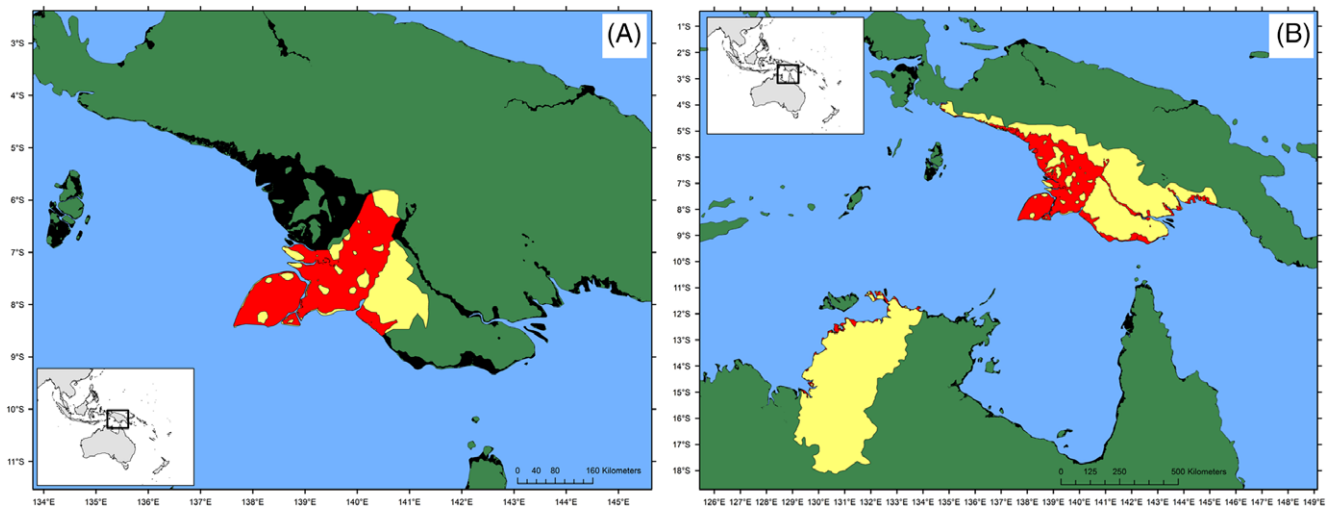


Fig. 3. Projected impact of sea level rise (SLR) on the geographic range of (A) *Chelodina reimanni* (Chelidae) in southern New Guinea, and (B) *Carettochelys insculpta* (Carettochelyidae) in southern New Guinea and Northern Australia. Species geographic range is presented yellow, unmitigated 1-m SLR projection is shaded in black, and potential area of SLR impact overlap within species distribution area is indicated in red.

Table 3. Mean and range of per cent overlap of global mean sea level on georeferenced coastal freshwater turtle species ranges (N), arranged by region. Predicted overlap values are based on an unmitigated 2100 sea level rise prediction of 1 m increase in global mean sea level

Geographic region	N	Mean % overlap	Range of % overlap
Africa	21	0.8	0.02–5.2
Australia	22	2.1	0.0–19.7
Caribbean	4	3.7	0.6–6.9
Europe	4	0.9	0.7–1.2
North America	59	2.4	0.0–31.2
South America	48	2.5	0.0–29.2
Southeast Asia	69	2.9	0.0–17.4
New Guinea	14	20.8	3.2–64.9

turtles from 16 species from seven families and on sub-adults in only three species from three families. Rates of mass loss in starved aquatic turtles exposed to 35‰ salinity (i.e. 100% seawater) ranged from 0.3–7.6% per day for adults (Table 4), and 0.3–9.1% for sub-adults (Table 5).

