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Source: *Herpetological Monographs*, 2015, No. 29 (2015), pp. 1-27

Published by: Allen Press on behalf of the Herpetologists' League

Stable URL: https://www.jstor.org/stable/26358479

Herpetological Monographs, 29, 2015, 1–27

OCCURRENCE OF AMPHIBIANS IN SALINE HABITATS: A REVIEW AND EVOLUTIONARY PERSPECTIVE

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ABSTRACT: Amphibians are well known as osmotically sensitive organisms due to their highly permeable skin and eggs and, as such, biologists have mostly discounted their presence in saline environments. Yet, from the 1800s to the present day, scientists have repeatedly found amphibians living and breeding in a variety of saline coastal and inland habitats. Despite this plethora of observations, their presence in these habitats is still mostly ignored, and the last (and only) complete literature review documenting amphibians in brackish and saline habitats was completed over 50 yr ago. Here we provide a review of the literature of amphibians in saline waters and present data on 144 species, in 28 families, on every continent except Antarctica. In doing so, we make the case that salt tolerance in amphibians may not be as rare as generally assumed. Through classifying habitats and studies, we conclude that the abilities of dozens of species to locally adapt to coastal and inland saline habitats have been extensively studied, although more work on most observed species is still needed. Our understanding of the evolutionary processes leading to this adaptation is also in its infancy. We summarize the existing knowledge on this subject and present a possible framework toward the development of an evolutionary model of amphibian adaptation to salt, based on genetic variation for salt tolerance in populations and the nature of selection events in osmotically stressful environments. Finally, we discuss some possible limitations on the ability of amphibians to tolerate salt water. Understanding the abilities and constraints of amphibian populations to adapt to salt will become more critical as humans continue to impact the world's freshwater resources through climate change, landscape modification, and pollution, and these habitats thus become increasingly stressful for amphibians.

Key words: Adaptation; Anura; Brackish; Caudata; Coastal; Frog; Road deicing salts; Salamander; Newt; Salt; Toad

> "These animals and their spawn are immediately killed (with the exception as far as known, of one Indian species) by sea-water."
>
> —Charles Darwin (1872)

FOR NEARLY as long as biologists have been aware of amphibian intolerance of salt water, they have been fascinated by exceptions to this rule. Thus, in discussing the general lack of amphibians on islands, Darwin (1872) amended his statement on amphibian intolerance of salt water in the 6th edition of *Origin of the Species* to include the parenthetical exception "…of one Indian species." "I may add," he wrote to Alfred Russel Wallace a few years later (probably referring to *Fejervarya cancrivora*), "that there is an Indian toad which can resist salt water and haunts the seaside" (Darwin 1876). While on the voyage of the Beagle in Port Desire, Patagonia, Argentina in January 1834, Darwin noted that a "*Rana*… is bred in and inhabits water far too salt to drink" (Darwin 1834), a habitat Bell (1843) agreed was "remarkable" when identifying the frog as *Leiuperus salarius* (= *Pleurodema bufoninum*).

Since Darwin, countless other biologists and naturalists have found other frogs, toads, salamanders, and newts "haunting the seaside" and remarked on these fascinating exceptions to the rule of amphibian intolerance of salt water (Table 1). Neill (1958) compiled these anecdotes into his opus, "The occurrence of amphibians and reptiles in saltwater areas, and a bibliography." This paper is the only complete review of amphibians in saline habitats to date, and it includes mostly anecdotal notes of occurrence of amphibians in habitats impacted by salt water. At the time of its publication, very little work had been completed on amphibian osmoregulatory physiology, including the now-classic work of Malcolm S. Gordon and colleagues (e.g., Gordon et al. 1961); very few of the species mentioned in Neill's publication had been tested for salt tolerance nor had the salinity of their habitats been measured. This pattern of what we would today call natural history notes makes up the bulk of the literature on amphibians and salinity, and it persisted as the norm from the 1800s to the early 1950s. Nevertheless, Neill's (1958) compilation of over 40 species of amphibians showing some evidence of salt tolerance provided the first glimpse that such tolerance may be more widespread than originally assumed.

In the 1960s and 1970s, Malcolm S. Gordon (e.g., Gordon et al. 1961), Uri Katz (e.g., Katz 1973), Ronald H. Alvarado (e.g., Alvarado and Moody 1970), and others completed seminal osmoregulatory physiology studies on amphibians and their ability to regulate salts. Much of this work focused on the physiological ability of the Asian Crab-eating Frog, *Fejervarya* (= *Rana*) *cancrivora*, and the European Green Toad, *Bufotes* (= *Bufo*) *viridis* (= *balearicus*) to inhabit coastal habitats with salinities approaching that of full-strength seawater. Although many observers, including Darwin (1872), had long commented on the presence of these species in tidal mangroves, beaches, and in some cases actually in the sea, Gordon, Katz, and their colleagues demonstrated experimentally how these animals achieved this remarkable tolerance. Their elucidations of the mechanisms of urea hypersynthesis and retention and Na^+ and Cl^- uptake to increase the osmolarity of the body fluids and plasma to be isotonic with the surrounding seawater (e.g., Gordon et al. 1961; Gordon 1962; Gordon and Tucker 1965, 1968; Katz 1973, 1975) are now considered classic works in amphibian physiology (reviewed by Balinsky 1981; Katz 1989; Shoemaker et al. 1992). This mechanism has since been discovered in other salt-tolerant species, e.g., *Ambystoma tigrinum* (Kirschner et al. 1971; Romspert and McClanahan 1981; Gasser and Miller 1986), *Batrachoseps* spp. (Jones and Hillman 1978), *Rhinella marinus* (Liggins and Grigg 1985), *Epidalea calamita* (Gomez-Mestre et al. 2004), and *Pseudacris regilla* (Weick 1980).

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TABLE 1.—Amphibians reported from saline habitats and the nature of the habitat and study. C = coastal, I = inland, N = natural, A = anthropogenic; FA = full article, NHN = natural history note, TD = thesis or dissertation; S = salinity-focused, NS = not salinity-focused.

Species	Life stage	Habitat	Location	Measured salinity	Tested tolerance	Field observation	Lab physiology	Paper type	Reference
Gymnophiona									
Typhlonectidae									
Atretochoana eiselti	Adult	Tidal stream, tidal pool (C/N)	Brazil	No	No	Yes	No	FA/NS	Hoogmoed et al. 2011
Caudata									
Ambystomatidae									
Ambystoma maculatum	Adult, juvenile	Beach, under driftwood (C/N)	USA	No	No	Yes	No	NHN/NS	Hardy 1952
	Eggs	Roadside pools (I/A)	USA	Yes	Yes	Yes	No	FA/S	Turtle 2000; Brady 2012
	Adults, eggs, larvae	Roadside pools (I/A)	USA	Yes	Yes	Yes	No	FA/S	Karraker et al. 2008
Ambystoma opacum	Adults, larvae	Beach ponds with salt spray (C/N)	USA	No	No	Yes	No	NHN/NS	Hardy 1972
Ambystoma talpoideum	Adults, larvae	Coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/S	Gunzburger et al. 2010
Ambystoma taylori	Adult, larvae	Saline lake (I/N)	Mexico	Yes	Yes	Yes	No	FA/NS	Taylor 1943; Brandon et al. 1981
Ambystoma tigrinum	Larvae	Saline, alkaline pond (I/N)	USA	Yes	Yes	Yes	Yes	FA/S	Gasser and Miller 1986
	Larvae/neotenic adults	Saline lake (I/N)	USA	Yes	No	Yes	No	FA/S/NHN /NS/FA/NS	Young 1924; Larson 1968; Held and Peterka 1974
	Larvae/neotenic adults	Saline lake (I/N)	USA	Yes	No	Yes	Yes	FA/S	Duerr and Ness 1970
	Larvae	Saline lake (I/N)	Canada	Yes	No	Yes	No	NHN/S	Hammer 1986
	Larvae		USA	No	Yes	No	Yes	FA/S	Kirschner et al. 1971
	Adults		USA	No	Yes	No	Yes	FA/S	Romspert and McClanahan 1981
Dicamptodon tenebrosus	Larvae	Tidal stream (C/N)	USA	No	No	Yes	No	NHN/S	Ferguson 1956
	Larvae	Tidal stream (C/N)	USA	Yes	No	Yes	No	NHN/S	Hopkins and Hopkins in press
Amphiumidae									
Amphiuma means	Adults, larvae	Coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/S	Gunzburger et al. 2010
Plethodontidae									
Batrachoseps gavilanensis	Adults	Beach, under driftwood (C/N)	USA	No	Yes	Yes	Yes	FA/S	Licht et al. 1975
Batrachoseps pacificus	Adults	Beach, under driftwood (C/N)	USA	No	No	Yes	No	FA/NS	Hansen et al. 2005
Eurycea quadridigitata	Adults, larvae	Coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/S	Gunzburger et al. 2010
Salamandridae									
Lissotriton helveticus	Larvae	Brackish tidal pool (C/N)	UK	Yes	No	Yes	No	NHN/S	Spurway 1943
	Adults	Island pond with sea spray (C/N)	UK	Yes	No	Yes	No	FA/NS	Pyefinch 1937
	Adults	Coastal saline wetland (C/N)	France	Yes	No	Yes	No	FA/S	Thirion 2014
Lissotriton vulgaris	Adults, larvae, eggs	Brackish tidal pools (C/N)	UK	No	No	Yes	No	NHN/S	Hardy 1943
	Adults, eggs	Baltic Sea (C/N)	Sweden	No	No	Yes	No	NHN/S	Hagström 1981
	Adults	Saline lake (I/N)	Russia (W. Siberia)	Yes	No	Yes	No	FA/S	Decksbach 1922
Notophthalmus viridescens	Adults	Brackish water (I/N)	USA	No	No	Yes	No	NHN/NS	Pawling 1939
	Adults		USA	No	No	No	Yes	FA/S	Wittig and Brown 1977

TABLE 1.—Continued.

Species	Life stage	Habitat	Location	Measured salinity	Tested tolerance	Field observation	Lab physiology	Paper type	Reference
	Adults, larvae	Coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/S	Gunzburger et al. 2010
Pleurodeles poireti	Adults	Brackish ponds, estuarine marshes (C/N)	Algeria	No	No	Yes	No	FA/NS	Samraoui et al. 2012
Salamandra salamandra	Adults	Semi-arid pools (I/N)	Israel	No	Yes	Yes	Yes	FA/S	Degani 1981
Taricha granulosa	Adults	Tidal stream (C/N)	USA	No	No	Yes	No	NHN/S	Ferguson 1956
	Adults	Tidal stream (C/N)	USA	Yes	No	Yes	No	NHN/S	Hopkins and Hopkins in press
	Eggs, larvae	Inland pond (I/A)	USA	No	Yes	No	No	FA/S	Hopkins et al. 2013b, 2014
Triturus dobrogicus	Neotenic adult	Saline soda pan (I/N)	Hungary	Yes	No	Yes	No	NHN/S	Mester et al. 2013
Triturus marmoratus	Adults	Brackish marsh (C/N)	France	Yes	No	Yes	No	FA/S	Thirion 2014
Sirenidae									
Siren lacertina	Adults	Mangrove swamp (C/N)	USA	Yes	No	Yes	No	NHN/S	Boss and Chesnes 2014
Anura									
Alytidae									
Discoglossus galganoi	Adults	Brackish water	Spain	No	No	Yes	No	FA/NS	Nöllert and Nöllert 1992
Discoglossus pictus	Larvae	Coastal saline lake, brackish lagoon (C/N)	Morocco	Yes	No	Yes	No	FA/NS	El Hamoumi et al. 2007
	Larvae	Salt marshes, estuaries, brackish ponds (C/N)	Tunisia, Algeria, France	Yes	Yes	Yes	No	FA/NS	Knoepffler 1962
Discoglossus sardus	Larvae	Salt marshes, estuaries, brackish ponds (C/N)	Tunisia, Algeria, France	Yes	Yes	Yes	No	FA/NS	Knoepffler 1962
Bombinatoridae									
Bombina variegata	Adults, larvae	Brackish ditch (I/N)	France	Yes	No	Yes	No	TD/S	Florentin 1899
	Larvae	Saline discharges/flows (I/N)	Germany	No	No	Yes	No	FA/NS	Knoepffler 1962
Bufonidae									
Amietophrynus mauritanicus	Adults, larvae	Beach, stream on beach (C/N)	Algeria	No	No	Yes	No	NHN/NS	Bellairs and Shute 1954
	Adults	Brackish pond (C/N)	Algeria	No	No	Yes	No	FA/NS	Samraoui et al. 2012
Anaxyrus americanus	Adults	Tidal marsh (C/N)	Canada	Yes	No	Yes	No	FA/NS	Ouellet et al. 2009
	Adults, eggs	Tidal marsh (C/N)	USA	Yes	No	Yes	No	NHN/S	Kiviat and Stapleton 1983
	Adults, eggs, larvae	Roadside wetlands (I/A)	Canada	Yes	Yes	Yes	No	FA/S	Collins and Russell 2009
	Larvae	Road deicing salt (I/A)	USA	No	Yes	No	No	FA/S	Dougherty and Smith 2006
	Eggs, larvae	Road deicing salt (I/A)	USA	No	Yes	No	No	FA/S	Snodgrass et al. 2008
Anaxyrus boreas	Adults	Beach, ocean (C/N)	USA	No	No	Yes	No	FA/NS	Storer 1925
	Adults, larvae	Saline hot spring, lake (I/N)	USA	Yes	No	Yes	No	FA/NS	Brues 1932
	Adults	Saline lake (I/N)	USA	No	No	Yes	No	FA/NS	Brues 1932
Anaxyrus fowleri	Adults	Beach, beach ponds with salt spray, coastal islands, ocean (C/N)	USA	No	No	Yes	No	FA/NHN/NS	Wright and Wright 1938; Engels 1952; Hardy 1972
Anaxyrus quercicus	Adults, larvae	Beach, coastal islands, coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/NS	Engels 1952; Gunzburger et al. 2010
Anaxyrus terrestris	Adults, larvae	Beach, coastal islands, coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/NS/S/NHN/S	Allen 1932; Smith and List 1955; Neill 1958; Gunzburger et al. 2010
	Larvae	Inland freshwater	USA	No	Yes	No	No	FA/S	Brown and Walls 2013
Bufo bufo	Adults, eggs	Brackish pools (C/N)	UK	No	No	Yes	No	NHN/S	Hardy 1943
	Larvae	Freshwater pond (C/N)	Italy	Yes	Yes	Yes	Yes	FA/S	Bernabò et al. 2013
	Larvae	Brackish island pool (C/N)	Norway	Yes	No	Yes	No	NHN/S	Hagström 1981
	Larvae	Brackish ditch (I/N)	France	Yes	No	Yes	No	TD/S	Florentin 1899

TABLE 1.—Continued.

Species	Life stage	Habitat	Location	Measured salinity	Tested tolerance	Field observation	Lab physiology	Paper type	Reference
Bufotes balearicus	Larvae	Pond (C/N)	Italy	Yes	Yes	Yes	Yes	FA/S	Bernabò et al. 2013
Bufotes boulengeri	Larvae	Coastal saline lake, brackish lagoon (C/N)	Morocco	Yes	No	Yes	No	FA/NS	El Hamoumi et al. 2007
	Adults	Brackish water (C/N)	Algeria, Egypt	No	No	Yes	No	FA/NS	Werner 1909
Bufotes variabilis	Adults	Beach (C/N)	Iran	No	No	Yes	No	FA/NS	Schmidt 1955
	Adults	Shores of hypersaline lake (I/N)	Iran	No	No	Yes	No	FA/NS	Asem et al. 2014
Bufotes viridis	Larvae	Saline, muddy pools (I/N)	Austria	No	No	Yes	No	FA/NS	Knoepffler 1962
	Adults	Brackish pools, ocean (sound) (C/N)	Sweden	Yes	No	Yes	No	FA/NS	Gislén and Kauri 1959
	Adults		Belgium, Yugoslavia, Italy, Israel	No	Yes	No	Yes	FA/S	Gordon 1962; Tercafs and Schoffeniels 1962; Katz 1973, 1975
	Adults, eggs	Baltic Sea (C/N)	Sweden	No	No	Yes	No	NHN/S	Mertens 1926; Hagström 1981
	Adults, eggs	Brackish water (C/N)	Europe	No	No	Yes	No	FA/NS	Boulenger 1897–1898
Duttaphrynus melanostictus	Adult	Brackish ponds/estuary (C/N)	India	Yes	No	Yes	No	FA/NS	Annandale 1907
	Adult	Saline mangrove swamp (C/N)	Bangladesh	No	No	Yes	No	FA/NS	Rahman and Asaduzzaman 2010
	Adult	Pond (C/N)	India	No	Yes	No	Yes	FA/S	Chakko 1968
	Larvae	Pond (C/N)	Hong Kong	No	Yes	No	No	FA/S	Strahan 1957; Karraker et al. 2010
	Adult	Brackish mangrove swamp (C/N)	Singapore	No	No	Yes	No	NHN/NS	Chan and Goh 2010
Epidalea calamita	Adults, eggs	Brackish pools, tidal pools, estuaries (C/N)	UK	No	No	Yes	No	FA/NS	Boulenger 1897–1898, 1920a; Hardy 1943
	Adults, eggs	Baltic Sea (C/N)	Europe	No	No	Yes	No	FA/NHN/NS	Mertens 1926; Hagström 1981
	Eggs, larvae	Brackish beach pool (C/N)	UK	Yes	Yes	Yes	No	FA/S	Beebee 1985
	Adults, eggs	Ocean (bay) (C/N)	Sweden	Yes	No	Yes	No	FA/NS	Gislén and Kauri 1959
	Larvae	Saline pools on Frisian Islands (C/N)	Germany	No	No	Yes	No	FA/NS	Knoepffler 1962
		Saline tidal marsh (C/N)	France	No	No	Yes	No	FA/NS	Knoepffler 1962
	Larvae	Coastal saline wetlands, salt marsh (C/N)	France	Yes	No	Yes	No	FA/S	Thirion 2014
	Eggs, larvae, juvenile	Brackish ponds (I/N)	Spain	Yes	Yes	Yes	No	FA/S	Gomez-Mestre and Tejedo 2003, 2004, 2005; Gomez-Mestre et al. 2004
	Larvae	Brackish ponds (I/N)	Spain	Yes	Yes	Yes	Yes	FA/S	Gomez-Mestre et al. 2004
Incilius nebulifer	Eggs, larvae	Ditch (C/N)	USA	No	Yes	No	Yes	FA/S	Alexander et al. 2012
Incilius valliceps	Adults, eggs	Brackish coastal salt Marshes, wetlands impacted by storm tides (C/N)	USA	No	No	Yes	No	FA/NS	Burger et al. 1949; Neill 1958; Mueller 1985
Peltophryne lemur	Adults, eggs	Brackish pools (C/N)	Puerto Rico	Yes	No	Yes	No	TD/NS	Matos-Torres 2006
	Adults	Mangrove swamps (C/N)	British Virgin Islands	No	No	Yes	No	FA/NS	Grant 1932
Rhinella arenarum	Adults, larvae	Brackish salt flats stream (I/N)	Argentina	Yes	Yes	Yes	Yes	FA/S	Ruibal 1962
Rhinella crucifer	Larvae	Brackish estuary (C/N)	Brazil	Yes	No	Yes	No	NHN/S	Guix and Lopes 1989

TABLE 1.—Continued.

Species	Life stage	Habitat	Location	Measured salinity	Tested tolerance	Field observation	Lab physiology	Paper type	Reference
Rhinella dorbignyi	Adults, eggs	Coastal lagoon with artificially opened sand bar (C/N/A)	Brazil	Yes	No	Yes	No	FA/S	Moreira et al. 2015
Rhinella marina	Adults	Brackish pools, beach, mangroves (C/N)	Australia	No	No	Yes	No	FA/NS	van Beurden and Grigg 1980
	Adults		Australia	No	Yes	No	Yes	FA/S	Liggins and Grigg 1985
	Eggs, larvae		USA (Hawaii)	No	Yes	No	No	NHN/S	Ely 1944
	Adults, eggs, larvae	Temporal pools on beach (C/N)	Costa Rica	No	No	Yes	No	FA/NS	Sasa et al. 2009
	Adults, larvae	Saline mangroves, brackish swamp/forest (C/N)	Puerto Rico	Yes	Yes	Yes	No	FA/S	Rios-López 2008
Strauchbufo raddei	Adult	Beach, ocean (C/N)	China	No	No	Yes	No	NHN/S	Shaw 1934
Ceratophryidae									
Chacophrys pierottii	Adults	Brackish salt flats pools (I/N)	Argentina	No	No	Yes	No	FA/NS	Cei 1955
Lepidobatrachus asper	Adults	Brackish salt flats pools (I/N)	Argentina	Yes	Yes	Yes	Yes	FA/S	Ruibal 1962
Craugastoridae									
Craugastor fitzingeri	Adults	Beach (C/N)	Costa Rica	No	No	Yes	No	FA/NS	Sasa et al. 2009
Cycloramphidae									
Thoropa taophora	Adults, larvae	Intertidal zone of seashore (C/N)	Brazil	No	No	Yes	No	FA/NS	Sazima 1971; Brasileiro et al. 2010
	Adults	Intertidal zone of seashore (C/N)	Brazil	No	No	Yes	Yes	FA/S	Abe and Bicudo 1991
	Adults, larvae	Rocky beach (C/N)	Brazil	No	No	Yes	No	FA/NS	Muralidhar et al. 2014
Dendrobatidae									
Hyloxalus littoralis	Adults	Pond on beach (C/N)	Peru	No	No	Yes	No	FA/NS	Péfaur 1984
Dicroglossidae									
Euphlyctis cyanophlyctis	Adult	Brackish ponds/estuary (C/N)	India	Yes	No	Yes	No	FA/NS	Annandale 1907
	Adult	Pond (C/N)	India	No	Yes	No	Yes	FA/S	Chakko 1968
	Adults	Tidal mangrove swamp (C/N)	India, Bangladesh	No	No	Yes	No	FA/NS	Rahman and Asaduzzaman 2010; Jena et al. 2013
Euphlyctis hexadactylus	Adults	Tidal mangrove swamp (C/N)	India	No	No	Yes	No	FA/NS	Jena et al. 2013
Fejervarya cancrivora	Adults	Tidal mangrove swamp (C/N)	India	No	No	Yes	No	FA/NS	Satheeshkumar 2011; Jena et al. 2013
	Adults	Tidal stream, mangrove forest (C/N)	Myanmar	No	No	Yes	No	FA/NS	Wogan et al. 2008
	Adults	Beach, ocean (C/N)	South Asia	No	No	Yes	No	FA/NS	Boulenger 1920b
	Adults	Brackish pools (C/N)	Philippines	No	No	Yes	No	FA/NS	Alcala 1962
	Adults	Brackish water mangrove swamps (C/N)	Singapore	No	No	Yes	No	NHN/NS	Chan and Goh 2010
	Larvae	Intertidal zone on beach, crab burrows (C/N)	Philippines	Yes	No	Yes	No	NHN/S	Pearse 1911
	Larvae	Mangrove tidal pools (C/N)	Philippines	Yes	Yes	Yes	No	NHN/S	Dunson 1977
	Adults, eggs, larvae	Mangrove swamps (C/N)	Thailand	Yes	Yes	Yes	Yes	FA/S	Uchiyama et al. 1990
	Larvae	Mangrove tidal pools (C/N)	Thailand	Yes	Yes	Yes	Yes	FA/S	Gordon and Tucker 1965
	Adults	Mangrove swamps (C/N)	Thailand	Yes	Yes	Yes	Yes	FA/S	Gordon et al. 1961; Gordon and Tucker 1968
	Adults	Brackish water at estuary mouth (C/N)	Thailand	No	No	Yes	No	FA/NS	Smith 1927

TABLE 1.—Continued.

Species	Life stage	Habitat	Location	Measured salinity	Tested tolerance	Field observation	Lab physiology	Paper type	Reference
	Adults	Mangrove tidal pools (C/N)	Indonesia	Yes	Yes	Yes	Yes	FA/S	Wygoda et al. 2011
Fejervarya limnocharis	Adult	Brackish tidal streams (C/N)	Southeast Asia	No	No	Yes	No	FA/NS	Boulenger 1912
	Larvae	Brackish island tide pools (C/N)	Taiwan	Yes	Yes	Yes	Yes	FA/S	Wu and Kam 2009; Wu et al. 2012
	Larvae	Ponds (C/N)	Hong Kong	No	Yes	No	No	FA/S	Karraker et al. 2010
	Larvae	Freshwater ditch (C/N)	Thailand	Yes	Yes	No	Yes	FA/S	Gordon and Tucker 1965
Fejervarya moodiei	Adults, larvae	Beach, crab burrows in intertidal zone, brackish swamps (C/N)	Philippines	No	No	Yes	No	FA/S/NS	Taylor 1943; Brown et al. 2013
Fejervarya orissaensis	Adults	Tidal mangrove swamp (C/N)	India	No	No	Yes	No	FA/NS	Jena et al. 2013
Hoplobatrachus crassus	Adults	Tidal mangrove swamp (C/N)	India	No	No	Yes	No	FA/NS	Jena et al. 2013
Fejervarya rugulosus	Adults	Tidal irrigation ditches (C/N)	Malaysia	Yes	Yes	Yes	No	FA/S	Davenport and Huat 1997
Fejervarya tigerinus	Adult	Brackish ponds/estuary (C/N)	India	Yes	No	Yes	No	FA/NS	Annandale 1907
	Adult		Vietnam	No	Yes	No	Yes	FA/S	Gordon et al. 1961
	Adults	Tidal mangrove swamp (C/N)	India	No	No	Yes	No	FA/NS	Jena et al. 2013
Zakerana syhadrensis	Adults	Tidal mangrove swamp (C/N)	India	No	No	Yes	No	FA/NS	Jena et al. 2013
Eleutherodactylidae									
Eleutherodactylus caribe	Adults	Coastal mangroves (C/N)	Haiti	No	No	Yes	No	FA/NS	Hedges and Thomas 1992
Eleutherodactylus coqui	Adults	Brackish swamp/forest (C/N)	Puerto Rico	Yes	No	Yes	No	FA/S	Rios-López 2008
Eleutherodactylus jamaicensis	Adults	Supratidal area of beach, under coconut husks (C/N)	Jamaica	No	No	Yes	No	NHN/NS	Grant 1939
Eleutherodactylus luteolus	Adults	Beach (C/N)	Jamaica	No	No	Yes	No	FA/NS	Goin 1953
Eleutherodactylus martinicensis	Adults	Beach (C/N)	Antigua	No	No	Yes	No	NHN/NS	Lynn 1957
Eleutherodactylus planirostris	Adults	Stones/beach at edge of Ocean (C/N)	USA	No	No	Yes	No	NHN/S	Neill 1958
Hylidae									
Acris crepitans	Adults, larvae	Beach ponds with salt spray (C/N)	USA	No	No	Yes	No	NHN/NS	Hardy 1972
Acris gryllus	Adults, larvae	Coastal marsh with storm surge, brackish pools on sand dunes near ocean (C/N)	USA	Yes	No	Yes	No	FA/NS/S	Burger et al. 1949; Neill 1958; Gunzburger et al. 2010
Aparasphenodon bokermanni	Adults	Brackish tidal river (C/N)	Brazil	No	No	Yes	No	FA/NS	Pombal 1993
Dendropsophus microcephalus	Adults	Mangroves (C/N)	Colombia	No	No	Yes	No	NHN/NS	Alvarez-León and De Ayala-Monedero 2000
Hyla cinerea	Adults	Brackish pools in coastal salt marsh (C/N)	USA	No	No	Yes	No	FA/NS/NHN/S	Burger et al. 1949; Neill 1958
	Adults	Ponds subject to salt spray from Chesapeake Bay (C/N)	USA	Yes	No	Yes	No	FA/NS	Hardy 1953

Table 1.—Continued.

Species	Life stage	Habitat	Location	Measured salinity	Tested tolerance	Field observation	Lab physiology	Paper type	Reference
	Adults, eggs	Brackish pool (C/N)	USA	No	No	Yes	No	NHN/NS	Peterson et al. 1952
	Larvae	Bay (C/N)	USA	Yes	No	Yes	No	NHN/S	Diener 1965
	Adults, larvae	Coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/S	Gunzburger et al. 2010
	Larvae	Inland freshwater pond (I/N)	USA	No	Yes	No	No	FA/S	Brown and Walls 2013
Hyla femoralis	Adults, larvae	Coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/S	Gunzburger et al. 2010
Hyla gratiosa	Adults, larvae	Coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/S	Gunzburger et al. 2010
Hyla meridionalis	Adults	Brackish pond (C/N)	Algeria	No	No	Yes	No	FA/NS	Samraoui et al. 2012
	Larvae	Coastal saline wetlands, salt marshes (C/N)	France	Yes	No	Yes	No	FA/S	Thirion 2014
Hyla sarda	Adults	Brackish ponds (C/N)	Europe	No	No	Yes	No	FA/NS	Nöllert and Nöllert 1992
Hyla savignyi	Adults	Shores of hypersaline lake (I/N)	Iran	No	No	Yes	No	FA/NS	Asem et al. 2014
Hyla versicolor	Adults	Beach, pools affected by sea spray (C/N)	USA	No	No	Yes	No	FA/NS/NHN/S	Viosca 1923; Neill 1958
	Larvae	Road deicing salts (I/A)	USA	No	Yes	No	No	FA/S	Chambers 2011; Van Meter and Swan 2014
Hypsiboas geographicus	Larvae	Brackish estuary (C/N)	Brazil	Yes	No	Yes	No	NHN/S	Guix and Lopes 1989
Hypsiboas pulchellus	Adults	Coastal lagoon with artificially opened sand bar (C/N/A)	Brazil	Yes	No	Yes	No	FA/S	Moreira et al. 2015
Litoria aurea	Larvae	Fresh and brackish (secondary salinization) wetland (I/A)	Australia	Yes	Yes	Yes	No	FA/S	Christy and Dickman 2002; Kearney et al. 2012
	Adults, larvae	Brackish estuary (C/N)	Australia	Yes	No	Yes	No	FA/S	Hamer et al. 2002
	Adults, larvae	Ponds adjacent to ocean and coastal lagoons (C/N)	Australia	Yes	No	Yes	No	FA/NS	Pyke et al. 2002, 2013
Litoria caerulea	Adults, larvae	Pond adjacent to coastal lagoon (C/N)	Australia	Yes	No	Yes	No	FA/NS	Pyke et al. 2002
Litoria cyclorhyncha	Adults, larvae	Saline creek (I/N/A)	Australia	Yes	No	Yes	No	NHN/S	Janicke and Roberts 2010
Litoria dentata	Adults, larvae	Pond adjacent to coastal lagoon (C/N)	Australia	Yes	No	Yes	No	FA/NS	Pyke et al. 2002
Litoria peronii	Adults, larvae	Pond adjacent to coastal lagoon (C/N)	Australia	Yes	No	Yes	No	FA/NS	Pyke et al. 2002
Litoria tyleri	Adults, larvae	Pond adjacent to coastal lagoon (C/N)	Australia	Yes	No	Yes	No	FA/NS	Pyke et al. 2002
Osteopilus pulchrilineatus	Adults	Coastal mangroves (C/N)	Haiti	No	No	Yes	No	FA/NS	Hedges and Thomas 1992
Osteopilus septentrionalis	Adults, eggs	Brackish pool (C/N)	USA	No	No	Yes	No	NHN/S	Peterson et al. 1952; Neill 1958
	Adults	Mangroves (C/N)	USA	No	No	Yes	No	FA/NS	Glorioso et al. 2012
	Larvae	Inland freshwater	USA	No	Yes	No	No	FA/S	Brown and Walls 2013
Pseudacris clarkii	Adults	Salt marshes very close to ocean (with crabs) (C/N)	USA	No	No	Yes	No	FA/NS	Smith and Sanders 1952
Pseudacris crucifer	Adults	Tidal marsh (C/N)	Canada	Yes	No	Yes	No	FA/NS	Ouellet et al. 2009
	Adults, eggs, larvae	Roadside wetlands (I/A)	Canada	Yes	Yes	Yes	No	FA/S	Collins and Russell 2009
	Adults, larvae	Beach ponds with salt spray (C/N)	USA	No	No	Yes	No	NHN/NS	Hardy 1972
Pseudacris maculata	Adults	Tidal marsh (C/N)	Canada	Yes	No	Yes	No	FA/NS	Ouellet et al. 2009
Pseudacris nigrita	Adults, larvae	Coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/S	Gunzburger et al. 2010

Table 1.—Continued.

Species	Life stage	Habitat	Location	Measured salinity	Tested tolerance	Field observation	Lab physiology	Paper type	Reference
Pseudacris ocularis	Adults, larvae	Coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/S	Gunzburger et al. 2010
Pseudacris regilla	Adults	Saline island pools (C/N)	USA	No	No	Yes	No	NHN/NS	Murray 1955
	Adults, larvae, eggs	Beach and cliff pools in spray zone, near tide mark (C/N)	USA	Yes	Yes	Yes	Yes	TD/S	Roberts 1970
	Adults	Saline hot spring (I/N)	USA	Yes	No	Yes	No	FA/NS	Brues 1932
	Adults	Brackish oceanic bay and alkaline marsh (C/N)	USA	Yes	Yes	Yes	Yes	TD/S	Weick 1980
	Adults, eggs, larvae	Brackish marsh, tidal estuary (C/N)	USA	Yes	No	Yes	No	FA/S	Smith and Reis 1997
Pseudis paradoxa	Adults, juveniles	Mangroves, saline swamp, tidal river (C/N)	Trinidad	No	No	Yes	No	FA/NS	Downie et al. 2010
Scinax ruber	Adults	Mangroves (C/N)	Colombia	No	No	Yes	No	NHN/NS	Alvarez-León and De Ayala-Monedero 2000
Scinax squalirostris	Adults	Coastal lagoon with artificially opened sand bar (C/N/A)	Brazil	Yes	No	Yes	No	FA/S	Moreira et al. 2015
Smilisca baudinii	Adults, eggs, larvae	Mangroves (C/N)	Costa Rica	No	No	Yes	No	FA/NS	Sasa et al. 2009
Trachycephalus typhonius	Adults, eggs, larvae	Mangroves (C/N)	Costa Rica	No	No	Yes	No	FA/NS	Sasa et al. 2009
Leptodactylidae									
Leptodactylus albilabris	Adults, larvae	Brackish swamp/forest (C/N)	Puerto Rico	Yes	Yes	Yes	No	FA/S	Rios-López 2008
Leptodactylus gracilis	Adults	Coastal lagoon with artificially opened sand bar (C/N/A)	Brazil	Yes	No	Yes	No	FA/S	Moreira et al. 2015
Leptodactylus latrans	Adults	Crab burrows in mangrove swamps (C/N)	Brazil	No	No	Yes	No	NHN/S	Ferreira and Tonini 2010
	Adults	Coastal lagoon with artificially opened sand bar (C/N/A)	Brazil	Yes	No	Yes	No	FA/S	Moreira et al. 2015
Leptodactylus macrosternum	Adults	Mangrove swamp (C/N)	Brazil	Yes	No	Yes	No	NHN/NS	Andrade et al. 2012
Leptodactylus melanonotus	Adults, eggs, larvae	Ponds on beach (C/N)	Costa Rica	No	No	Yes	No	FA/NS	Sasa et al. 2009
Leptodactylus nesiotus	Adults	Brackish swamp (C/N)	Trinidad	No	No	Yes	No	FA/NS	Ponssa et al. 2010
Leptodactylus pentadactylus	Adults	Mangrove swamp (C/N)	Guyana	No	No	Yes	No	NHN/NS	Crawford and Jones 1933
Physalaemus biligonigerus	Adults	Coastal lagoon with artificially opened sand bar (C/N/A)	Brazil	Yes	No	Yes	No	FA/S	Moreira et al. 2015
Physalaemus gracilis	Adults	Coastal lagoon with artificially opened sand bar (C/N/A)	Brazil	Yes	No	Yes	No	FA/S	Moreira et al. 2015
Physalaemus henselii	Adults	Coastal lagoon with artificially opened sand bar (C/N/A)	Brazil	Yes	No	Yes	No	FA/S	Moreira et al. 2015
Pleurodema bufoninum	Adults, eggs	Salt water (C/N)	Argentina	No	No	Yes	No	NHN/NS	Darwin 1834; Bell 1843
Pleurodema nebulosum	Adults	Brackish salt flats pools (I/N)	Argentina	Yes	Yes	Yes	Yes	FA/S	Ruibal 1962
Limnodynastidae									
Limnodynastes dumerili	Larvae	Saline wetlands/secondary salinization (I/A)	Australia	Yes	No	Yes	No	FA/S	Smith et al. 2007

TABLE 1.—Continued.