From observational and experimental studies, it appears that several freshwater species cannot survive for extended periods (e.g. >7 days) in marine environments as exposure leads to mortality, and thus the time tolerated in brackish water is highly variable among freshwater turtle species (Dunson, 1979). For instance, for *Kinostemon leucostomum*, *Terrapene carolina*, *Amyda cartilaginea*, and *Pelodiscus sinensis*, individuals died in relatively high-salinity water (~35‰) after 1 week or less (Bentley *et al.*, 1967; Dunson, 1979; Dunson & Seidel, 1986). Conversely, *M. terrapin* and *Chelodina expansa* remained healthy after several weeks and months of exposure to 100% seawater (i.e. 35‰ salinity; Bentley *et al.*, 1967; Cowan, 1974; Scheltinga, 1991). Furthermore,

populations of *B. borneensis*, a species that frequently occurs in estuarine habitats of SE Asia, survived for at least 14 days in 100% seawater (Dunson & Moll, 1980), and populations of *Pseudemys nelsoni*, a habitat generalist of the southeastern USA, tolerated 100% seawater for up to 24 days (Dunson & Seidel, 1986). In addition, the Chinese softshell turtle (*Pelodiscus sinensis*) appears to be tolerant of increased salinity for short periods, as it survived in up to 50% seawater (17.5‰ salinity) for up to a week (Lee *et al.*, 2006); similarly, the largest of the long-necked turtles, *C. expansa*, survived at 15‰ for 50 days (Bower *et al.*, 2016).

(2) Behavioural, physiological, and morphological homeostatic mechanisms

To survive in brackish environments, freshwater turtles implement various behavioural, physiological, and morphological homeostatic mechanisms (Fig. 4). Flexible behaviour of multiple freshwater turtle species in the absence of physiological adaptations allows them to temporarily occupy brackish water environments (Greenberg & Maldonado, 2006). Behavioural mechanisms include activities like movements between saline and freshwater areas, frequent retreats to freshwater sources higher upstream, and reduced feeding and drinking that would result in ingestion of higher salinity water (Hart & Lee, 2006; Harden, Midway, & Williard, 2015; Bower *et al.*, 2016). For example, *M. terrapin* and *B. baska* can identify high-salinity conditions and avoid drinking or feeding when water salinity is too high (Davenport & Ward, 1993). Additionally, *M. terrapin* can quickly rehydrate if given access to freshwater sources (Davenport & Macedo, 1990), and can survive for extended periods in marine environments by drinking rainwater floating on the sea surface (Dunson, 1985).

In addition to behaviour, many species of freshwater turtle show some capacity to occupy brackish waters temporarily by

Table 4. Rates of mass loss in starved adult freshwater turtles exposed to various salinities. As a reference, seawater salinity on average is 35‰, or 3.5% total dissolved salt. – indicates that turtles maintained their mass over the duration of the experiment

Family	Species	Mean loss (%) per day	Reference
Geoemydidae	<i>Batagur baska</i>		
	17.5‰ salt	1.22	Davenport & Wong (1986)
	26.25‰ salt	1.53	Davenport & Wong (1986)
	35‰ salt	1.80	Davenport & Wong (1986)
Emydidae	<i>Batagur borneoensis</i>		
	35‰ salt	1.13	Davenport & Wong (1986)
	<i>Pseudemys nelsoni</i>		
	35‰ salt	0.30–0.40	Dunson & Seidel (1986)
	<i>Trachemys decussata</i>		
	35‰ salt	0.84	Dunson & Seidel (1986)
	<i>Malaclemys terrapin</i>		
	35‰ salt	0.30–0.32	Robinson & Dunson (1976); Dunson (1986)
	34‰ salt	—	Davenport & Macedo (1990)
	<i>Chrysemys picta</i>		
35‰ salt	1.80	Robinson & Dunson (1976); Dunson (1986)	
Kinosternidae	<i>Clemmys guttata</i>		
	35‰ salt	2.20	Dunson (1986)
	35‰ salt	2.40	Dunson & Seidel (1986)
	<i>Kinosternon baurii</i>		
	35‰ salt	1.30–1.70	Dunson (1979)
	<i>Kinosternon subrubrum</i>		
	35‰ salt	2.10	Dunson (1986); Dunson & Seidel (1986)
	<i>Kinosternon leucostomum</i>		
	2.40	Dunson (1979)	
	<i>Sternotherus odoratus</i>		
17.5‰ salt	2.30	Dunson (1981)	
35‰ salt	7.60	Dunson (1986)	
35‰ salt	3.30	Dunson (1986)	
Trionychidae	<i>Kinosternon baurii</i>		
	35‰ salt	2.80	Dunson & Seidel (1986)
	35‰ salt	2.30	Dunson (1981)
	<i>Trionyx ferox</i>		
Chelidae	17.5‰ salt	2.80	Dunson & Seidel (1986)
	35‰ salt	4.50	Dunson (1981)
Chelydridae	<i>Chelodina expansa</i>		
	15‰ salt	—	Bower <i>et al.</i> (2016)
Chelydridae	<i>Emydura macquarii</i>		
	15‰ salt	—	Bower <i>et al.</i> (2016)
Chelydridae	<i>Chelydra serpentina</i>		
	13.9‰ salt	0.75	Kinneary (1993)
	35‰ salt	0.40–1.40	Dunson (1986)