Species	Life stage	Habitat	Location	Measured salinity	Tested tolerance	Field observation	Lab physiology	Paper type	Reference
Limnodynastes peronii	Larvae	Saline wetlands/secondary salinization (I/A)	Australia	Yes	No	Yes	No	FA/S	Smith et al. 2007
	Adults, larvae	Pond adjacent to coastal lagoon (C/N)	Australia	Yes	No	Yes	No	FA/NS	Pyke et al. 2002
Limnodynastes tasmaniensis	Larvae	Saline wetlands/secondary salinization (I/A)	Australia	Yes	No	Yes	No	FA/S	Smith et al. 2007
Neobatrachus sudelli	Larvae	Saline wetlands/secondary salinization (I/A)	Australia	Yes	No	Yes	No	FA/S	Smith et al. 2007
Microhylidae									
Gastrophryne carolinensis	Adults, eggs	Ponds subject to salt spray from Chesapeake Bay (C/N)	USA	Yes	No	Yes	No	FA/NS	Hardy 1953
	Adults, eggs	Brackish water Florida Keys (C/N)	USA	No	No	Yes	No	NHN/NS	Peterson et al. 1952
	Adults	Beach, brackish water near beach, salt marsh (C/N)	USA	No	No	Yes	No	FA/NS	Viosca 1923; Neill 1958
	Larvae	Inland freshwater	USA	No	Yes	No	No	FA/S	Brown and Walls 2013
Glyphoglossus molossus	Adults	Tidal portion of delta (C/N)	Myanmar	No	No	Yes	No	FA/NS	Theobald 1868
Myobatrachidae									
Crinia riparia	Adults	Saline creek (I/N)	Australia	Yes	No	Yes	No	FA/NS	Odendaal and Bull 1982
Crinia signifera	Adults	Saline creek (I/N)	Australia	Yes	No	Yes	No	FA/NS	Odendaal and Bull 1982
	Larvae	Brackish tide pools (C/N)	Australia	No	No	Yes	No	FA/NS	Mokany and Shine 2003
Odontophrynidae									
Odontophrynus maisuma	Adults, eggs	Coastal lagoon with artificially opened sand bar (C/N/A)	Brazil	Yes	No	Yes	No	FA/S	Moreira et al. 2015
Pelobatidae									
Pelobates cultripes	Larvae	Coastal saline wetlands, lagoons, and salt marshes (C/N)	France	Yes	No	Yes	No	FA/S	Thirion 2014
	Adults	Coastal wetlands with tsunami storm surge (C/N)	France	Yes	No	Yes	No	FA/S	Thirion 2002
	Eggs	Coastal wetlands (C/N)	France	No	Yes	No	No	TD/NS	Thirion 2006
Pelobates fuscus	Eggs, larvae	Inland pond polluted with road deicing salts (I/A)	Romania	Yes	Yes	Yes	No	FA/S	Stanescu et al. 2013
Pelodytidae									
Pelodytes punctatus	Larvae	Coastal saline wetlands, lagoons, and salt marshes (C/N)	France	Yes	No	Yes	No	FA/S	Thirion 2014
Pipidae									
Xenopus laevis	Juveniles	Brackish pond (I/N)	USA	No	Yes	Yes	Yes	FA/S	Munsey 1972
	Larvae	Road deicing salts (I/A)	USA	No	Yes	No	No	FA/S	Dougherty and Smith 2006
	Adults		USA	No	Yes	No	Yes	FA/S	McBean and Goldstein 1967
Ranidae									
Lithobates berlandieri	Adults	Hypersaline lagoon (C/N)	USA	Yes	No	Yes	No	NHN/S	McCoid 2005
Lithobates catesbeianus	Adults	Tidal brackish water (C/N)	USA (Hawaii)	No	No	Yes	No	NHN/NS	La Rivers 1948
	Adults, larvae	Beach ponds with salt spray (C/N)	USA	No	No	Yes	No	NHN/NS	Hardy 1972
	Eggs, larvae	Road deicing salt (I/A)	USA	No	Yes	No	No	FA/S	Matlaga et al. 2014
	Larvae		USA	No	No	No	Yes	FA/S	Alvarado and Moody 1970
	Larvae		USA	No	Yes	No	No	FA/S	Brown and Walls 2013

Table 1.—Continued.

Species	Life stage	Habitat	Location	Measured salinity	Tested tolerance	Field observation	Lab physiology	Paper type	Reference
Lithobates clamitans	Eggs, larvae	Road deicing salt (I/A)	USA	No	Yes	No	No	FA/S	Dougherty and Smith 2006; Karraker 2007
	Adults, eggs, larvae	Roadside wetlands (I/A)	Canada	Yes	Yes	Yes	No	FA/S	Collins and Russell 2009
	Adults	Brackish marshes (C/N)	USA	No	No	Yes	No	NHN/S	Neill 1958
Lithobates grylio	Adults	Salt marshes (C/N)	USA	No	No	Yes	No	FA/NS/NHN/S	Viosca 1923; Neill 1958
	Adults, larvae	Coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/S	Gunzburger et al. 2010
	Adults	Brackish swamp/forest (C/N)	Puerto Rico	Yes	No	Yes	No	FA/S	Rios-López 2008
Lithobates palmipes	Adults	Beach (C/N)	Guyana	No	No	Yes	No	NHN/NS	Crawford and Jones 1933
Lithobates pipiens	Adults	Saline lake (I/N)	USA	Yes	No	Yes	No	FA/NS	Young 1924
	Adults	Tidal marsh (C/N)	USA	No	No	Yes	No	FA/NS	Klemens et al. 1987
Lithobates sphenocephalus	Adults	Salt marshes (C/N)	USA	Yes	Yes	Yes	Yes	FA/S	Christman 1974
	Adults	Salt marshes, intertidal zone, bay, mangrove swamps (C/N)	USA	No	No	Yes	No	NHN/S	Neill 1958
	Adult, larvae	Coastal wetland with storm surge (C/N)	USA	Yes	No	Yes	No	FA/S	Gunzburger et al. 2010
	Adults	Brackish bay (C/N)	USA	No	No	Yes	No	FA/NS	Duellman and Schwartz 1958
	Larvae		USA	No	Yes	No	No	FA/S	Brown and Walls 2013
Lithobates sylvaticus	Adults	Tidal marsh (C/N)	Canada	Yes	No	Yes	No	FA/NS	Ouellet et al. 2009
	Adults, eggs, larvae	Roadside wetlands with deicing salt (I/A)	USA	Yes	Yes	Yes	No	FA/S	Karraker et al. 2008; Brady 2013
	Larvae	Road deicing salts (I/A)	USA	No	Yes	No	No	FA/S	Sanzo and Hecnar 2006; Langhans et al. 2009; Chambers 2011; Harless et al. 2011
	Eggs, larvae	Road deicing salts (I/A)	USA	No	Yes	No	No	FA/S	Snodgrass et al. 2008; Petranka and Doyle 2010
Lithobates yavapaiensis	Adults, eggs	Saline creek (connects to Salton Sea) (I/N)	USA	Yes	Yes	Yes	No	FA/S	Ruibal 1959
Pelophylax perezi	Eggs	Saline lake (I/N)	Spain	Yes	Yes	Yes	No	FA/S	Ortiz-Santaliestra et al. 2010
	Adults	Saline waters (I/N)	Spain	Yes	No	Yes	No	FA/S	Margalef 1956
	Larvae	Coastal saline wetlands, salt marshes (C/N)	France	Yes	No	Yes	No	FA/S	Thirion 2014
	Adults, eggs, larvae	Tide pools (C/N)	Portugal	Yes	No	Yes	No	NHN/S	Sillero and Ribeiro 2010
Pelophylax ridibundus	Adults	Baltic sea (C/N)	Europe	No	No	Yes	No	FA/NS	Mertens 1926
	Adults	Coastal dune pond (C/N)	France	Yes	No	Yes	No	FA/S	Thirion 2014
	Adults	Saline water (I/N)	Germany	Yes	No	Yes	No	FA/S	Thienemann 1926
	Adults	Arid (I/N)	Israel	No	Yes	No	Yes	FA/S	Katz 1975
	Adults	Shores of hypersaline lake (I/N)	Iran	No	No	Yes	No	FA/NS	Asem et al. 2014
	Adults	Saline lake (I/N)	Algeria	Yes	No	Yes	No	FA/NS	Beadle 1943
Pelophylax saharicus	Adults	Brackish pond (C/N), brackish marsh (I/N)	Algeria	No	No	Yes	No	FA/NS	Samraoui et al. 2012
	Adults, eggs, larvae	Saline water (I/N)	Algeria	Yes	No	Yes	No	TD/S	Florentin 1899
Rana draytonii	Adults, eggs, larvae	Brackish marsh, tidal estuary (C/N)	USA	Yes	No	Yes	No	TD/S / FA/S	Smith and Reis 1997; Reis 1999
Rana luteiventris	Adults	Saline hot springs and mudflats (I/N)	USA	Yes	No	Yes	No	FA/NS	Brues 1932; Hovingh 1993
Rana macrocnemis	Adults	Brackish coastal and desert aquatic habitats (C/I/N)	Iran	No	No	Yes	No	FA/NS	Bahmani et al. 2014
Rana temporaria	Adults, larvae, eggs	Brackish tidal pools (C/N)	UK	No	No	Yes	No	NHN/S	Hardy 1943

Table 1.—Continued.

Species	Life stage	Habitat	Location	Measured salinity	Tested tolerance	Field observation	Lab physiology	Paper type	Reference
	Adults	Baltic Sea (C/N)	Europe	No	No	Yes	No	FA/NS	Mertens 1926
	Eggs	Inland ponds (I/N)	Germany	Yes	Yes	Yes	No	FA/S	Viertel 1999
	Eggs	Brackish ditch (I/N)	France	Yes	No	Yes	No	TD/S	Florentin 1899
Rhacophoridae									
Buergeria japonica	Adults, eggs	Beach, tidal streams (C/N)	Japan	No	No	Yes	No	FA/NS	Goris and Maeda 2005
	Adults, eggs	Beach, tidal streams (C/N)	Japan	Yes	No	Yes	No	FA/S	Haramura 2004, 2011
	Eggs	Beach, tidal streams (C/N)	Japan	No	Yes	Yes	No	FA/S	Haramura 2007a
	Larvae	Tidal stream (C/N)	Japan	Yes	No	Yes	No	FA/S	Haramura 2007b
	Adults, eggs		Japan	No	No	Yes	No	FA/S	Haramura 2008
Polypedates maculatus	Adults	Tidal mangrove swamp (C/N)	India, Bangladesh	No	No	Yes	No	FA/NS	Rahman and Asaduzzaman 2010; Jena et al. 2013
Polypedates megacephalus	Larvae	Pond (C/N)	Hong Kong	No	Yes	No	No	FA/S	Karraker et al. 2010
Rhinodermatidae									
Rhinoderma darwinii	Adult	Beach (C/N)	Chile	No	No	Yes	No	NHN/NS	Crump 2002
Scaphiopodidae									
Spea hammondii	Adults	Saline hot spring (I/N)	USA	Yes	No	Yes	No	FA/NS	Brues 1932

The remarkable finding that physiological adaptations allowed *Fejervarya cancrivora* in particular to survive in practically marine habitats with daily predictable sources of tidal salinity captivated biologists, and nearly all subsequent work on amphibian salt tolerance and adaptation has been written in reference to this and only one or two other (i.e., *Bufotes viridis*, *Xenopus laevis*) species (Shoemaker et al. 1992). Thus, statements emphasizing these putative model species have remained common to this day, despite evidence that this pattern may be much more widespread. Indeed, most authors introduce their findings of salt tolerance in their study species by writing something to the effect of: "Salt tolerance is extremely rare in amphibians, and until the present study, has only been documented in the Crab-eating Frog and the Green Toad."

The perception that salt tolerance exists only in a few amphibian species has long persisted in the scientific community (with a few exceptions, e.g., Neill 1958; Balinsky 1981) and has perhaps biased its members in prematurely discounting the presence of amphibians in certain habitats. Herpetologist Edward H. Taylor, in describing "a new ambystomatid salamander adapted to brackish water" (Ambystoma subsalsum [= *taylori*]; Taylor 1943:152), provides a typical example:

"Dr. Hobart Smith and I visited Lake Alchichica in 1932, but because of the salinity of the water we made no effort to collect salamanders, presuming that they could not occur. In 1939 Mr. Dyfrig McH. Forbes, unaware that salt water is usually not tolerated by amphibians, investigated the lake and succeeded in obtaining two ambystomid larvae."

Gadow (1901) stated that "Common salt is poison to the Amphibia," and there is no doubt that amphibians are indeed osmotically challenged organisms due to their permeable skin and eggs (Shoemaker and Nagy 1977). A plethora of studies have found that salt can lead to increased mortality, developmental deformities, physiological stress, and the alteration of growth and development at (e.g., Ely 1944; Ruibal 1959; Beebee 1985; Padhye and Ghate 1992; Viertel 1999; Turtle 2000; Chinathamby et al. 2006; Dougherty and Smith 2006; Collins and Russell 2009; Karraker and Ruthig 2009; Langhans et al. 2009; Chambers 2011; Duff et al. 2011; Harless et al. 2011; Alexander et al. 2012; Hopkins et al. 2013a,b; Hua and Pierce 2013) and across different life-history stages (i.e., carry-over effects; Petranka and Doyle 2010; Wu et al. 2012; Hopkins et al. 2014). This general intolerance has been demonstrated repeatedly (and as such will not be a focus of this review) and, perhaps as a result, there are no truly marine- or saline-specialist amphibian species. Still, the mere presence of so many species of amphibians inhabiting salt-water areas around the world suggests that these animals may be a lot more adaptable than has been suggested for over a century.

Our review challenges the perception of widespread salt intolerance in amphibians by attempting to compile all documented evidence (including a re-examination of Neill 1958) of these animals inhabiting brackish and saline environments whether coastal, inland, natural, or anthropogenically altered. This comes at a critical incipient time, as the biological community begins to become more-fully aware of the ability of amphibians to survive in these habitats around the world. Indeed, almost half (44%) of the references in this review describing amphibians in saline habitats, or their tolerances of salt, were published since 2000, and in the last year and a half alone (January 2013–October 2014) an additional 20 species have been described as inhabiting brackish and saline habitats. With so much burgeoning interest in this topic, it is worth stepping back and analyzing our current state of knowledge on the topic. In addition, while there appears to be much recent interest in documenting the occurrence of amphibians in these habitats, we still know very little regarding how adaptations allowing amphibians to live in these habitats might evolve. We thus conclude this review by outlining an evolutionary model of understanding amphibian adaptation to saline environments. Such studies will be important as freshwater resources become increasingly saline in a world of rising sea levels (Gornitz 1995; Nicholls et al. 1999; Purcell et al. 2008; Rios-López 2008), road deicing salt application (Environment Canada 2001; Thunqvist 2004; Kaushal et al. 2005; Cañedo-Argülles et al. 2013), and secondary salinization (Williams 2001; Christy and Dickman 2002; Chinathamby et al. 2006; Kearney et al. 2012), and we attempt to understand the ability of vulnerable groups such as amphibians to adapt and survive in these habitats.

MATERIALS AND METHODS

Review of the Literature

We reviewed the scientific literature for reports of amphibians inhabiting brackish or saline environments. For pre-1950s, we relied heavily (but not exclusively) on Neill's (1958) compilation. In doing so, we tried to locate the studies referenced, verify that they met our criteria for inclusion, and classified each study into specific categories (see below). Unlike Neill (1958), we did not include reports of amphibians that were found dead or sickly in saline habitats (e.g., Carl 1949; Neill 1958) or second-hand accounts of frog calling, for example, in areas that might have been brackish or near (but not on) a beach (Bellairs and Shute 1954, as cited in Neill 1958). We included Neill's personal observations, but did not include unverified second-hand accounts in Neill's paper unless the species in question had also been described in a saline habitat in another publication. For post-1950s, we relied heavily on internet searches for scholarly works involving amphibians and saline habitats and included published accounts from natural history surveys, studies of local adaptation or salinity tolerance, natural history notes, or books. While there is a multitude of studies on amphibian osmoregulatory physiology and the effects of road deicing salts on amphibian survival, we did not include species whose tolerance had been physiologically tested but never reported, even anecdotally, in saline habitats in the field (e.g., *Ambystoma gracile*, Alvarado and Dietz 1970a). We did include some physiological studies of species observed by others in saline habitats, even if the authors had not collected their study subjects from these habitats (e.g., *Lithobates catesbeianus*, Alvarado and Moody 1970). In summary, our criteria for inclusion in this review were that at least one author had found at least one life-history stage of the species alive and healthy in a saline environment, and that the account had been published. Species names follow Frost (2014).

Classification of Habitats

Our literature review for amphibians inhabiting saline environments revealed a diversity of habitats. These included habitats naturally influenced by oceanic salt including beaches, lagoons, salt marshes, mangrove swamps, tidal ponds, pools, streams, estuaries, pools affected by sea spray, oceans, and bays. All of these habitats were classified as coastal/natural (C/N) in Table 1. Other naturally saline habitats included inland seas, saline lakes and ponds, saline hot springs, and temporary desert ponds and streams recorded as saline. These were classified as inland/natural (I/N) in Table 1. We also included habitats (mostly inland) that are affected by anthropogenic sources of salt, such as road deicing salts or secondary salinization, and classified these as such (anthropogenic vs. natural; i.e., A vs. N). Finally, we listed the geographic location of each occurrence.

Classification of Studies

To clarify our understanding of amphibian salt tolerance, we classified all studies/observations in several ways. We recorded (Yes/No) in Table 1 whether the study measured the salinity of the reportedly saline environment in which the amphibian was found. Conservatively, those studies that simply reported that the water was definitely brackish but did not report salinity measurements (e.g., Peterson et al. 1952) were not scored as having measured environmental salinity. We also listed whether the authors made a field observation of the animal in a saline environment (Yes/No) and if they subsequently tested salinity tolerance (typically in the laboratory; Yes/No). Those studies that measured some additional aspect of physiological adaptation to salt in the laboratory were also noted. Finally, we classified papers as either being a full-length article (FA), natural history note (NHN), or thesis/dissertation (TD) and whether the focus of the paper was on salt tolerance (S) or not (NS).

Estimating Environmental and Experimental Salinity Tolerance Limits

For every species where environmental salinity was measured at the time of field observation, we determined the maximum salinity concentration in which the animal was found. There are many measurement units used in the salinity literature, with very little standardization or consistency (e.g., conductivity, specific conductance, mOsm/L, g/L, mg/mL, mequiv/L, specific gravity, ppt [parts per thousand], ppm [parts per million], psu [practical salinity unit]). To facilitate accurate comparison among species and studies, we converted all values into ppt (g/L Cl^-). For those species whose salt tolerance had been experimentally examined in the laboratory, we determined the maximum upper limit of tolerance by arbitrarily defining this as the concentration of salt in which $\geq$50% of individuals survived. For nonlethal measures, we recorded the upper limit as that concentration which first caused a statistically significant negative effect.