regulating osmotic pressures relative to saline environments. One mechanism to reduce water loss – the repartitioning of intercellular fluids and increasing concentrations of plasma urea to maintain osmotic balance (Gilles-Baillien, 1970) – is present in almost all freshwater turtles that can tolerate prolonged exposure to seawater (e.g. *Pelodiscus sinensis*, *Emydura macquarii*, *Chelodina expansa*, *C. longicollis*; Lee *et al.*, 2006). In addition, bladder fluids can accumulate high salt concentrations, and thus some turtles can excrete excess salts with urea (Gilles-Baillien, 1973) including through their mouth (Ip *et al.*, 2012). Populations within species can also exhibit variable levels of local adaptation. For example, individual snapping turtles (*Chelydra serpentina*) that hatched from eggs of adults living in saltwater marshes grew faster at higher

salinities than those from parents living in freshwater creeks (Dunson, 1986).

The most widely distributed estuarine turtle is *M. terrapin*. It occurs along the Atlantic and Gulf coasts of the USA (from Florida Keys north to Massachusetts and west to Texas), where it is restricted to brackish waters with relatively high salinities [27–34‰ (Wood, 1977) and 11–34‰ (Dunson, 1985; see Ernst & Lovich, 2009)]. *M. terrapin* can increase red blood cell counts when exposed to seawater, thus aiding in the removal of ammonia and urea from muscle tissue (Gilles-Baillien, 1973). This species is also the only non-marine turtle species indisputably shown to have a functional lachrymal gland (i.e. salt gland; Babonis & Brischoux, 2012), which is situated near their eyes and is

Table 5. Rates of mass loss in starved sub-adult freshwater turtles exposed to various salinities. As a reference, seawater salinity on average is 35‰, or 3.5% total dissolved salt

Species	Family	Mean loss (%) per day	Reference
<i>Trachemys decussata</i> 17.5‰ salt	Emydidae	0.59	Dunson & Seidel (1986)
		0.36	Dunson & Seidel (1986)
		0.80	Dunson & Seidel (1986)
<i>Chelydra serpentina</i> 17.5‰ salt 14‰ salt 35‰ salt	Chelydridae	1.20–1.70	Dunson (1986)
		0.32–0.86	Kinneary (1993)
		7.40–9.10	Dunson (1986)
<i>Batagur borneoensis</i> 17.5‰ salt 35‰ salt	Geoemydidae	0.90	Dunson & Moll (1980)
		1.40	Dunson & Moll (1980)

a series of ducts over the lateral surface of the nictitating membrane (Dunson & Dunson, 1975). During periods of immersion in seawater, *M. terrapin* use this gland to excrete excess salt (Dunson & Dunson, 1975). Their lachrymal gland is similar in structure to those in other freshwater turtles (Cowan, 1969), but in *M. terrapin* these glands are much larger, function to minimize water loss, and, therefore,

play a significant role in maintaining internal salt balance. Other species, such as *C. longicollis*, are suspected of having functional lachrymal glands (Chessman, 1984), given their relatively high tolerance to salinity among freshwater turtles (Bower, Death, & Georges, 2012; Bower, Hodges, & Georges, 2013), but evidence to date remains inconclusive.

Similar to *M. terrapin*, the lachrymal gland controls salt influx in sea turtles. However, the relative size of the lachrymal glands in *M. terrapin* (0.03–0.04% of individual body mass) and adult sea turtles differs. For example, the gland is almost twice the size of the brain in the leatherback sea turtle (*Dermochelys coriacea*) (Lutz, 1997). Similarly, green sea turtle (*Chelonia mydas*) hatchlings have proportionally larger salt glands (0.3% body mass) compared to their adult counterparts (0.05% body mass), and size is negatively correlated with sodium influx (Dunson & Heatwole, 1986). Additionally, other adult sea turtles, *Caretta caretta* and *Lepidochelys olivacea*, have lachrymal glands that range from 0.05 to 0.07% body mass (Lutz, 1997). Altogether, these observations suggest that size of the lachrymal gland relative to body mass may be an important trait for efficient salt excretion and osmoregulation in turtles, and *M. terrapin* has evolved proportionally sized and similarly functioning lachrymal glands to those of adult sea turtles.

Finally, morphological variation also influences an individual turtles' salinity tolerance. For example, net water loss is inversely proportional to body size, providing larger turtles with increased tolerance (Dunson, 1986). This relationship may be why freshwater turtles in brackish water environments frequently have larger body sizes than their conspecifics from freshwater locales (Pritchard, 2001), a phenomenon often reported with nesting turtles found