RESULTS AND DISCUSSION

Phylogenetic Breadth

We identified a total of 144 amphibian species, from 65 genera and 28 families, as having representative individuals or populations inhabiting saline habitats (Table 1). This list included representatives from 1 of the 10 caecilian families (10%), 5 of the 9 caudate families (56%), and 22 of the 56 anuran families (39%), representing an impressive breadth across the

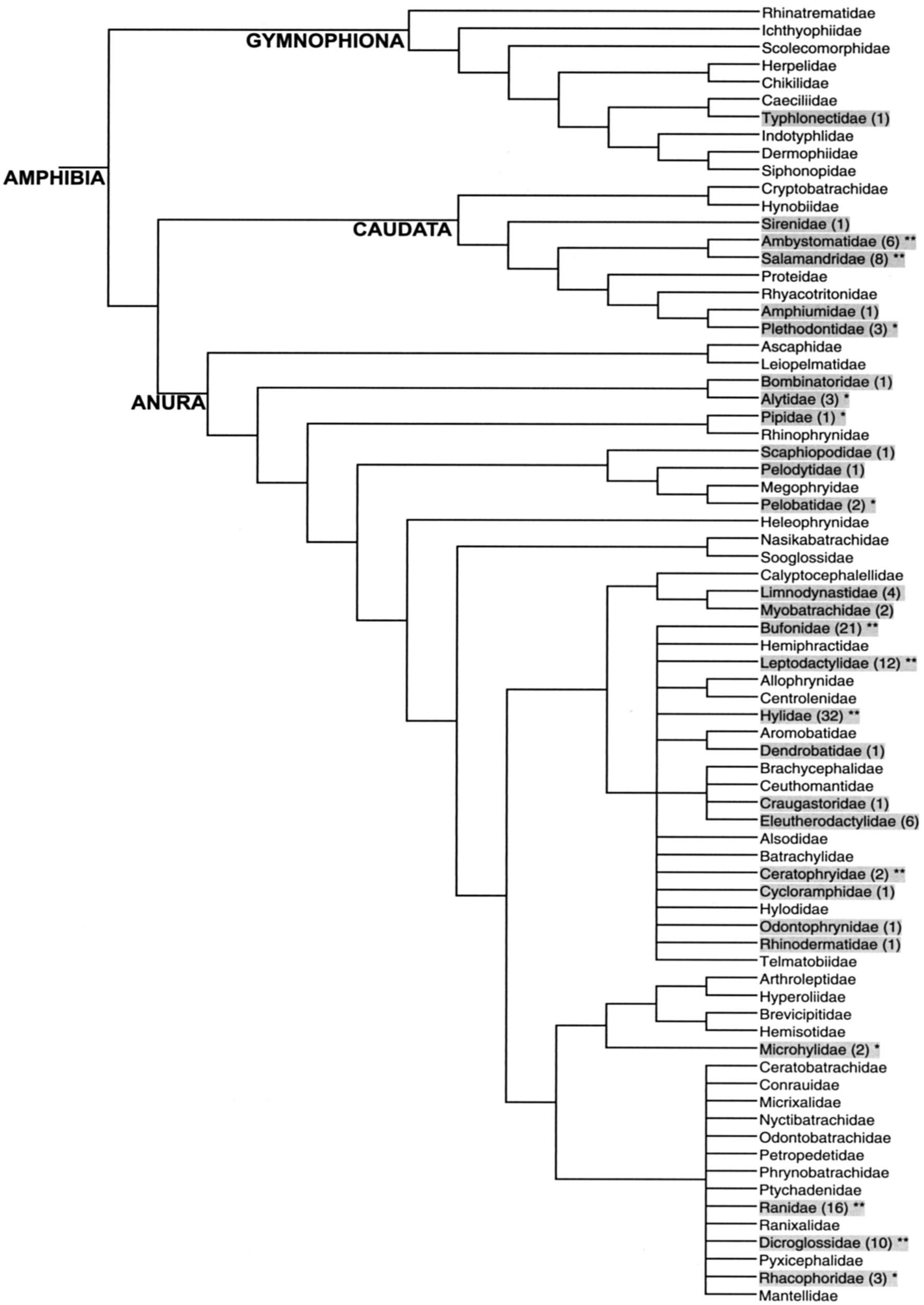

FIG. 1.—Phylogeny of amphibian families (Frost 2014) highlighting those with salt-tolerant representatives. The number of known salt-tolerant species is included in parentheses and families with well-studied species are indicated with asterisks (see Table 2A for ** and Table 2B,C for *).

amphibian tree of life (Fig. 1). This review adds 103 species to the number (41) recorded by Neill (1958). The majority of species described here are anurans (124 vs. 19 caudates and 1 caecilian), but this is not surprising given the relative diversity of frogs and toads compared to other amphibians (6431 anurans vs. 687 caudates and 200 caecilians; Frost 2014).

The large cosmopolitan families Hylidae (32 salt-tolerant species), Bufonidae (21 species), and Ranidae (16 species),

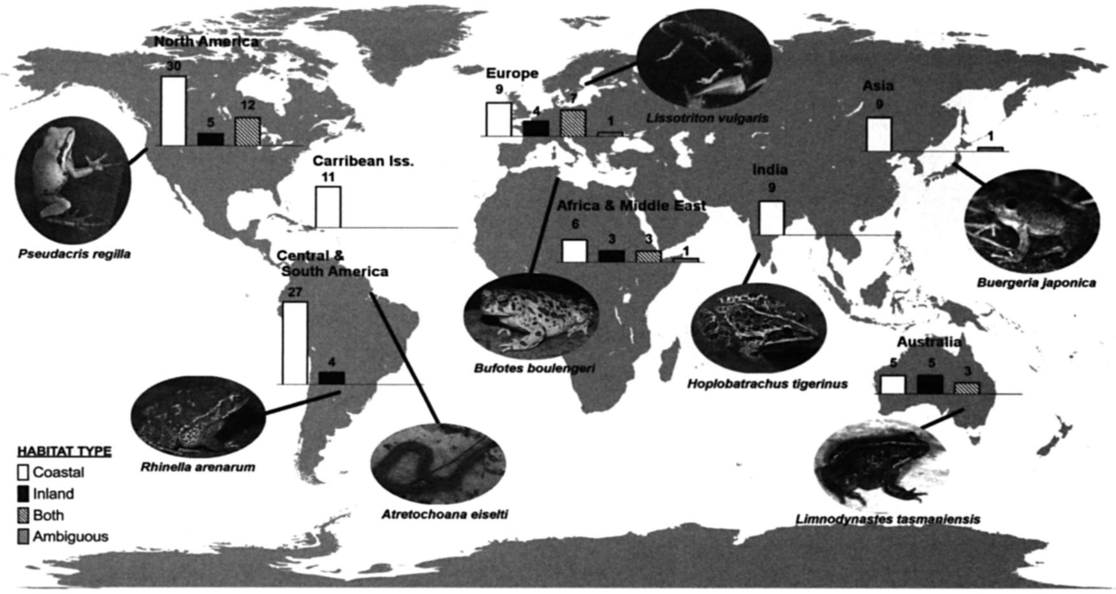

FIG. 2.—Global geographic distribution of salt-tolerant amphibian species and the habitat types in which they are found: Coastal = white bars, Inland = black bars, Both coastal and inland = hatched bars, Ambiguous/not listed = gray bars. Numbers of species are indicated above each bar. Photos show representative species found in saline habitats from each continent: *Pseudacris regilla* (photo by Oregon Department of Fish and Wildlife), *Rhinella arenarum* (photo by A. Kwet), *Bufotes boulengeri* (photo by Manuelgvs), *Lissotriton vulgaris* (photo by Viridiflavus), *Hoplobatrachus tigerinus* (photo by Balaram Mahalder), *Buergeria japonica* (photo by Pseudolapiz), *Atretochoana eiselti* (photo by M. Hoogmoed), *Limnodynastes tasmaniensis* (photo by EDB).

as well as the Central and South American Leptodactylidae (12 species) and the Asian species of the Dicroglossidae (10 species), dominated the anurans in this review whereas Salamandridae (8 species) and Ambystomatidae (6 species) made up the majority of salt-tolerant caudates (Fig. 1). Only a couple of individual representatives of one species of aquatic caecilian, *Atretochoana eiselti*, were found in a tidal stream and pool in Brazil (Hoogmoed et al. 2011). The only other hint of salt tolerance in caecilians comes from a study (Measey et al. 2007) of *Schistometopum thomense* (Dermophiidae) on oceanic islands off the coast of West Africa. This species is considered endemic to these islands and is a rare example of an amphibian (let alone a caecilian) on a purely oceanic island. The best explanation for its occurrence on these islands is oceanic transport on vegetation rafts, which would imply a probable tolerance of oceanic salinity (Measey et al. 2007). While these hints of possible salt tolerance in caecilians are certainly suggestive, our understanding of adaptation to salt in this group of little-studied amphibians is clearly still very much in its infancy.

Geographical and Habitat Distribution

Salt-tolerant amphibians have been reported from all continents except Antarctica (i.e., on every continent where amphibians are found), with the majority of species from North America and, with the exception of Australia, the majority located in naturally saline coastal areas (Figs. 2, 3). A larger count from North America may have more to do with a bias in the number of researchers from this region studying this topic, rather than to a biological phenomenon, especially given that the majority of the world's anuran species are found in the tropics rather than North America. Regardless, it seems that wherever amphibians occur there are examples of salt tolerance having evolved, often in both coastal and inland habitats (Figs. 2, 3).

Although most studies of adaptation to saline habitats have been conducted on natural systems (~95%), a few (e.g., Christy and Dickman 2002; Karraker 2007; Janicke and Roberts 2010; Brady 2012; Kearney et al. 2012; Hopkins et al. 2013b) highlight the importance of examining adaptation in response to anthropogenic sources of salt, principally secondary salinization due to landscape modification and agricultural runoff in Australia and road deicing salt application in North America (e.g., Fig. 3C). While myriad studies have documented the adverse effects of this salinization on amphibians in both habitat types, it appears that some amphibian populations and species have the potential to adapt to artificially elevated levels of salinity in their habitats. This makes sense given amphibians' long evolutionary history of adapting to naturally saline environments, which may give them an edge on adapting to anthropogenic salt (NaCl) over other pollutants (but see later section on "Limitations of Salt Tolerance"). Interestingly, the distinction between natural vs. anthropogenic salinization can also be blurred, as is the case with salt water intrusion into freshwater bodies due to rising sea levels associated with human-induced climate change (Nicholls et al. 1999). In addition, the influx of seawater into natural coastal estuaries, lagoons, and wetlands can also be heavily managed, causing salinities to change dramatically when artificial barriers are purposely breached (Smith and Reis 1997; Moreira et al. 2015). Several species of anurans have been found inhabiting and breeding in these natural/anthropogenic brackish water bodies (Smith and Reis 1997; Moreira et al. 2015) and, intriguingly, it is possible that this management technique actually promotes vs. discourages amphibian occupancy (Moreira et al. 2015).

Degree of Understanding

Our data compilation and summary reveals a fairly comprehensive picture of the evolved salt tolerance in at

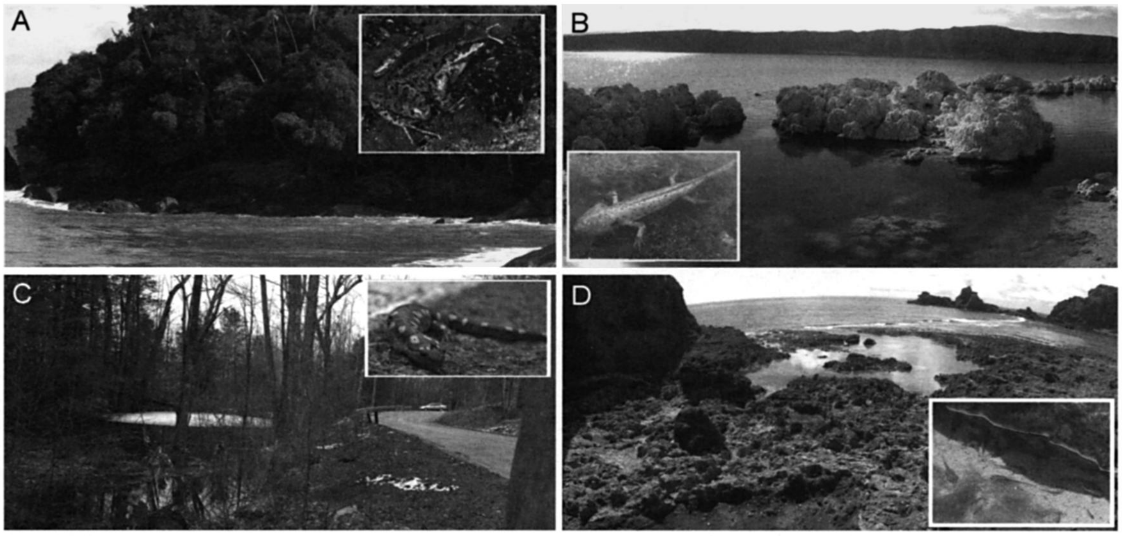

FIG. 3.—Examples of different types of saline habitats and their amphibian inhabitants. (A) *Thoropa taophora* (Cycloramphidae) on a rocky seashore in Brazil (note presence of mussels and barnacles next to frog in inset; Photo by I. Sazima; see Brasileiro et al. 2010). (B) Neotenic *Ambystoma taylori* (Ambystomatidae) in inland saline Lake Alchichica, Mexico (photos by E. De Troya, R. Daniel; see Taylor 1943). (C) *Ambystoma maculatum* (Ambystomatidae) breeding in a roadside pond salinized by road deicing salts in the eastern United States (photo by S. Brady; see Brady 2012). (D) *Fejervarya limnocharis* (Dicroglossidae) tadpoles in tide-pools on islands off the coast of Taiwan (photo by C.-S. Wu; see Wu and Kam 2009).

least 42 species of amphibians across 27 genera and 14 families (Table 2, Figs. 4, 5). Of these, 17 species (~12% of all studied species [Fig. 4] and over half of them from Dicroglossidae or Bufonidae) have been observed in saline habitats in the wild where the environmental salinity of the habitat was measured, the salt tolerance of at least one life-history stage was tested, and some physiological work was performed (Table 2A). Another 21 species have been studied in all but their physiology (Table 2B), and 4 other species have been found in purportedly saline habitats, and their salinity tolerance examined thoroughly (including physiologically), but habitat salinity was not measured (Table 2C). The remaining 102 species and their habitats have not been studied in as much detail, and reports of their tolerance remain somewhat anecdotal (Fig. 4). Some have been tested experimentally for tolerance and, in many cases, environmental salinity was measured. However, in over a quarter of all species, tolerance, environmental salinity, and/or laboratory physiology were not examined (Fig. 4). Regardless, their mere presence in putatively saline environments is highly suggestive of salt tolerance. Much more detailed work needs to be done on these species and undoubtedly many others.

Of the 144 species found to inhabit saline habitats, only 24 have had all their life-history stages (eggs, larvae, adults/postmetamorphic juveniles) reported in these habitats or examined for salt tolerance. A total of 131 species have been recorded and/or examined as adults, 75 as larvae, and only 35 as eggs. There is some apparent consensus in the literature that amphibian embryos are most sensitive to salt, followed by larvae, with adults being most tolerant (Gordon et al. 1961; Roberts 1970; Beebee 1985; Padhye and Ghate 1992; Chinathamby et al. 2006; Brand et al. 2010; Petranka and Doyle 2010; Bernabò et al. 2013; Hopkins et al. 2014; Thirion 2014), although there are also some dissenting data and evidence that sensitivity can also change with age within a particular life stage (see Alexander et al. 2012). This may be due to differences in the physiological abilities and mechanisms of different life-history stages to regulate salt. Although very little work has been conducted on embryonic physiology, to the best of our knowledge eggs have extremely limited osmoregulatory abilities (Gosner and Black 1957; Karraker and Gibbs 2011) while larvae mainly rely on ionic exchange through gill and integumentary Na^+ pumps (Alvarado and Dietz 1970b; Alvarado and Moody 1970; Gomez-Mestre et al. 2004; Bernabò et al. 2013). Adult amphibians rely on both this integumentary ionic exchange and the ability to hypersynthesize and retain urea to increase body osmolarity (reviewed by Shoemaker and Nagy 1977; Balinsky 1981; Katz 1989). While some species inhabiting saline habitats appear to avoid egg deposition in highly saline water (e.g., Viertel 1999; Haramura 2008, 2011), perhaps due to this apparent sensitivity of eggs many other species do indeed breed in these habitats, and eggs and larvae have been found in saline waters for numerous species (Table 1). More research needs to be conducted on this topic, especially on early life-history stages for which we have a relative paucity of knowledge, before broad generalizations can be made regarding salt tolerance across life-history stages in amphibians.

Type of Published Work

Over a third of published works were full-length articles with a focus on amphibian adaptation to salinity (Fig. 6). Including natural history notes and theses/dissertations, just over half of all articles were focused on salt (Fig. 6). This emphasizes the importance of non–salt-tolerance literature in reporting on the habits and habitats of amphibians. Many of these articles were general field notes and natural history surveys from the late 1800s–early 1900s, some focused on amphibians (e.g., Boulenger 1897–1898) and others not (e.g., Annandale 1907). More-recent articles on faunistic surveys of certain habitats (e.g., Chan and Goh 2010; Jena et al. 2013), range extensions (e.g., Alvarez-León and De Ayala-Monedero 2000; Wogan et al. 2008), and general natural history notes (e.g., Crump 2002) of particular species were equally valuable.

TABLE 2.—Well-studied salt-tolerant amphibian species.

Family	Species
A. Species comprehensively studied (environmental salinity, tolerance, field observation, lab physiology)	
Ambystomatidae	*Ambystoma tigrinum*
Bufonidae	*Bufo bufo*
	Bufotes balearicus
	Bufotes viridis
	Duttaphrynus melanostictus
	Epidalea calamita
	Rhinella arenarum
	Rhinella marinus
Ceratophryidae	*Lepidobatrachus asper*
Dicroglossidae	*Euphlyctis cyanophlyctis*
	Fejervarya cancrivora
	Fejervarya limnocharis
	Hoplobatrachus tigerinus
Hylidae	*Pseudacris regilla*
Leptodactylidae	*Pleurodema nebulosum*
Ranidae	*Lithobates sphenocephalus*
	Pelophylax ridibundus
B. Species where all but lab physiology was tested (environmental salinity, tolerance, field observation)	
Ambystomatidae	*Ambystoma maculatum*
	Ambystoma taylori
Salamandridae	*Taricha granulosa*
Alytidae	*Discoglossus pictus*
	Discoglossus sardus
Bufonidae	*Anaxyrus americanus*
	Anaxyrus terrestris
Dicroglossidae	*Hoplobatrachus rugulosus*
Hylidae	*Hyla cinerea*
	Litoria aurea
	Pseudacris crucifer
Leptodactylidae	*Leptodactylus albilabris*
Microhylidae	*Gastrophryne carolinensis*
Pelobatidae	*Pelobates cultripes*
	Pelobates fuscus
Ranidae	*Lithobates clamitans*
	Lithobates sylvaticus
	Lithobates yavapaiensis
	Pelophylax perezi
	Rana temporaria
Rhacophoridae	*Buergeria japonica*
C. Species where all but environmental salinity was tested (tolerance, field observation, lab physiology)	
Plethodontidae	*Batrachoseps gavilanensis*
Salamandridae	*Salamandra salamandra*
Pipidae	*Xenopus laevis*
Ranidae	*Lithobates catesbeianus*

A full review of unpublished dissertations and theses was not completed for this review, but their potential importance to the field is clearly illustrated by the case of *Pseudacris regilla*. Our knowledge of salt tolerance in this species now rivals that of the most well-known salt-tolerant amphibians (Table 2A), but only due to the unpublished dissertation of James O. Roberts (1970) and the thesis of David L. Weick (1980). These authors found animals in brackish coastal waters, recorded environmental salinity, tested tolerance of locally adapted populations, and determined the osmoregulatory physiology of animals in these populations. Without these studies, knowledge of salt tolerance in *P. regilla* would be confined to anecdotal notes (Table 1). It is probable that there are many other species of fully investigated, salt-tolerant amphibians residing in the pages of unpublished dissertations and theses that have not made it into this review.

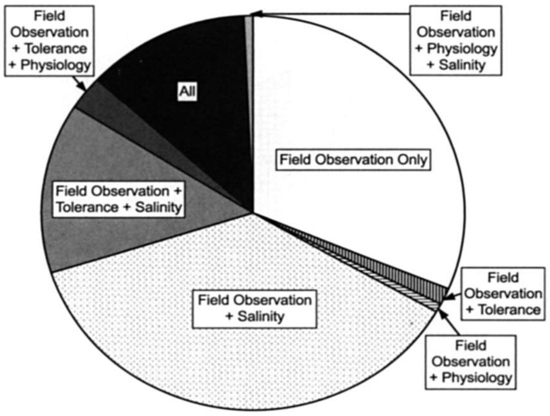

FIG. 4.—Proportions of the different aspects of salt tolerance tested in amphibian species. Black corresponds to species listed in Table 2A; gray to species listed in Table 2B,C. White are those species that have not been investigated as thoroughly (i.e., not in Table 2).