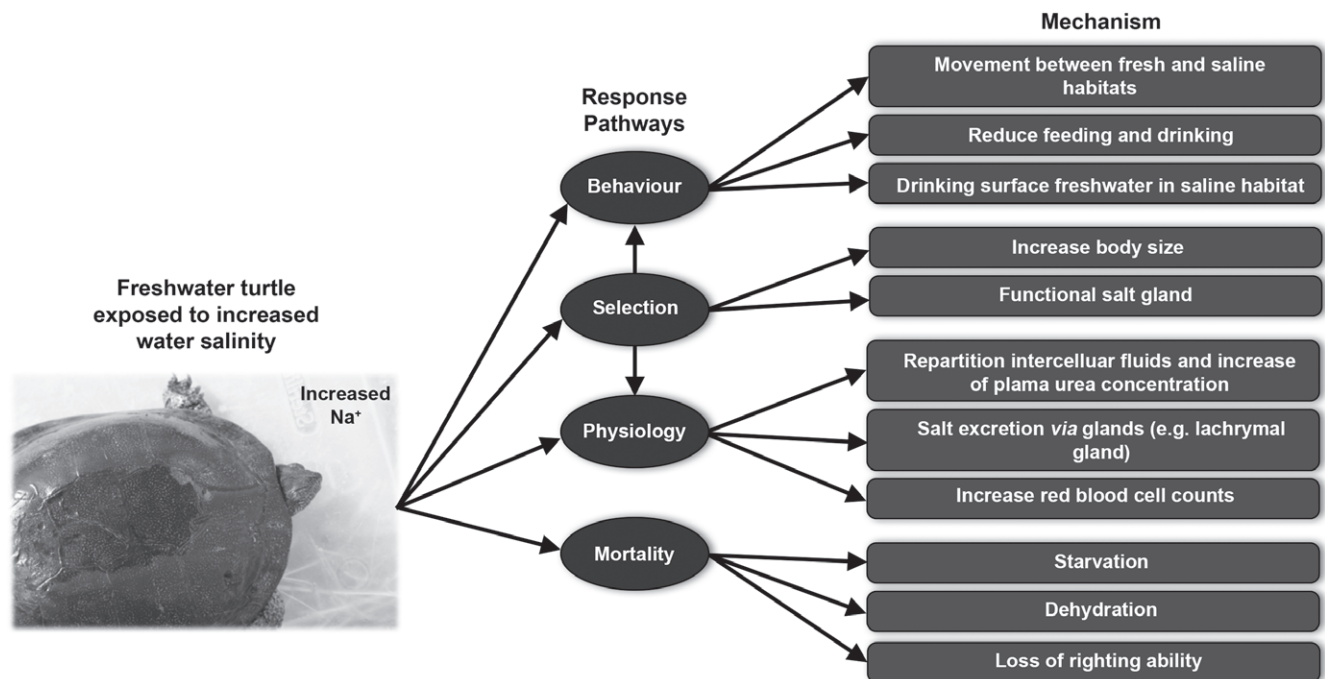


Fig. 4. Pathways of water salinity exposure response and mechanisms in freshwater turtles described in the literature.

in brackish water (Dunson & Mazzotti, 1989; Kinneary, 1993). For example, one study showed that in the family Carettochelyidae, *Carettochelys insculpta* that migrate to coastal brackish waters to lay eggs were significantly larger than those that did not (Eisemberg *et al.*, 2015). Such an explanation is not exclusive, however, as increased body size in turtles migrating to offshore islands may also reduce the risk of predation, increase the capacity of individuals to migrate effectively (Moll & Moll, 2004), or provide a selective advantage in salinity tolerance (Eisemberg *et al.*, 2015).

(3) Origins and evolutionary perspective of salinity tolerance

Freshwater turtles are one of the most evolutionarily conserved reptile taxa, with many species retaining ancestral traits that extend back approximately 210 million years (Joyce & Gauthier, 2004). There are two competing hypotheses for aquatic *versus* terrestrial origins of turtles. Fossil evidence from extinct species like *Proganochelys quenstedti* and *Palaeochersis talampayensis* suggests that early turtle evolution occurred in terrestrial habitats (Joyce & Gauthier, 2004). However, these findings were challenged with the discovery of *Odontochelys*, the oldest known turtle fossil that appears to have occupied brackish or river delta environments (Li *et al.*, 2008), which has led many evolutionary biologists to hypothesize that turtles first evolved in marine environments (see Reisz & Head, 2008). More recent interpretations of morphological and molecular-based phylogenies support the origin of multiple radiations of turtles and suggest that stem turtles originated in terrestrial environments, whereas crown turtle species originated in freshwater systems (Lyson *et al.*, 2010). Using this latest interpretation of the fossil record, it appears that many turtle taxa independently evolved the ability to inhabit brackish or marine environments throughout the evolutionary history of turtles.

In extant aquatic turtle species, their occurrence in saline habitats appears to vary depending on region and phylogenetic position. To clarify broad phylogenetic associations with brackish water use among species and within turtle families, we provide a phylogenetic visual representation of 240 coastal turtle species (phylogeny from R.C. Thomson, P.Q. Spinks & H.B. Shaffer, in preparation) and colour code their level of use of saline habitats (Fig. 2). In general, there are multiple families (e.g. Emydidae, Chelydridae, Carettochelyidae, Kinosternidae, and Trionychidae) that have closely related species commonly seen in brackish water environments. A majority of these species are located in North America and Southeast Asia (Fig. 1). The increased incidence of brackish water habitat use from these regions and the grouping of salt-tolerant species within the phylogeny could reflect greater availability of brackish water habitats in these regions compared to other regions of the world (e.g. greater niche space, allowing more species to evolve to use them). Alternatively, the increased use of brackish water in these areas could be due to the concentration of research and reporting in these areas relative to other areas, or simply data

deficiency for species in other regions. For instance, one anecdotal record suggested that all species of *Graptemys* ($N = 13$), with the exception of *Graptemys versa*, have been detected in brackish waters (Schwartz & Dutcher, 1961); however, further published documentation on *Graptemys* could not be found. Thus, there are likely significant gaps in our current knowledge of brackish water use by freshwater and estuarine turtle species in the literature. For example, very few salinity-tolerance studies or studies reporting occurrences in salt water focus on species from the families Chelidae and Pelomedusidae, both of which evolved from species within an extinct group of turtle (Bothremyidae) that possibly inhabited brackish environments (Winkler & Sanchez-Villagra, 2006; Klein *et al.*, 2016). Therefore, knowledge of salt tolerance in freshwater and estuarine turtles is likely incomplete, especially within specific groups and geographic regions.