Finally, the importance of natural history notes and short observations, making up just under a quarter of the references in this review (Fig. 6), cannot be overstated. These observations were commonplace 100 yr ago but are now published in only a few journals (e.g., Herpetological Review, Herpetology Notes, Herpetological Natural History). They provide valuable insights into a remarkable worldwide phenomenon and may serve as the starting point for more-intensive studies. For example, Ferguson's (1956) natural history note of observations of *Taricha granulosa* near the ocean inspired our own studies on *Taricha* salt tolerance (Hopkins et al. 2013b, 2014).

We have now established that salt tolerance in amphibians is not as rare as previously thought, and many of the proximate physiological mechanisms that these animals use in these challenging environments have been elucidated in detail for some species. However, our understanding of the ultimate question, how amphibian populations evolve to be salt-tolerant, is still in its infancy. Given the number of times

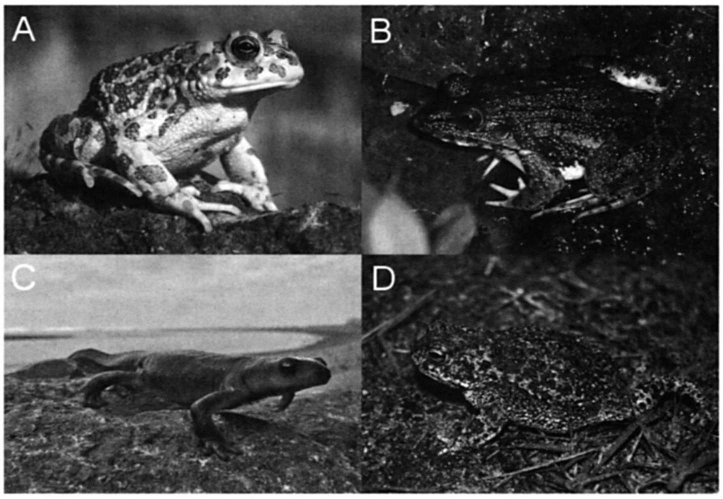

FIG. 5.—Examples of well-studied amphibians inhabiting saline habitats (Table 2). (A) *Bufotes balearicus* (= *viridis*) (Bufonidae) in Europe, Africa, and the Middle East (photo by R. Bartz). (B) *Fejervarya cancrivora* (Dicroglossidae) from mangrove swamps in Southeast Asia and India (photo by W.A. Djatmiko). (C) *Taricha granulosa* (Salamandridae) from a tidal stream in North America (photo by GRH). (D) *Epidalea calamita* (Bufonidae) from a saline desert pond in Spain (photo by I. Gomez-Mestre).

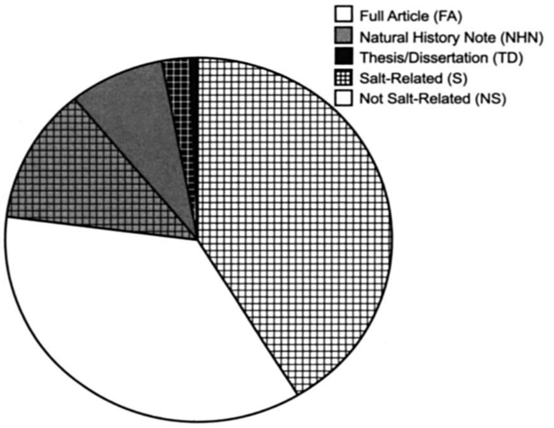

FIG. 6.—Classification—of the literature as full articles (FA), natural-history notes (NHN), dissertations or theses (TD), and if the work was focused on salt tolerance (S) or not (NS).

tolerance has occurred, phylogenetically (Fig. 1) and geographically (Fig. 2), and continues to evolve in a rapidly changing world (e.g., Brady 2012), our understanding of variation, selective forces, differential survival, and heritability is still mostly unexplored. We now turn our attention to this evolutionary approach: How does a salt-naïve population evolve and locally adapt to become a more–salt-tolerant population or species? Although additional empirical work in this area is needed, we review the current state of knowledge, and provide a basic framework for considering this question, in the hopes of stimulating development of an evolutionary model of amphibian adaptation to saline habitats.

TOWARD AN EVOLUTIONARY MODEL OF AMPHIBIAN ADAPTATION TO SALINE HABITATS

Genetic Nature of Salinity Tolerance

Populations can adapt to novel or challenging environments in two ways, either through the propagation of new mutations or through natural selection acting on standing genetic variation in traits (Barrett and Schluter 2007). While the propagation of new mutations can be effective, it is generally a much-slower process with a lower probability of fixation than is selection exploiting existing standing genetic variation (Barrett and Schluter 2007). Surprisingly few studies have examined standing variation for salinity tolerance in amphibians, but those that have looked have found it (Roberts 1970; Gomez-Mestre and Tejedo 2003, 2004; Hopkins et al. 2013b). Significant variation in salinity tolerance has been examined among sibships of Natterjack Toads (*Epidalea calamita*) inhabiting fresh and saline lakes in Spain (e.g., Fig. 5D; Gomez-Mestre and Tejedo 2003, 2004) as well as in Pacific Tree-Frogs (*Pseudacris regilla*) in Oregon, USA (Roberts 1970). Roberts (1970: 32) wrote: "It was observed that, even in tests run on animals from salt sensitive areas, there were always a few animals that survived the highest levels of salt in the test solutions. This suggested that there was at least a measure of plasticity, with respect to salinity tolerance, in the gene pool." These findings are similar to what has been found with Rough-Skinned Newts (*Taricha granulosa*; e.g., Fig. 5C) on the Pacific Coast of North America (Hopkins et al. 2013b). In a salt-naïve population inhabiting an inland pond, some females had 100% survival of eggs in salt water whereas others from the same population had 100% mortality, representing a significant female × salt interaction and the potential for local adaptation (Hopkins et al. 2013b).

While variation is critical for natural selection, it is so only in the degree to which it is heritable. Broad-sense heritability in salinity tolerance has been found in locally adapted Natterjack Toad (*Epidalea calamita*) populations, which increased with increased salinity (up to $H^2 = 0.50$; Gomez-Mestre and Tejedo 2004). However, narrow-sense estimates of heritability did not necessarily follow the same pattern, possibly due to other additive effects including maternal effects. Maternal effects of female or egg size were not found, however, to have any significant effect on either local adaptation (Brady 2012) or variation (Hopkins et al. 2013b) in other salt-tolerant amphibians (tests on eggs). Thus, there appears to be modest evidence that salt tolerance is genetic in nature. The fact that a high degree of genetic population subdivision (high interpopulation Q_{ST} values) for salinity tolerance persists in *E. calamita* is especially important in the face of molecular evidence indicating otherwise little genetic population differentiation and moderate to high gene flow (F_{ST}) between fresh and saline populations of toads (Gomez-Mestre and Tejedo 2004). The fact that local adaptation may have occurred in populations of toads in the face of this significant gene flow and presumed migration reveals the intense nature of the selective pressures of salinity.

To date, these studies remain the only hints of the genetic nature of salinity adaptation in amphibians. To the best of our knowledge, no molecular studies have identified genes for salt tolerance in amphibians or compared the genetic profiles of locally adapted populations. While very little knowledge is currently available on genetic variation in salt tolerance within populations, we predict that, if examined, one would find significant standing genetic variation in salinity tolerance in salt-naïve populations of many amphibian species and that this variation is key to their adaptive ability. The sheer number of salt-tolerant species worldwide, and their apparently deep evolutionary relationships (Fig. 1), indicates that alleles for salinity tolerance (if they exist) in amphibians are most likely old and have been pretested by selection (Barrett and Schluter 2007) in many species and populations inhabiting naturally saline environments. This would help explain the rapid evolution of salt tolerance observed in some inland populations in response to anthropogenic application of salt (e.g., Brady 2012; Fig. 3C), as the pace of evolution by natural selection is much faster with standing genetic variation than for new mutations. Adaptation to anthropogenic change has indeed been predicted to be primarily the result of standing genetic variation (Barrett and Schluter 2007; Bell 2013). Fully understanding the genetic nature of salinity tolerance clearly is the biggest, and most pressing, hurdle that remains in our elucidation of the evolution of amphibian adaptation to both natural and anthropogenic salt.

Origins of Salt Tolerance

The fact that alleles for salt tolerance might exist in amphibian populations is not surprising considering the primary importance of osmoregulatory functioning in these animals. Amphibians, due to their permeable skin and egg membranes, are highly sensitive to water loss at all life-stages and in all its forms (Shoemaker and Nagy 1977; Katz 1989). At the same time, amphibians generally live in environments deficient of salts, and thus their skin has evolved to be very efficient at transporting Na^+ and Cl^- ions into the body (Shoemaker and Nagy 1977). Efficient osmoregulation is a key trait under intense selective pressure in these animals. This is true whether the animal lives in arid conditions, where it must burrow in soil to aestivate, or in hyperosmotic saline aquatic systems, and amphibians can be found in both habitats (Katz 1989). Indeed, some species found in both arid and saline aquatic environments, such as the toad *Bufotes viridis* (= *balearicus*, Fig. 5A; Degani et al. 1984; Katz 1989) and the salamander *Ambystoma tigrinum* (Delson and Whitford 1973), appear to use the same osmoregulatory physiological mechanism, overactive urea synthesis and retention, to achieve tolerance of hyperosmotic conditions in both habitats. Thus, salinity tolerance in amphibians might have its evolutionary origins as an exaptation of tolerance to arid conditions (Gomez-Mestre and Tejedo 2005). Conversely, adaptation to arid conditions might be an exaptation to salt tolerance (Hoffman 2014). It has been proposed, for example, that *Bufotes viridis* initially evolved in aquatic environments with fluctuating salinity and then dispersed to arid environments once this adaptation to increased ion concentrations had evolved (Hoffman 2014). Degani (1981) found support for a link between aridity and salinity tolerance in *Salamandra salamandra*, as salamanders from semiarid areas of Israel were more tolerant of saline aquatic conditions than were animals from moist habitats. When explicitly testing this exaptation hypothesis with the toad *Epidalea calamita*, however, Gomez-Mestre and Tejedo (2005) could find no support for it and concluded that drought tolerance and salinity tolerance may have evolved independently in this species. Support for this conclusion also comes from the fact that the osmoregulatory physiological mechanisms amphibians employ pre- and postmetamorphosis appear to be fundamentally different, with larvae regulating salts through ionic exchange and juveniles and adults primarily relying on the overactive synthesis and retention of urea (Gomez-Mestre et al. 2004; Gomez-Mestre and Tejedo 2005; Bernabò et al. 2013). As the physiological mechanism larvae employ for regulating increased ion concentrations would not work for postmetamorphic individuals facing drought conditions, this decoupling of osmoregulatory mechanisms pre- and postmetamorphosis suggests that drought tolerance and salinity tolerance may have evolved independently (Gomez-Mestre and Tejedo 2005). In addition, although there are certainly amphibian species such as these that occur in both arid and saline habitats, there arguably are more that occur in coastal habitats (Fig. 2) where salinity tolerance in the face of oceanic salt would be highly beneficial. In direct contrast to Darwin's (1859) views on the matter, it now appears that salt tolerance in coastal amphibians may have resulted in the ability of these animals to disperse across oceans (Vences et al. 2003; Measey et al. 2007).

It is possible that ecological factors, including biotic interactions, could drive diversification of amphibians into saline habitats. Salinity is known as a driving force governing the composition of aquatic ecological communities (Gunter 1956), and recent work has suggested that salinity can affect the interactions of amphibians with other community members (e.g., food-web dynamics) both directly and indirectly (Petranka and Doyle 2010; Chambers 2011; Van Meter et al. 2011; Petranka and Francis 2013; Moreira et al. 2015; Van Meter and Swan 2014). Adaptation to salinity could certainly lead to novel predation opportunities for amphibians in these environments, as has been shown in some South American anurans eating marine invertebrates, for example (Sazima 1971; Brasileiro et al. 2010; Ferreira and Tonini 2010). It is also possible that salinity intolerance of freshwater invertebrate predators could lead amphibians to adapt to saline habitats to escape predation pressure (Moreira et al. 2015; although this must be balanced by potentially increased pressure from marine predators; Pyke et al. 2013). Differential susceptibility to salt can also affect amphibian species diversity and community composition in saline habitats (Karraker et al. 2008; Collins and Russell 2009; Karraker et al. 2010; Brown and Walls 2013; Gallagher et al. 2014; Moreira et al. 2015). Thus, an escape from competitors or predators, or novel prey opportunities (in short, changes in community composition and structure), may be driving forces in the evolution of salt tolerance in amphibians. Research on this topic, however, remains relatively speculative and correlative at this time. The demonstration of definitive causal links between salinity, community composition, ecological interactions, and selective advantages for amphibians still needs to be completed and is an important endeavor for future investigation.

The Nature of Selection in Osmotically Stressful Environments

For amphibians in osmotically stressful environments, events that favor salinity tolerance may be predictable or unpredictable; this can have important consequences for evolution (Badyaev 2005; Parsons 2005). Regular, predictable exposure to salt is typified by amphibians inhabiting mangrove swamps, where daily tidal cycles temporarily increase salinity in a predictable way (e.g., Jena et al. 2013). The most-familiar example of this is Crab-Eating Frogs of Southeast Asia, *Fejervarya cancrivora* (Fig. 5B), the most well-known euryhaline amphibian, whose physiological mechanisms for dealing with this predictable source of salinity were described by Gordon et al. (1961). In addition, amphibians may be able to adapt with the help of gradual acclimation to gradually increasing salinity in some environments where salinity is primarily elevated through evaporation (Gomez-Mestre and Tejedo 2003; Wu et al. 2014). Although these selection pressures may be common in some environments, amphibians in many other environments may experience much-more unpredictable, dramatic salinity selection events. Indeed, it has been argued that dramatically fluctuating salinity levels are the norm, rather than the exception, in most environments (Wu et al. 2012; Kearney et al. 2014).

Stochastic coastal storm events can periodically wash seawater into otherwise mostly freshwater or tidal habitats (Thirion 2002; Gunzburger et al. 2010; Pyke et al. 2013; Hopkins and Hopkins in press). This habitat can thus change dramatically and unpredictably and so, even though an area may be fresh for much of the time, extreme "pulses of selection" exist to maintain saline-adapted animals in this habitat (Gunzburger et al. 2010). Bell (2013: 3) notes, "A catastrophic event that threatens the survival of a population is likely to occur only at long intervals, but when it does occur, it will have a decisive effect on the subsequent history of that population, because the resistant types that survive may have previously been very rare. Thus, the long-term fate of a population will often be governed by the extreme values of environmental and genetic variation." Most amphibians found in coastal habitats live in rock pools, streams, and beach areas affected by sea spray, waves, and storms (Table 1, Fig. 3A,D). Roberts (1970) typified these observations for coastal Pacific Tree-Frogs (*Pseudacris regilla*): "One population sampled in this study came from a 'freshwater' pool within 5 m of mean high tide and the tadpoles and eggs were collected in a shower of salt spray." Amphibians in coastal areas increasingly have to deal with storm surges and inundations of habitats with seawater during extreme weather events (e.g., tsunamis, hurricanes, etc.) as they increase in frequency with climate change (Thirion 2002; Gunzburger et al. 2010; Brown and Walls 2013). Thus, amphibians in these habitats have been forced to evolve tolerance in response to these intermittent salinity events (Gunzburger et al. 2010; Brown and Walls 2013; Moreira et al. 2015). The salinity of coastal areas can also be affected by anthropogenic management activities, such as artificially opening and closing estuaries, resulting in the same pattern of disruptive, intermittent salinity inundation (Moreira et al. 2015).

Road deicing events also result in extreme, transient spikes of salinity in roadside aquatic habitats, not unlike a coastal storm event (Whitfield and Wade 1992, 1996), and habitat degradation and the changing of agricultural practices are also leading to extreme and unpredictable fluctuations of salinity in many inland habitats (Kearney et al. 2014). Unpredictable episodes of selection therefore probably play some of the most important roles in amphibian adaption to salt in both inland and coastal natural and anthropogenically altered environments. Our understanding of how amphibians adapt to these fluctuating environments is still, however, mostly unexplored. Kearney et al. (2014) provide a much-needed first look at this subject, and their results suggest that animals experiencing transient salinity react very differently than do those experiencing constant salinity. Much more work is needed on this subject, as understanding the frequency, predictability, and nature of selection events clearly is key to our understanding of adaptation in these environments (Parsons 2005; Bell 2013).

Limitations of Salt Tolerance

A final note should be made on possible limits to amphibian adaptation to salt. While there is extensive and important literature on the limitations of adaptation in general (Parsons 2005; Bell 2013), specific points salient to amphibian salt tolerance in particular can be made here.

First, there may be limits to the concentration of salt to which certain amphibians can adapt. Our review of the literature where environmental salinity was measured and/or salt tolerance was determined experimentally in the laboratory (Table 3) indicates that despite amphibians (and especially anurans) being found in, and found to be tolerant of, an extremely wide range of salinities (0.11–39 ppt; Table 3), the majority of species are found in habitats with maximum salinities of ~2–13 ppt and have a median maximum experimental tolerance of ~9–12 ppt (Fig. 7). This convergence may therefore represent a general upper limit of salt tolerance for most amphibian species—and was predicted (as 10 ppt) by Gomez-Mestre and Tejedo (2003) over 10 yr ago. It should be emphasized, however, that this general finding does not necessarily apply to all species or all populations of a particular species. In particular, we urge caution in directly comparing caudate and anuran species due to the relative paucity of knowledge on caudates, especially regarding experimental tolerance data (only 4 caudate species examined versus 39 anurans; Fig. 7). In addition, for this analysis (Table 3; Fig. 7) we chose the highest salt tolerance level found for a species, not the average among populations. There are certainly many species included here where deleterious effects were seen in individuals from certain populations at lower salinities than were seen in other populations and where many of the populations were not found in waters as salty as the one population we chose to represent the maximum for this species. In addition, there are clearly several species of anurans that are found in, and can tolerate, extremely high salinities (Table 3; Fig. 7). Although the most well-known of these euryhaline amphibians are Crab-eating Frogs (*Fejervarya cancrivora*) in salinities up to 39 ppt (35 ppt measured environmentally; Gordon et al. 1961; Gordon and Tucker 1968; Dunson 1977; Uchiyama et al. 1990), North America's Rio Grande Leopard Frogs (*Lithobates berlandieri*; McCoid 2005) and Australia's Spotted-Thighed Tree Frogs (*Litoria cyclorhyncha*; Janicke and Roberts 2010) have also been found in salinities rivaling or exceeding *F. cancrivora* (39 ppt, and 37.4 ppt, respectively).

One of the ways that euryhaline amphibians such as *Fejervarya cancrivora* and *Bufotes viridis* are able to tolerate such high salinities in the laboratory is through gradual acclimation to increasing salinity (Gordon et al. 1961; Gordon 1962; Gordon and Tucker 1968; Katz 1973). Acclimation may increase tolerance in these and other species (e.g., Licht et al. 1975; Wu et al. 2014) through physiological means such as increased Na^+/K^+-ATPase expression, allowing larvae to more-efficiently maintain osmotic homeostasis (Bernabò et al. 2013; Wu et al. 2014). The effects of acclimation do not appear to be universal, however, and in some cases may have either no effect (Kearney et al. 2014) or even inhibit adaptation (e.g., Hua and Pierce 2013). Acclimation to gradually increasing salinities may be a realistic ecological scenario in some habitats, such as saline desert ponds, where evaporation leads to increasing salinity over time (Gomez-Mestre and Tejedo 2003), but may be less ecologically realistic in other habitats where salinity may be governed more by dramatic unpredictable events such as storms and road deicing salt application (see above; Hopkins et al. 2014). Many species may therefore be limited in their adaptive abilities by a lower (but still effective and ecologically realistic) salinity limit to which they can respond immediately, without the need for gradual acclimation.