The southeastern USA and southeast Asia regions, where turtle diversity is high and where many freshwater turtle species reportedly occupy brackish water environments, have similar geological histories. Throughout geological time, these regions were influenced by glacial cycles and subsequent sea-level fluctuations, which functioned as isolation and vicariance mechanisms that shaped the evolutionary history of the regions (Sodhi *et al.*, 2004; Ennen *et al.*, 2016, 2017). The repeated inundation of freshwater systems with saltwater over time likely favoured salt-tolerant freshwater lineages, facilitating dispersal into coastal rivers and other coastal habitats from shared estuaries in these regions. For example, phylogenetic data suggest that the ancestor of the brackish-water-adapted North American *M. terrapin* gave rise to the freshwater ancestor of the genera *Trachemys*, *Pseudemys*, and *Graptemys* via a Miocene divergence (Gaffney & Meylan, 1988; Bickham *et al.*, 1996; Lamb & Osentoski, 1997; Thomson, Spinks, & Shaffer, 2017), which contradicted a previous hypothesis on *Graptemys* speciation put forth by Wood (1977). Although salinity tolerance data are scarce for *Graptemys* species, the fluctuating sea levels and repeated saltwater intrusion of freshwater systems during past glacial cycles of the Pliocene and Pleistocene corresponds with high endemism of *Graptemys* species inhabiting coastal drainages of the Gulf of Mexico (Lamb & Osentoski, 1997; Ennen *et al.*, 2017; Thomson *et al.*, 2017), suggesting a potential role of salinity tolerance in the evolution and distribution of *Graptemys*. Other geological periods also experienced high sea levels. For example, fossil pelomedusid eggshells from the late Miocene found in South America were potentially oviposited in terrestrial habitats adjacent to marine environments (Winkler & Sanchez-Villagra, 2006). In addition, a potential evolutionary pathway for salinity tolerance may have occurred in the late Cretaceous, as fossil remains of Bothremyidae (side-necked turtles) of Africa were documented in nearshore habitats with either salt or brackish waters (Klein *et al.*, 2016). Finally, a late Cretaceous marine-associated shark coprolite was found with a sub-adult trionychid turtle inclusion, suggesting that the turtle may have been eaten by the shark in brackish waters (Schwimmer, Weems, & Sanders, 2015). These ancient

divergence hypotheses could be the earliest examples of divergence of a brackish water vertebrate from an ancestral freshwater group to date.

In Europe and Asia, where freshwater turtles are recorded occupying brackish water in several studies, geographic ranges of turtles may have expanded or shifted more recently in the late Pleistocene–Holocene (Kukushkin & Jablonski, 2016), leaving isolated relict populations in either freshwater or brackish water environments. In addition, some freshwater turtle species and tortoises are capable of long-distance transoceanic dispersal (Gerlach, Muir, & Richmond, 2006; Vamberger *et al.*, 2014; Cheke *et al.*, 2016), whereas others have been dispersed by humans. Thus, ranges may have shifted more recently into saline environments, generating contemporary brackish water records (Kukushkin & Jablonski, 2016). Furthermore, in Australia, wide-ranging aquatic turtles found in large catchments tolerating expanses of saline conditions reflects an extensive history of evolutionary adaptation to salinity as well as a recent adaptation to dry periods (Bower *et al.*, 2016). During extended periods of drought, freshwater turtles could have been isolated in ponds with high salinity, forcing these turtles to adapt or perish (Bower *et al.*, 2016). In North America, populations of *Actinemys marmorata* inhabit brackish water tidal sloughs, which may again be a result of recent drought-induced isolation.

Finally, extant aquatic turtle species that are considered brackish water specialists (e.g. *M. terrapin*) are often in direct contact with, adjacent to, or closely related to solely freshwater species. Their genetic differences may be a result of allopatric speciation as suggested above. However, secondary contact, and continued differences in salinity tolerance, may point to parapatric speciation (Dunson & Travis, 1994). Parapatric speciation, resulting from extreme salinity variation between marine and estuarine ecosystems across the globe, could explain distinct differences in salinity tolerance among co-occurring aquatic turtle species and their continued genetic isolation. While these hypotheses fit with current extant freshwater turtle coastal distributions, there are gaps that remain in our understanding of the origins of brackish water use and the evolution of salinity tolerance of freshwater turtles.

(4) Sea level rise

Global SLR driven by thermal expansion, melting glaciers and ice sheets, and reduction of water storage on land may severely affect the long-term stability of coastal brackish water ecosystems (e.g. estuaries, mangroves, and tidal marsh) and their wildlife inhabitants (Kirwan *et al.*, 2010; Mengel *et al.*, 2016). Based on our review of the literature, freshwater turtles depend on and use these coastal habitats during multiple life-history phases and to meet their nesting, basking, foraging, and aestivation requirements. However, under unmitigated upper SLR predictions (~1 m by 2100), global coastal wetland losses may reach 78% (Spencer *et al.*, 2016), and could impact the geographic range of approximately 90% of coastal freshwater turtles in some

way. Consequently, some freshwater turtles are predicted to be at risk of significant habitat loss due to projected SLR (Hunter *et al.*, 2015; Woodland, Rowe, & Henry, 2017). Freshwater turtles that use coastal brackish water habitats are expected to be vulnerable to SLR because they will either need to adapt physiologically or adjust behaviourally (i.e. migrate) in response to potential increased variance in water salinity and reduced habitat availability. While this loss of habitat affects only part of the range of many species, it may act synergistically with many other processes that are simultaneously threatening freshwater turtles (e.g. consumptive exploitation, habitat destruction and degradation, human development, water pollution, and water diversion). Thus, future research directed at life-history, behavioural, and physiological responses of freshwater turtles to saltwater inundation and SLR may be of critical value to conservation managers in regions of the world where SLR is predicted to have the greatest effects on species' ranges.

IV. CONCLUSIONS

(1) Despite the physiological challenges posed by saline environments, we document the existence of variable tolerances of different freshwater turtle species ranging from completely intolerant to highly tolerant of saline waters. We identify regions of the world in need of research on the physiological and behavioural salinity tolerances of freshwater turtles, especially Oceania, where coastal species may be exceedingly vulnerable to projected SLR.

(2) We find that there may be under-appreciated mechanisms allowing freshwater turtles to deal with various salinities at different life-history phases. Precisely defining mechanisms and corresponding tolerances should be a priority for species that are likely to be most affected by coastal inundation and salinization of freshwater habitats from droughts, climate change, and SLR.

(3) Similarly, we propose a useful phylogenetic and spatial framework for prioritizing future research focused on mechanisms of salt tolerance, the capacity for populations to respond, and correspondingly, identifying levels of susceptibility across the globe (e.g. regional and species-targeted conservation applications).

(4) While freshwater turtles access brackish water habitats on every continent where turtles occur, the exclusive dependence of some species on brackish water habitats makes them highly vulnerable to projected SLR.

(5) In response to 2100 SLR projections and their expected impacts on sensitive freshwater turtles, we suggest integrating region-specific physiological and phylogenetic vulnerability assessments to effectively target species, clades, or localities of concern for conservation prioritization. Specifically, for managers to predict, prioritize, and mitigate effects of SLR and extreme weather events (e.g. hurricanes, droughts) on coastal freshwater species, conservation practitioners will need to use data on species-specific salinity

tolerances and behavioural, demographic, and growth responses to salinity gradients. These studies should also be accompanied by research on current species distributions and assemblage composition along salinity gradients (i.e. freshwater to brackish ecosystems), especially in global turtle biodiversity hotspots.

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