Despite the evidence that amphibian populations can locally adapt to saline environments, for some populations evidence is emerging that this may not always be possible (Brady 2013). In habitats subjected to anthropogenic salt, the pace of salinization may take place faster than adaptation can occur—and this, combined with severely reduced population sizes, a loss of genetic diversity, asymmetrical

TABLE 3.—Maximum salinity concentrations (ppt Cl^-) measured in the field where amphibians were observed, and maximum salt tolerance limits measured in the lab for amphibian species where these were measured (see Methods text for full definition of tolerance). The references given are for those maximum values listed here and do not represent the range of values in which species have been found or have been experimentally found to be tolerant.

Species	Life stage	Environmental salinity (ppt)	Experimental tolerance (ppt)	Reference
Caudata				
Ambystomatidae				
Ambystoma maculatum	Eggs, larvae	1.56	0.145	Karraker et al. 2008
Ambystoma talpoideum	Adults, larvae	4.9		Gunzburger et al. 2010
Ambystoma taylori	Larvae	8.3		Taylor 1943
Ambystoma tigrinum	Larvae		10.29	Gasser and Miller 1986
	Larvae	15		Duerr and Ness 1970
Dicamptodon tenebrosus	Larvae	1		Hopkins and Hopkins in press
Amphiumidae				
Amphiuma means	Adults, larvae	4.9		Gunzburger et al. 2010
Salamandridae				
Lissotriton helveticus	Larvae	21.95		Spurway 1943
Lissotriton vulgaris	Adults	17		Decksbach 1922
Notophthalmus viridescens	Adults, larvae	4.9		Gunzburger et al. 2010
Salamandra salamandra	Adults		12.9	Degani 1981
Taricha granulosa	Adults	1.4		Hopkins and Hopkins in press
Triturus dobrogicus	Neotenic adult	1.72		Mester et al. 2013
Triturus marmoratus	Adults	1		Thirion 2014
Plethodontidae				
Batrachoseps gavilanensis	Adult		17	Licht et al. 1975
Eurycea quadridigitata	Adults, larvae	4.9		Gunzburger et al. 2010
Sirenidae				
Siren lacertina	Adults	4		Boss and Chesnes 2014
Anura				
Alytidae				
Discoglossus pictus	Larvae	6.08	10	Knoepffler 1962
Discoglossus sardus	Larvae	9	13	Knoepffler 1962
Bombinatoridae				
Bombina variegata	Adults, larvae	13		Florentin 1899
Bufonidae				
Anaxyrus americanus	Adults	2		Ouellet et al. 2009
	Larvae		3.9	Collins and Russell 2009
Anaxyrus boreas	Adults, larvae	4.5		Brues 1932
Anaxyrus quercicus	Adults, larvae	4.9		Gunzburger et al. 2010
Anaxyrus terrestris	Adults, larvae	4.9		Gunzburger et al. 2010
	Larvae		10	Brown and Walls 2013
Bufo bufo	Larvae		4.8	Bernabò et al. 2013
	Larvae	8		Florentin 1899
Bufotes balearicus	Larvae	0.11	6.4	Bernabò et al. 2013
Bufotes boulengeri	Larvae	0.21		El Hamoumi et al. 2007
Bufotes viridis	Adults	20		Gislén and Kauri 1959
	Adults		25	Tercafs and Schoffeniels 1962
Duttaphrynus melanostictus	Adults	12.87		Annandale 1907
			11.2	Chakko 1968
Epidalea calamita	Eggs, larvae	22	10	Gomez-Mestre and Tejedo 2003
Incilius nebulifer	Eggs, larvae		4	Alexander et al. 2012
Peltophryne lemur	Adults, eggs	2.16		Matos-Torres 2006
Rhinella arenarum	Adults, larvae	4	10	Ruibal 1962
Rhinella crucifer	Larvae	18		Guix and Lopes 1989
Rhinella marina	Adults, larvae	20.5		Rios-López 2008
	Adults		16	Liggins and Grigg 1985
Ceratophryidae				
Lepidobatrachus asper	Adults, larvae	4	10	Ruibal 1962
Dicroglossidae				
Euphlyctis cyanophlyctis	Adults	12.87		Annandale 1907
			8	Chakko 1968
Fejervarya cancrivora	Adults, larvae	35	39	Gordon et al. 1961
Fejervarya limnocharis	Larvae	12		Wu and Kam 2009
	Larvae		9.6	Gordon and Tucker 1965
Hoplobatrachus rugulosus	Adults	5	10.2	Davenport and Huat 1997
Hoplobatrachus tigerinus	Adults	12.87		Annandale 1907
	Adults		9	Gordon et al. 1961
Eleutherodactylidae				
Eleutherodactylus coqui	Adults	20.5		Rios-López 2008
Hylidae				
Acris gryllus	Adults, larvae	4.9		Gunzburger et al. 2010
Hyla cinerea	Adults	15		Hardy 1953

TABLE 3.—Continued.

Species	Life stage	Environmental salinity (ppt)	Experimental tolerance (ppt)	Reference
	larvae		10	Brown and Walls 2013
Hyla femoralis	Adults, larvae	4.9		Gunzburger et al. 2010
Hyla gratiosa	Adults, larvae	4.9		Gunzburger et al. 2010
Hyla meridionalis	Adult, larvae	9		Thirion 2014
Hypsiboas geographicus	Larvae	4.5		Guix and Lopes 1989
Hypsiboas pulchellus	Adults	2.5		Moreira et al. 2015
Litoria aurea	Larvae	7.3		Pyke et al. 2002
	Larvae		5.6	Kearney et al. 2012
Litoria caerulea	Adult, larvae	6		Pyke et al. 2002
Litoria cyclorhyncha	Adults, larvae	37.4		Janicke and Roberts 2010
Litoria dentata	Adult, larvae	6		Pyke et al. 2002
Litoria peronii	Adult, larvae	6		Pyke et al. 2002
Litoria tyleri	Adult, larvae	6		Pyke et al. 2002
Osteopilus septentrionalis	Larvae		12	Brown and Walls 2013
Pseudacris crucifer	Adults, larvae	0.59	2.9	Collins and Russell 2009
Pseudacris maculata	Adults	2		Ouellet et al. 2009
Pseudacris nigrita	Adults, larvae	4.9		Gunzburger et al. 2010
Pseudacris ocularis	Adults, larvae	4.9		Gunzburger et al. 2010
Pseudacris regilla	Adults, larvae	7.2		Smith and Reis 1997
	Adults, larvae		9.5	Roberts 1970
Scinax squalirostris	Adults	2.5		Moreira et al. 2015
Leptodactylidae				
Leptodactylus albilabris	Adults, larvae	20.5	4	Rios-López 2008
Leptodactylus gracilis	Adults	2.5		Moreira et al. 2015
Leptodactylus latrans	Adults	2.5		Moreira et al. 2015
Leptodactylus macrosternum	Adults	6.4		Andrade et al. 2012
Physalaemus biligonigerus	Adults	2.5		Moreira et al. 2015
Physalaemus gracilis	Adults	2.5		Moreira et al. 2015
Physalaemus henselii	Adults	2.5		Moreira et al. 2015
Pleurodema nebulosum	Adults	8	10	Ruibal 1962
Limnodynastidae				
Limnodynastes dumerili	Larvae	4		Smith et al. 2007
Limnodynastes peronii	Adults, larvae	6		Pyke et al. 2002
Limnodynastes tasmaniensis	Larvae	3.9		Smith et al. 2007
Neobatrachus sudelli	Larvae	2.64		Smith et al. 2007
Microhylidae				
Gastrophryne carolinensis	Adults, eggs	15		Hardy 1953
	Larvae		5	Brown and Walls 2013
Myobatrachidae				
Crinia riparia	Adults	1.75		Odendaal and Bull 1982
Crinia signifera	Adults	0.85		Odendaal and Bull 1982
Odontophrynidae				
Odontophrynus maisuma	Adults, eggs	2.5		Moreira et al. 2015
Pelobatidae				
Pelobates cultripes	Adult	35		Thirion 2014
	Egg		6	Thirion 2014
Pelobates fuscus	Larvae, eggs	0.6	4	Stanescu et al. 2013
Pelodytidae				
Pelodytes punctatus	Larvae	9		Thirion 2014
Pipidae				
Xenopus laevis	Juveniles		14	Munsey 1972
Ranidae				
Lithobates berlandieri	Adults	39		McCoid 2005
Lithobates catesbeianus	Larvae		10	Brown and Walls 2013
Lithobates clamitans	Adults, eggs, larvae	0.59	3.1	Collins and Russell 2009
Lithobates grylio	Adults	20.5		Rios-López 2008
Lithobates pipiens	Adults	15		Young 1924
Lithobates sphenocephalus	Adults	12.4	10.8	Christman 1974
Lithobates sylvaticus	Adults	2		Ouellet et al. 2009
	Larvae		7.5	Harless et al. 2011
Lithobates yavapaiensis	Adults, eggs	9	5	Ruibal 1959
Pelophylax perezi	Adults, larvae	28		Sillero and Ribeiro 2010
	Eggs		1	Ortiz-Santaliestra et al. 2010
Pelophylax ridibundus	Adults	4		Beadle 1943
	Adults		8.8	Katz 1975
Pelophylax saharicus	Adults, larvae, eggs	11		Florentin 1899
Rana draytonii	Adults, larvae	7.2		Smith and Reis 1997

TABLE 3.—Continued.

Species	Life stage	Environmental salinity (ppt)	Experimental tolerance (ppt)	Reference
Rana pretiosa	Adults	7.6		Brues 1932
Rana temporaria	Eggs	4		Florentin 1899
			4.5	Viertel 1999
Rhacophoridae				
Buergeria japonica	Adults, eggs	2		Haramura 2004, 2011
	Eggs		1	Haramura 2007a
Polypedates megacephalus	Larvae		6.6	Karraker et al. 2010
Scaphiopodidae				
Spea hammondii	Adults	7.4		Brues 1932

gene flow, altered migration, and inbreeding depression due to habitat fragmentation and degradation from multiple stressors, may limit the evolutionary responsiveness of these populations (Bell 2013; Brady 2013). These processes can result in maladapted vs. locally adapted populations, as has been found in Wood Frogs (*Lithobates sylvatica*) inhabiting anthropogenically salted roadside ponds (Brady 2013). These populations continue to persist, however; thus, while the animals may experience lower survival, increased malformations, etc. in their home roadside environment (Brady 2013), this also does not necessarily preclude them from inhabiting this habitat. Spotted Salamanders (*Ambystoma maculatum*) also appear to be able to locally adapt to increased salinity in these same ponds (Brady 2012), and Wood Frog populations have been found elsewhere inhabiting saline environments such as tidal marshes (Table 1; Ouellet et al. 2009). These limitations to adaptation thus appear to be species-, population-, and habitat-specific, and more work is needed to be able to predict the responses of populations to salinity.

A final limit to adaptation, especially relevant in anthropogenically altered saline habitats, is the chemical nature of the salt and the evolutionary history amphibians have in regulating it. Several amphibian species, otherwise somewhat tolerant of NaCl, have been found to be susceptible to non–NaCl-based salts such as $MgCl_2$ (Dougherty and Smith 2006; Harless et al. 2011). In Rough-Skinned Newts (*Taricha granulosa*), significant interfamily variation exists in egg survival in response to both NaCl and $MgCl_2$, which affect eggs similarly (Hopkins et al. 2013b). However, larval survival is significantly lower in $MgCl_2$ than in NaCl (Hopkins et al. 2014), as has been found in anuran tadpoles (Dougherty and Smith 2006; Harless et al. 2011). It appears that eggs do not have substantial osmoregulatory ability and therefore are equally affected by both salts, whereas larvae have the ability to regulate Na^+, but not Mg^{2+}, through gill and integumentary Na^+ pumps (Hopkins et al. 2014). This probably reflects the long evolutionary history that amphibians have with NaCl, but not $MgCl_2$, in various naturally saline habitats around the world (Drever 1997). Na^+, but not Mg^{2+}, also has a long evolutionary history as being one of the most-common vertebrate osmolytes (Shoemaker and Nagy 1977). Thus, it appears that the adaptive ability of amphibians to particular types of salt may be limited by their physiological means of regulating the salt in question, a product of their evolutionary history with the chemical (Hopkins et al. 2014). This has particularly important consequences for the ability of amphibians to adapt to anthropogenic sources of salt, such as road deicing salts, which are often increasingly not NaCl-based (e.g., Harless et al. 2011). $MgCl_2$ is now the second most-commonly used road deicing salt in North America (National Transportation Research Board 2007) and is used exclusively in some regions. Amphibian populations in these areas may thus be constrained in their ability to adapt to this evolutionarily more "foreign" salt. Future management decisions regarding the selection and application of road deicing salts should take into account this evolutionary perspective (Hopkins et al. 2014).

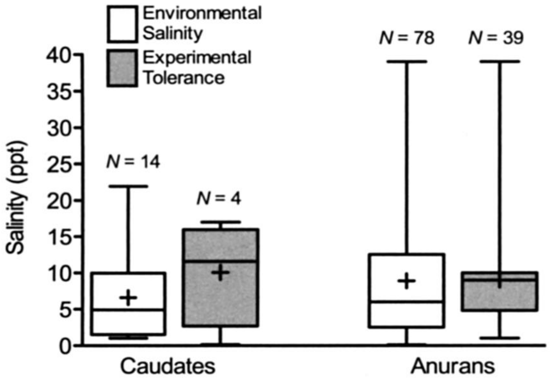

FIG. 7.—Maximum salinity concentrations (ppt Cl^-) measured in the field where amphibians were observed (white bars) and maximum salt tolerance limits measured in the lab (gray bars) for caudates and anurans (see Methods text for full definition of tolerance). The range of concentrations is displayed (minimum to maximum error bars). Upper and lower box limits represent 3rd (75th percentile) and 1st (25th percentile) quartiles, respectively, with the line in the box representing the median (2nd quartile). Means are shown as plus (+) symbols. *N* numbers indicate the number of species examined.

CONCLUSIONS

Salt tolerance has evolved in over 100 amphibian species around the world as populations have adapted to exploit coastal and inland saline habitats. The known number of salt-tolerant or salt-adapted species continues to grow rapidly (i.e., 20 since 2013) as we examine amphibian adaptation to both natural and anthropogenic sources of salt. We now understand salinity tolerance in over a dozen species around the world to a similar extent as well-known examples such as *Fejervarya cancrivora* and *Bufotes viridis*. Despite this progress, the vast majority of species and families have still not been examined in any depth, and we know very little about salt tolerance and physiological adaptations in most amphibians. More research is needed, especially on under-studied groups (such as caecilians and caudates) and life stages (such as eggs), and in areas outside of North America.

With over 7200 amphibian species, the number of known salt- tolerant species (144) remains relatively small. However, it is also evident that, while amphibians are osmotically sensitive, they are not helpless, and many are certainly capable of evolving and adapting to saline habitats around the world. As researchers begin to appreciate this worldwide phenomenon, we anticipate that many more salt-tolerant species and populations will be revealed. We encourage biologists to contact us regarding these findings so this review may be updated in the future.

While we have established that salt tolerance in amphibians is not as rare as previously thought, our understanding of how such tolerance evolves is still in its infancy. Populations appear to be able to adapt through exploiting existing genetic variation in salt tolerance in osmotically stressful, unpredictable environments. However, most species have not been examined in an evolutionary light, and we still know very little regarding the genetic nature of salinity tolerance, the variation in tolerance that might exist within populations, and selective pressures, including ecological interactions and the temporal nature of selection events, which might lead to adaptation. Finally, as habitats become increasingly impacted by anthropogenic change, including salinization, it is important to understand what might limit salinity adaptation in amphibians as well as why some populations or species may struggle to evolve and/or be constrained by their evolutionary history. This evolutionary perspective, where we seek to understand the factors that regulate the abilities (and constraints) of populations to evolve, is critical both in looking back at those "Indian toads… haunting the seaside" (Darwin 1872) and forward at those species facing new saline stressors, whether they be road deicing salts, landscape modification, or the formation of new seaside haunts as sea levels rise in a changing world.

Acknowledgments.—Research on amphibian salinity adaptation in the Brodie and French labs has been supported by the Utah State University Department of Biology and Ecology Center, the Society for Northwestern Vertebrate Biology, and a fellowship from the Natural Sciences and Engineering Research Council of Canada to GRH. We thank S.S. French for additional support and A.H. Savitzky, M.L. Crump, S.S. French, and Z.M. Hopkins for providing valuable comments on an earlier version of the manuscript. We are grateful to M. Koo (AmphibiaWeb) for assistance with Fig. 1 and to I. Gomez-Mestre, I. Sazima, C-S. Wu, S. Brady, and M. Hoogmoed for the kind permission to use and reprint their photos in Figures 2, 3, and 5. All other photos were used under Creative Commons license from Wikimedia or Flickr. Finally, we thank I. Gomez-Mestre, M. Harvey, and three anonymous reviewers for their valuable comments and ideas to improve the manuscript and A. Durso and T. Grant for providing information on species.

LITERATURE CITED

Abe, S., and E.P.W. Bicudo. 1991. Adaptations to salinity and osmoregulation in the frog *Thoropa miliaris* (Amphibia, Leptodactylidae). Zoologischer Anzeiger 227: 5–6.

Alcala, A.C. 1962. Breeding behavior and early development of frogs of Negros, Philippine Islands. Copeia 1962: 679–726.

Alexander, L.G., S.P. Lailvaux, J.H.K. Pechmann, and P.J. De Vries. 2012. Effects of salinity on early life stages of the Gulf Coast toad, *Incilius nebulifer* (Anura: Bufonidae). Copeia 2012: 106–114.

Allen, M.J. 1932. A survey of the amphibians and reptiles of Harrison County, Mississippi. American Museum Novitates 542: 1–20.

Alvarado, R.H., and T.H. Dietz. 1970a. Effect of salt depletion on hydromineral balance in larval *Ambystoma gracile:* I. Ionic composition. Comparative and Biochemical Physiology 33: 85–92.

Alvarado, R.H., and T.H. Dietz. 1970b. Effect of salt depletion on hydromineral balance in larval *Ambystoma gracile:* II. Kinetics of ion exchange. Comparative and Biochemical Physiology 33: 93–110.

Alvarado, R.H., and A. Moody. 1970. Sodium and chloride transport in tadpoles of the bullfrog *Rana catesbeiana*. American Journal of Physiology 218: 1510–1516.

Alvarez-León, R., and R.M. De Ayala-Monedero. 2000. Frogs associated to the swamps of the Colombian Caribbean. Revista de Biología Tropical 48: 724.

Andrade, E.B., T.B.L. Júnior, J.M.A.L. Júnior, and J.R.S.A. Leite. 2012. Predation by native fish and feeding by crab species on *Leptodactylus macrosternum* Mirando-Ribeiro, 1926 (Anura: Leptodactylidae) in northeastern Brazil. Herpetology Notes 5: 173–175.

Annandale, N. 1907. The fauna of brackish ponds at Port Canning, Lower Bengal. Records of the Indian Museum (A Journal of Indian Zoology) 1: 35–43.

Asem, A., A. Eimanifar, M. Djamali, P. De los Rios, and M. Wink. 2014. Biodiversity of the hypersaline Urmia Lake National Park (NW Iran). Diversity 6: 102–132.

Badyaev, A.V. 2005. Stress-induced variation in evolution: From behavioural plasticity to genetic assimilation. Proceedings of the Royal Society B 272: 877–886.

Bahmani, Z., R. Karamiani, N. Rastergar-Pouyani, A. Gharzi, and R.K. Browne. 2014. The amphibian fauna of Kurdistan Province, Western Iran. Amphibian and Reptile Conservation 9: 31–35.

Balinsky, J.B. 1981. Adaptation of nitrogen metabolism to hyperosmotic environment in Amphibia. Journal of Experimental Zoology 215: 335–350.

Barrett, R.D.H., and D. Schluter. 2007. Adaptation from standing genetic variation. Trends in Ecology and Evolution 23: 38–44.

Beadle, L.C. 1943. An ecological survey of some inland saline waters of Algeria. Journal of the Linnean Society of London, Zoology 43: 218–242.

Beebee, T.J.C. 1985. Salt tolerances of natterjack toad (*Bufo calamita*) eggs and larvae from coastal and inland populations in Britain. Herpetological Journal 1: 14–16.

Bell, G. 2013. Evolutionary rescue and the limits of adaptation. Philosophical Transactions of the Royal Society B 368: 1–6.

Bell, T. 1843. Reptiles. Elder and Co., UK.

Bellairs, A., and C.C.D. Shute. 1954. Notes on the herpetology of an Algerian beach. Copeia 1954: 224–226.

Bernabò, I., A. Bonacci, F. Coscarelli, M. Tripepi, and E. Brunelli. 2013. Effects of salinity stress on *Bufo balearicus* and *Bufo bufo* tadpoles: Tolerance, morphological gill alterations and Na^+/K^+-ATPase localization. Aquatic Toxicology 132–133: 119–133.

Boss, H., and T. Chesnes. 2014. *Siren lacertina*. (Greater Siren) habitat. Herpetological Review 45: 302.

Boulenger, G.A. 1897–1898. The Tailless Batrachians of Europe. The Ray Society, UK.

Boulenger, G.A. 1912. A Vertebrate Fauna of the Malay Peninsula from the Isthmus of Kra to Singapore Including the Adjacent Islands: Reptilia and Batrachia. Taylor and Francis, UK.

Boulenger, G.A. 1920a. British batrachians. Proceedings of the South London Entomological and Natural History Society 1919–1921: 23–31.

Boulenger, G.A. 1920b. A monograph of the South Asian, Papuan, Melanesian, and Australian frogs of the genus *Rana*. Records of the Indian Museum (A Journal of Indian Zoology) 20: 1–226.

Brady, S.P. 2012. Road to evolution? Local adaptation to road adjacency in an amphibian (*Ambystoma maculatum*). Scientific Reports 2: 1–5. DOI: 10.1038/srep00235.

Brady, S.P. 2013. Microgeographic maladaptive performance and deme depression in response to roads and runoff. PeerJ 1: e163. DOI: http://dx.doi.org/10.7717/peerj.163

Brand, A., J.W. Snodgrass, M.T. Gallagher, R.E. Casey, and R. Van Meter. 2010. Lethal and sublethal effects of embryonic and larval exposure of *Hyla versicolor* to stormwater pond sediments. Archives of Environmental Contamination and Toxicology 58: 325–331.

Brandon, R.A., E.J. Maruska, and W.T. Rumph. 1981. A new species of neotenic *Ambystoma* (Amphibia, Caudata) endemic to Laguna Alchichica, Puebla, Mexico. Bulletin of the Southern California Academy of Sciences 80: 112–125.

Brasileiro, C.A., M. Martins, and I. Sazima. 2010. Feeding ecology of *Thoropa taophora* (Anura: Cycloramphidae) on a rocky seashore in southeastern Brazil. South American Journal of Herpetology 5: 181–188.

Brown, M.E., and S.C. Walls. 2013. Variation in salinity tolerance among larval anurans: Implications for community composition and the spread of an invasive, non-native species. Copeia 2013: 543–551.

Brown, R.M., C.D. Siler, C.H. Oliveros, and A.C. Diesmos. 2013. The amphibians and reptiles of Luzon Island, Philippines, VIII: The herpetofauna of Cagayan and Isabela Provinces, northern Sierra Madre Mountain Range. ZooKeys 266: 1–120.

Brues, C.T. 1932. Studies on the fauna of North American hot springs. Proceedings of the American Academy of Arts and Sciences 67: 185–303.

Burger, W.L., P.W. Smith, and H.M. Smith. 1949. Notable records of reptiles and amphibians in Oklahoma, Arkansas, and Texas. Journal of the Tennessee Academy of Sciences 24: 130–134.

Cañedo-Argüelles, M., B.J. Kefford, C. Piscart, N. Prat, R.B. Schäfer, and C.-J. Schulz. 2013. Salinization of rivers: An urgent ecological issue. Environmental Pollution 173: 157–167.

Carl, G.C. 1949. Extensions of known ranges of some amphibians in British Columbia. Herpetologica 5: 139.

Cei, J.M. 1955. Chacoan batrachians in central Argentina. Copeia 1955: 291–293.

Chakko, G. 1968. Salinity tolerances in some south Indian anurans. Proceedings of the Indian Academy of Sciences B 67: 233–236.

Chambers, D.L. 2011. Increased conductivity affects corticosterone levels and prey consumption in larval amphibians. Journal of Herpetology 45: 219–223.

Chan, S.H., and C. Goh. 2010. Frogs of Sungei Buoh wetland reserve (Amphibia: Anura). Nature in Singapore 3: 103–116.

Chinathamby, K., R.D. Reina, P.C.E. Bailey, and B.K. Lees. 2006. Effects of salinity on the survival, growth and development of tadpoles of the brown tree frog, *Litoria ewingii*. Australian Journal of Zoology 54: 97–105.

Christman, S.P. 1974. Geographic variation for salt water tolerance in the frog *Rana sphenocephala*. Copeia 1974: 773–778.

Christy, M.T., and C.R. Dickman. 2002. Effects of salinity on tadpoles of the green and golden bell frog (*Litoria aurea*). Amphibia-Reptilia 23: 1–11.

Collins, S.J., and R.W. Russell. 2009. Toxicity of road salt to Nova Scotia amphibians. Environmental Pollution 157: 320–324.

Crawford, S.C., and E.P. Jones. 1933. Field notes on some amphibians from British Guiana. Copeia 2: 88–92.

Crump, M.L. 2002. Natural history of Darwin's frog, *Rhinoderma darwinii*. Herpetological Natural History 9: 21–30.

Darwin, C. 1834. Beagle animal notes. Pp. 186–187 in Charles Darwin's Zoology Notes and Specimen Lists from H.M.S. Beagle. R. Keynes (Ed.). Cambridge University Press, UK.

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. Murray, UK.

Darwin, C. 1872. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life, 6th ed. Murray, UK.

Darwin, C. 1876. Letter 391. To A.R. Wallace. Pp. 16 in More Letters of Charles Darwin: A Record of his Work in a Series of Hitherto Unpublished Letters. F. Darwin and A.C. Seward (Eds.). Murray, UK.

Davenport, J.M., and K.K. Huat. 1997. Salinity tolerance and preference in the frog *Rana rugulosa* Wiegmann. Herpetological Journal 7: 114–115.

Decksbach, N. 1922. Die Salzwassertierwelt Mittelrusslands. Archiv füer Hydrobiologie 14: 191–195.

Degani, G. 1981. Salinity tolerance and osmoregulation in *Salamandra salamandra* (L.) from different populations. Journal of Comparative Physiology 145: 133–137.

Degani, G., N. Silanikove, and A. Shkolnik. 1984. Adaptation of green toad (*Bufo viridis*) to terrestrial life by urea accumulation. Comparative and Biochemical Physiology 77A: 585–587.

Delson, J., and W.G. Whitford. 1973. Adaptation of the tiger salamander, *Ambystoma tigrinum*, to arid habitats. Comparative and Biochemical Physiology 46A: 631–638.

Diener, R.A. 1965. The occurrence of tadpoles of the green treefrog, *Hyla cinerea cinerea* (Schneider) in Trinity Bay, Texas. British Journal of Herpetology 3: 198–199.

Dougherty, C.K., and G.R. Smith. 2006. Acute effects of road de-icers on the tadpoles of three anurans. Applied Herpetology 3: 87–93.

Downie, J.R., E.G. Hancock, and A.P. Muir. 2010. The diet of the paradoxical frog *Pseudis paradoxa* in Trinidad, West Indies. Herpetological Journal 20: 111–114.

Drever, J.I. 1997. The Geochemistry of Natural Waters: Surface and Groundwater Environments. Prentice Hall, USA.

Duellman, W.E., and A. Schwartz. 1958. Amphibians and reptiles of southern Florida. Bulletin of the Florida State Museum 3: 181–324.

Duerr, F.G., and G.C. Ness. 1970. Non-protein-nitrogen levels and nitrogen excretion by *Ambystoma tigrinum* from saline lakes. American Zoologist 10: 287–326.

Duff, J.P., K. Colvile, J. Foster, and N. Dumphreys. 2011. Mass mortality of great crested newts (*Triturus cristatus*) on ground treated with road salt. Veterinary Record 168: 282.

Dunson, W.A. 1977. Tolerance to high temperature and salinity by tadpoles of the Philippine frog, *Rana cancrivora*. Copeia 1977: 375–378.

El Hamoumi, R., M. Dakki, and M. Thevenot. 2007. Etude écologique des larves d'anoures du Maroc. Bulletin de l'Institut Scientifique, Rabat, Section Sciences de la Vie 29: 27–34.

Ely, C. 1944. Development of *Bufo marinus* larvae in dilute sea water. Copeia 1944: 256.

Engels, W.L. 1952. Vertebrate fauna of North Carolina coastal islands II: Shackleford Banks. American Midland Naturalist 47: 702–742.

Environment Canada. 2001. Priority Substances List Assessment Report: Road Salts. Environment Canada, Canada.

Ferguson, D.E. 1956. Notes on the occurrence of some Oregon salamanders close to the Ocean. Copeia 1956: 120.

Ferreira, R.B., and J.F.R.T. Tonini. 2010. Living holed: *Leptodactylus latrans* occupying crabs' burrows. Herpetology Notes 3: 237–238.

Florentin, M.R. 1899. Études sur la faune des mares salées de Lorraine. Docteur des Sciences Naturelles dissertation, Université de Nancy, France.

Frost, D.R. 2014. Amphibian species of the world: An online reference. American Museum of Natural History, USA. Available at http://research.amnh.org/vz/herpetology/amphibia/index.php. Archived by WebCite at http://www.webcitation.org/6U0q9vUeU on 11 November 2014.

Gadow, H. 1901. Amphibia and reptiles. Cambridge Natural History 8: 1–668.

Gallagher, M.T., J.W. Snodgrass, A.B. Brand, R.E. Casey, S.M. Lev, and R.J. Van Meter. 2014. The role of pollutant accumulation in determining the use of stormwater ponds by amphibians. Wetlands Ecology and Mangement 22: 551–564.

Gasser, K.W., and B.T. Miller. 1986. Osmoregulation of larval blotched tiger salamanders, *Ambystoma tigrinum melanostictum*, in saline environments. Physiological Zoology 59: 643–648.

Gislén, T., and H. Kauri. 1959. Zoogeography of the Swedish amphibians and reptiles with notes on their growth and ecology. Acta Vertebratica 1: 197–397.

Glorioso, B.M., J.H. Waddle, M.E. Crockett, K.G. Rice, and H.F. Percival. 2012. Diet of the invasive Cuban Treefrog (*Osteopilus septentrionalis*) in pine rockland and mangrove habitats in South Florida. Caribbean Journal of Science 46: 346–355.

Goin, C.J. 1953. Rediscovery of the frog *Litoria luteola* Gosse in Jamaica. Occasional Papers of the Museum of the Institute of Jamaica 7: 1–4.

Gomez-Mestre, I., and M. Tejedo. 2003. Local adaptation of an anuran amphibian to osmotically stressful environments. Evolution 57: 1889–1899.

Gomez-Mestre, I., and M. Tejedo. 2004. Contrasting patterns of quantitative and neutral genetic variation in locally adapted populations of the natterjack toad, *Bufo calamita*. Evolution 58: 2243–2352.

Gomez-Mestre, I., and M. Tejedo. 2005. Adaptation or exaptation? An experimental test of hypotheses on the origin of salinity tolerance in *Bufo calamita*. Journal of Evolutionary Biology 18: 847–855.

Gomez-Mestre, I., M. Tejedo, E. Ramayo, and J. Estepa. 2004. Developmental alterations and osmoregulatory physiology of a larval anuran under osmotic stress. Physiological and Biochemical Zoology 77: 267–274.

Gordon, M.S. 1962. Osmotic regulation in the green toad (*Bufo viridis*). Journal of Experimental Biology 39: 261–270.

Gordon, M.S., and V.A. Tucker. 1965. Osmotic regulation in the tadpoles of the crab-eating frog (*Rana cancrivora*). Journal of Experimental Biology 42: 437–445.

Gordon, M.S., and V.A. Tucker. 1968. Further observations on the physiology of salinity adaptation in the crab-eating frog (*Rana cancrivora*). Journal of Experimental Biology 49: 185–193.

Gordon, M.S., K. Schmidt-Nielsen, and H.M. Kelly. 1961. Osmotic regulation in the crab-eating frog (*Rana cancrivora*). Journal of Experimental Biology 38: 659–678.

Goris, C.R., and N. Maeda. 2005. Guide to the Amphibians and Reptiles of Japan. Krieger Publishing Company, USA.

Gornitz, V. 1995. Sea-level rise: A review of recent past and near-future trends. Earth Surface Processes and Landforms 20: 7–20.

Gosner, K.L., and I.H. Black. 1957. The effects of acidity on the development and hatching of New Jersey frogs. Ecology 38: 256–262.

Grant, C. 1932. Herpetology of Tortola: Notes on Anegada and Virgin Gorda, British Virgin Islands. Journal of the Department of Agriculture, Puerto Rico 16: 339–346.

Grant, C. 1939. Additional data on Jamaican snakes of the genus *Dromicus*. Copeia 1939: 105–106.

Guix, J.C., and R.M. Lopes. 1989. Occurrence of *Hyla geographica* Spix and *Bufo crucifer* Wied tadpoles in brackish water environments in the Juréia region (Sao Paulo, SE Brazil). Amphibia-Reptilia 10: 185–192.

Gunter, G. 1956. Some relations of faunal distributions to salinity in estuarine waters. Ecology 37: 616–619.

Gunzburger, M.S., W.B. Hughes, W.J. Barichivich, and J.S. Staiger. 2010. Hurricane storm surge and amphibian communities in coastal wetlands of northwestern Florida. Wetlands Ecology and Mangement 18: 651–663.

Hagström, T. 1981. Tadpoles of the common toad (*Bufo bufo* L.) found in brackish water. Amphibia-Reptilia 2: 187–188.

Hamer, A.J., S.J. Lane, and M. Mahony. 2002. Management of freshwater wetlands for the endangered green and golden bell frog (*Litoria aurea*): Roles of habitat determinants and space. Biological Conservation 106: 413–424.

Hammer, U.T. 1986. Saline Lake Ecosystems of the World. Dr. W. Junk Publishers, the Netherlands.

Hansen, R.W., D.B. Wake, and G.M. Fellers. 2005. Batrachoseps pacificus (Cope, 1985): Species Account. Pp. 685–686 in Amphibian Declines: The Conservation Status of United States Species. M. Lannoo (Ed.). University of California Press, USA.

Haramura, T. 2004. Salinity and other abiotic characteristics of oviposition sites of the rhacophorid frog, *Buergeria japonica*, in coastal habitat. Current Herpetology 23: 81–84.

Haramura, T. 2007a. Salinity tolerance of eggs of *Buergeria japonica* (Amphibia, Anura) inhabiting coastal areas. Zoological Science 24: 820–823.

Haramura, T. 2007b. Microhabitat selection by tadpoles of *Buergeria japonica* inhabiting the coastal area. Journal of Ethology 25: 3–7.

Haramura, T. 2008. Experimental test of spawning site selection by *Buergeria japonica* (Anura: Rhacophoridae) in response to salinity level. Copeia 2008: 64–67.

Haramura, T. 2011. Use of oviposition sites by a Rhacophorid frog inhabiting a coastal area of Japan. Journal of Herpetology 45: 432–437.

Hardy, E. 1943. Newt larvae in brackish water (reply). Nature 151: 226.

Hardy, J.D., Jr. 1952. A concentration of juvenile spotted salamanders, *Ambystoma maculatum* (Shaw). Copeia 1952: 181–182.

Hardy, J.D., Jr. 1953. Notes on the distribution of *Mycrohyla carolinensis* in southern Maryland. Herpetologica 8: 162–166.

Hardy, J.D., Jr. 1972. Amphibians of the Chesapeake Bay region. Chesapeake Science 13: S123–S128.

Harless, M.L., C.J. Huckins, J.B. Grant, and T.G. Pypker. 2011. Effects of six chemical deicers on larval wood frogs (*Rana sylvatica*). Environmental Toxicology and Chemistry 30: 1637–1641.

Hedges, S.B., and R. Thomas. 1992. A new marsh-dwelling species of *Eleutherodactylus* from Haiti (Anura: Leptodactylidae). Journal of Herpetology 26: 191–195.

Held, J.W., and J.J. Peterka. 1974. Age, growth and food habits of the fathead minnow, *Pimephales promelas*, in North Dakota saline lakes. Transactions of the American Fisheries Society 103: 743–756.

Hoffman, J. 2014. Physiological response of *Bufo viridis* (Laurenti, 1768) populations across an aridity gradient. Alytes 30: 33–41.

Hoogmoed, M.S., A.O. Maciel, and J.T. Coragem. 2011. Discovery of the largest lungless tetrapod, *Atretochoana eiselti* (Taylor, 1968) (Amphibia: Gymnophiona: Typhlonectidae), in its natural habitat in Brazilian Amazonia. Boletim do Museu Paraense Emilio Goeldi Ciências Naturais 6: 241–262.

Hopkins, G.R., and Z.M. Hopkins. In press. Salty salamander: Occurrence of a *Dicamptodon tenebrosus* in a tidal stream. Northwestern Naturalist 96(2).

Hopkins, G.R., S.S. French, and E.D. Brodie Jr. 2013a. Increased frequency and severity of developmental deformities in rough-skinned newt (*Taricha granulosa*) embryos exposed to road deicing salts (NaCl & MgCl2). Environmental Pollution 173: 264–269.

Hopkins, G.R., S.S. French, and E.D. Brodie Jr. 2013b. Potential for local adaptation in response to an anthropogenic agent of selection: Effects of road deicing salts on amphibian embryonic survival and development. Evolutionary Applications 6: 384–392.

Hopkins, G.R., E. Brodie Jr., and S.S. French. 2014. Developmental and evolutionary history affect survival in stressful environments. PLoS One 9: e95174. DOI: 10.1371/journal.pone.0095174.

Hovingh, P. 1993. Aquatic habitats, life history observations, and zoogeographic considerations of the spotted frog (*Rana pretiosa*) in Tule Valley, Utah. Great Basin Naturalist 53: 168–179.

Hua, J., and B.A. Pierce. 2013. Lethal and sublethal effects of salinity on three common Texas amphibians. Copeia 2013: 562–566.

Janicke, G., and J.D. Roberts. 2010. *Litoria cyclorhyncha* saline habitat. Herpetological Review 41: 199–200.

Jena, S.C., S.K. Palita, and M.K. Mahapatra. 2013. Anurans of Bhitarkanika mangroves, Odisha, east coast of India. Check List 9: 400–404.

Jones, R.M., and S.S. Hillman. 1978. Salinity adaptation in the salamander *Batrachoseps*. Journal of Experimental Biology 76: 1–10.

Karraker, N.E. 2007. Are embryonic and larval green frogs (*Rana clamitans*) insensitive to road deicing salt? Herpetological Conservation and Biology 2: 35–41.

Karraker, N.E., and J.P. Gibbs. 2011. Road deicing salt irreversibly disrupts osmoregulation of salamander egg clutches. Environmental Pollution 159: 833–835.

Karraker, N.E., and G.R. Ruthig. 2009. Effect of road deicing salt on the susceptibility of amphibian embryos to infection by water molds. Environmental Research 109: 40–45.

Karraker, N.E., J.P. Gibbs, and J.R. Vonesh. 2008. Impacts of road deicing salt on the demography of vernal pool-breeding amphibians. Ecological Applications 18: 724–734.

Karraker, N.E., J. Arrigoni, and D. Dudgeon. 2010. Effects of increased salinity and an introduced predator on lowland amphibians in southern China: Species identity matters. Biological Conservation 143: 1079–1086.

Katz, U. 1973. Studies on the adaptation of the toad *Bufo viridis* to high salinities: Oxygen consumption, plasma concentration and water content of the tissues. Journal of Experimental Biology 58: 785–796.

Katz, U. 1975. NaCl adaptation in *Rana ridibunda* and a comparison with the euryhaline toad *Bufo viridis*. Journal of Experimental Biology 63: 763–773.

Katz, U. 1989. Strategies of adaptation to osmotic stress in anuran amphibia under salt and burrowing conditions. Comparative and Biochemical Physiology 93A: 499–503.

Kaushal, S.S., P.M. Groffman, G.E. Likens, K.T. Belt, W.P. Stack, V.R. Kelly, L.E. Band, and G.T. Gisher. 2005. Increased salinization of fresh water in the northeastern United States. Proceedings of the National Academy of Sciences of the United States of America 102: 13517–13520.

Kearney, B.D., P.G. Byrne, and R.D. Reina. 2012. Larval tolerance to salinity in three species of Australian anuran: An indication of saline specialisation in *Litoria aurea*. PLoS One 7: e43427. DOI: 10.1371/journal.pone.0043427.

Kearney, B.D., R.J. Pell, P.G. Byrne, and R.D. Reina. 2014. Anuran larval developmental plasticity and survival in response to variable salinity of ecologically relevant timing and magnitude. Journal of Experimental Zoology A 321: 541–549,

Kirschner, L.B., T. Kerstetter, D. Porter, and R.H. Alvarado. 1971. Adaptation of larval *Ambystoma tigrinum* to concentrated environments. American Journal of Physiology 220: 1814–1819.

Kiviat, E., and J. Stapleton. 1983. *Bufo americanus*. (American toad) estuarine habitat. Herpetological Review 14: 46.

Klemens, M.W., E. Kiviat, and R.E. Schmidt. 1987. Distribution of the northern leopard frog, *Rana pipiens*, in the lower Hudson and Housatonic river valleys. Northeastern Environmental Science 6: 99–101.

Knoepffler, L.P. 1962. Contribution à l'étude du genre Discoglosus (Amphibiens, Anoures). Vie et Milieu 12: 1–94.

La Rivers, I. 1948. Some Hawaiian ecological notes. The Wasmann Collector 7: 85–110.

Langhans, M., B. Peterson, A. Walker, G.R. Smith, and J.E. Rettig. 2009. Effects of salinity on survivorship of wood frog (*Rana sylvatica*) tadpoles. Journal of Freshwater Ecology 24: 335–336.

Larson, D.W. 1968. The occurrence of neotenic salamanders, *Ambystoma tigrinum diaboli* Dunn, in Devils Lake, North Dakota. Copeia 1968: 620–621.

Licht, P., M.E. Feder, and S. Bledsoe. 1975. Salinity tolerance and osmoregulation in the salamander *Batrachoseps*. Journal of Comparative Physiology 102: 123–134.

Liggins, G.W., and G.C. Grigg. 1985. Osmoregulation of the Cane toad, *Bufo marinus*, in salt water. Comparative and Biochemical Physiology 82A: 613–619.

Lynn, W.G. 1957. Notes on a collection of reptiles and amphibians from Antigua, B.W.I. Herpetologica 13:53–56.

Margalef, R. 1956. La vida en las aguas de elevado residuo salino de la provincia de Zamora. Publicaciones del Instituto de Biología Aplicada 26: 123–137.

Matlaga, T.H., C.A. Phillips, and D.J. Soucek. 2014. Insensitivity to road salt: An advantage for the American bullfrog? Hydrobiologia 721: 1–8.

Matos-Torres, J.J. 2006. Habitat characterization for the Puerto Rican Crested Toad (*Peltophryne [Bufo] lemur*) at Guánica State Forest, Puerto Rico. M.S. thesis, University of Puerto Rico, Puerto Rico.

McBean, R.L., and L. Goldstein. 1967. Ornithine-urea cycle activity in *Xenopus laevis*: Adaptation in saline. Science 157: 931–932.

McCoid, M.J. 2005. *Rana berlandieri* salinity tolerance. Herpetological Review 36: 437–438.

Measey, G.J., M. Vences, R.C. Drewes, Y. Chiari, M. Melo, and B. Bourles. 2007. Freshwater paths across the ocean: Molecular phylogeny of the frog *Ptychadena newtoni* gives insights into amphibian colonization of oceanic islands. Journal of Biogeography 34: 7–20.

Mertens, R. 1926. Amphibia, Reptilia. Die Tierwelt der Nord-und Ostee 12: 1–20.

Mester, B., N.J. Cozma, and M. Puky. 2013. First observation of facultative paedomorphosis in the Danube crested newt (*Triturus dobrogicus* Kiritzescu, 1903) and the occurrence of facultative paedomorphosis in two newt species from soda pans of the Danube-Tisza Interfluve (Kiskunság National Park, Hungary). North-Western Journal of Zoology 9: 443–445.

Mokany, A., and R. Shine. 2003. Oviposition site selection by mosquitoes is affected by cues from conspecific larvae and anuran tadpoles. Austral Ecology 28: 33–37.

Moreira, L.F.B., D.S. Knauth, and L. Maltchik. 2015. Intermittently closed estuaries and tadpole communities: Influence of artificial breaching. Estuaries and Coasts 38: 979–987.

Mueller, A.J. 1985. Vertebrate use of nontidal wetlands on Galveston Island, Texas. Texas Journal of Science 37: 215–225.

Munsey, L.D. 1972. Salinity tolerance of the African pipid frog, *Xenopus laevis*. Copeia 1972: 584–586.

Muralidhar, P., F.P. De Sá, C.F.B. Haddad, and K.R. Zamudio. 2014. Kin-bias, breeding site selection and female fitness in a cannibalistic Neotropical frog. Molecular Ecology 23: 453–463.

Murray, K.F. 1955. Herpetological collections from Baja California. Herpetologica 11: 33–48.

National Transportation Research Board. 2007. Guidelines for the Selection of Snow and Ice Control Materials to Mitigate Environmental Impacts. National Cooperative Highway Research Program Report 577. National Cooperative Highway Research Program, USA.

Neill, W.T. 1958. The occurrence of amphibians and reptiles in saltwater areas, and a bibliography. Bulletin of Marine Science of the Gulf and Caribbean 8: 1–97.

Nicholls, R.J., F.M.J. Hoozemans, and M. Marchand. 1999. Increasing flood risk and wetland losses due to global sea-level rise: Regional and global analyses. Global Environmental Change 9: S69–S87.

Nöllert, A., and C. Nöllert. 1992. Die Amphibien Europas. Franckh-Kosmos Verlags-GmbH and Company, Germany.

Odendaal, F.J., and C.M. Bull. 1982. A parapatric boundary between *Ranidella signifera* and *R. riparia* (Anura: Leptodactylidae) in South Australia. Australian Journal of Zoology 30: 49–57.

Ortiz-Santaliestra, M.E., M.J. Fernández-Benéitez, M. Lizana, and A. Marco. 2010. Adaptation to osmotic stress provides protection against ammonium nitrate in *Pelophylax perezi* embryos. Environmental Pollution 158: 934–940.

Ouellet, M., C. Fortin, and M.-J. Grimard. 2009. Distribution and habitat use of the Boreal Chorus Frog (*Pseudacris maculata*) at its extreme northeastern range limit. Herpetological Conservation and Biology 4: 277–284.

Padhye, A.D., and H.V. Ghate. 1992. Sodium chloride and potassium chloride tolerance of different stages of the frog, *Microhyla ornata*. Herpetological Journal 2: 18–23.

Parsons, P.A. 2005. Environments and evolution: Interactions between stress, resource inadequacy and energetic efficiency. Biological Reviews 80: 589–610.

Pawling, R.O. 1939. The amphibians and reptiles of Union County, Pennsylvania. Herpetologica 1: 165–169.

Pearse, A.S. 1911. Concerning the development of frog tadpoles in sea water. Phillippine Journal of Science 6: 219–220.

Péfaur, J.E. 1984. A new species of Dendrobatid frog from the coast of Peru. Journal of Herpetology 18: 492–494.

Peterson, H.W., R. Garrett, and J.P. Lantz. 1952. The mating period of the giant tree frog *Hyla dominicensis*. Herpetologica 8: 63.

Petranka, J.W., and E.J. Doyle. 2010. Effects of road salts on the composition of seasonal pond communities: Can the use of road salts enhance mosquito recruitment? Aquatic Ecology 44: 155–166.

Petranka, J.W., and R.A. Francis. 2013. Effects of road salts on seasonal wetlands: Poor prey performance may compromise growth of predatory salamanders. Wetlands 33: 707–715.

Pombal, J.P., and Jr. 1993. New species of *Aparashpenodon* (Anura: Hylidae) from southeastern Brazil. Copeia 1993: 1088–1091.

Ponssa, M.L., M.J. Jowers, and R.O. De Sá. 2010. Osteology, natural history notes, and phylogenetic relationships of the poorly known Caribbean frog *Leptodactylus nesiotus* (Anura: Leptodactylidae). Zootaxa 2646: 1–25.

Purcell, K.M., A.T. Hitch, P.L. Klerks, and P.L. Leberg. 2008. Adaptation as a potential response to sea-level rise: A genetic basis for salinity tolerance in populations of a coastal marsh fish. Evolutionary Applications 1: 155–160.

Pyefinch, K.A. 1937. The fresh and brackish waters of Bardsey Island (North Wales): A chemical and faunistic survery. Journal of Animal Ecology 6: 115–137.

Pyke, G.H., A.W. White, P.J. Bishop, and B. Waldman. 2002. Habitat-use by the Green and Golden Bell Frog *Litoria aurea* in Australia and New Zealand. Australian Zoologist 32: 12–31.

Pyke, G.H., S.T. Ahyong, A. Fuessel, and S. Callaghan. 2013. Marine crabs eating freshwater frogs: Why are such observations so rare? Herpetology Notes 6: 195–199.

Rahman, M.R., and M. Asaduzzaman. 2010. Ecology of Sundarban, Bangladesh. Journal of Science Foundation 8: 35–47.

Reis, D.K. 1999. Habitat characteristics of California red-legged frogs (*Rana aurora draytonii*): Ecological differences between eggs, tadpoles, and adults in a coastal brackish and freshwater system. M.S. thesis, San Jose State University, USA.

Rios-López, N. 2008. Effects of increased salinity on tadpoles of two anurans from a Caribbean coastal wetland in relation to their natural abundance. Amphibia-Reptilia 29: 7–18.

Roberts, J.O. 1970. Variations in salinity tolerance in the Pacific treefrog, *Hyla regilla*, in Oregon. Ph.D. dissertation [unpublished], Oregon State University, USA.

Romspert, A.P., and L.L. McClanahan. 1981. Osmoregulation of the terrestrial salamander, *Ambystoma tigrinum* in hypersaline media. Copeia 1981: 400–405.

Ruibal, R. 1959. The ecology of a brackish water population of *Rana pipiens*. Copeia 1959: 315–322.

Ruibal, R. 1962. Osmoregulation in amphibians from heterosaline habitats. Physiological Zoology 35: 133–147.

Samraoui, B., F. Samraoui, N. Benslimane, A. Alfarhan, and K.A.S. Al-Rasheid. 2012. A precipitous decline of the Algerian newt *Pleurodeles poireti* Gervais, 1835 and other changes in the status of amphibians of Numidia, north-eastern Algeria. Revue d'Écologie (Terre Vie) 67: 71–81.

Sanzo, D., and S.J. Hecnar 2006. Effects of road de-icing salt (NaCl) on larval wood frogs (*Rana sylvatica*). Environmental Pollution 140: 247–256.

Sasa, M., G.A. Chaves, and L.D. Patrick. 2009. Marine reptiles and amphibians. Pp. 459–468 in Marine Biodiversity of Costa Rica, Central America. I.S. Wehrtmann and J. Cortés (Eds.). Springer, the Netherlands.

Satheeshkumar, P. 2011. First record of a mangrove frog *Fejervarya cancrivora* (Amphibia: Ranidae) in the Pondicherry Mangroves, Bay of Bengal-India. World Journal of Zoology 6: 328–330.

Sazima, I. 1971. The occurrence of marine invertebrates in the stomach contents of the frog *Thoropa miliaris*. Ciência e Cultura 23: 647–648.

Schmidt, K.P. 1955. Amphibians and reptiles from Iran. Videnskabelige Meddeleser fra Dansk Naturhistorisk Forening 117: 193–207.

Shaw, T.-H. 1934. Notes on specimens of Radde's toad from Chefoo. The China Journal 20: 197–199.

Shoemaker, V.H., and K.A. Nagy. 1977. Osmoregulation in amphibians and reptiles. Annual Reviews of Physiology 39: 449–471.

Shoemaker, V.H., S.S. Hillman, S.D. Hillyard, D.C. Jackson, L.L. McClanahan, P.C. Withers, and M.L. Wygoda. 1992. Exchange of water, ions, and respiratory gases in terrestrial amphibians. Pp. 125–150 in Environmental Physiology of the Amphibians. M.E. Feder and W.W. Burggren (Eds.). University of Chicago Press, USA.

Sillero, N., and R. Ribeiro. 2010. Reproduction of *Pelophylax perezi* in brackish water in Porto (Portugal). Herpetology Notes 3: 337–340.

Smith, H.M., and O. Sanders. 1952. Distributional data on Texan amphibians and reptiles. Texas Journal of Science 2: 204–219.

Smith, J.J., and D.K. Reis. 1997. Pescadero Marsh Natural Preserve salinity, tidewater goby and red-legged frog monitoring for 1995–1996. Report number 3790-301-722(7), California Department of Parks and Recreation, San Jose State University, USA.

Smith, M.A. 1927. Contributions to the herpetology of the Indo-Australian region. Proceedings of the Zoological Society of London 1927: 199–225.

Smith, M.J., E.S.G. Schreiber, M.P. Scroggie, M. Kohout, K. Ough, J. Potts, R. Lennie, D. Turnbull, C. Jin, and T. Clancy. 2007. Associations between anuran tadpoles and salinity in a landscape mosaic of wetlands impacted by secondary salinisation. Freshwater Biology 52: 75–84.

Smith, P.W., and J.C. List. 1955. Notes on Mississippi amphibians and reptiles. American Midland Naturalist 53: 115–125.

Snodgrass, J.W., R.E. Casey, D. Joseph, and J.A. Simon. 2008. Microcosm investigations of stormwater pond sediment toxicity to embryonic and larval amphibians: Variation in sensitivity among species. Environmental Pollution 154: 291–297.

Spurway, H. 1943. Newt larvae in brackish water. Nature 151: 109–110.

Stanescu, F., R. Iosif, D. Székely, P. Székely, D. Rosioru, and D. Cogalniceanu. 2013. Salinity tolerance in *Pelobates fuscus* (Laurenti, 1768) tadpoles (Amphibia: Pelobatidae). Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa" 56: 103–108.

Storer, T.I. 1925. A Synopsis of the Amphibia of California. University of California Press, USA.

Strahan, R. 1957. The effect of salinity on the survival of larvae of *Bufo melanostictus* Schneider. Copeia 1957: 146–147.

Taylor, E.H. 1943. A new ambystomatid salamander adapted to brackish water. Copeia 3: 151–156.

Tercafs, R.R., and E. Schoffeniels. 1962. Adaptation of amphibians to salt water. Life Sciences 1: 19–23.

Theobald, Jr., W. 1868. Cataologue of the reptiles of British Birma, embracing the provinces of Pegu, Martaban, and Tenasserim; with descriptions of new or little-known species. Journal of the Linnean Society of London, Zoology 10: 4–67.

Thienemann, A. 1926. Erganzende Notizen zur Salzwasserfauna von Oldesloe. Mitteilunger der Geographischen Gesellschat und des Naturhistorischen Museums in Lübeck 31: 102–126.

Thirion, J.-M. 2002. Impact du raz de marée sur une population de Pélobate cultripède *Pelobates cultripes* (Cuvier, 1829) (Amphibia, Pelobatidae) dans un espace protégé de Charente-Maritime. Annales de la Société des sciences naturelles de la Charente-Maritime 9: 195–202.

Thirion, J.-M. 2006. Le Pélobate cultripède *Pelobates cultripes* (Cuvier, 1829) sur la façade Atlantique Française: Chorologie, écologie et conservation. Diplome de l'ecole pratique des Hautes estudes, Montpellier Université, France.

Thirion, J.-M. 2014. Salinity of the reproductive habitats of the Western Spadefoot Toad *Pelobates cultripes* (Cuvier, 1829), along the Atlantic coast of France (Anura: Pelobatidae). Herpetozoa 27: 13–20.

Thunqvist, E. 2004. Regional increase of mean chloride concentration in water due to the application of deicing salt. Science of the Total Environment 325: 29–37.

Turtle, S.L. 2000. Embryonic survivorship of the spotted salamander (*Ambystoma maculatum*) in roadside and woodland vernal pools in southeastern New Hampshire. Journal of Herpetology 34: 60–67.

Uchiyama, M., T. Murakami, and H. Yoshizawa. 1990. Notes on the development of the crab-eating frog, *Rana cancrivora*. Zoological Science 7: 73–78.

van Beurden, E.K., and G.C. Grigg. 1980. An isolated and expanding population of the introduced toad *Bufo marinus* in New South Wales. Australian Wildlife Research 7: 305–310.

Van Meter, R., and C.M. Swan. 2014. Road salts as environmental constraints in urban pond food webs. PLoS One 9: 1–12. DOI: 10.1371/journal.pone.0090168.

Van Meter, R.J., C.M. Swan, J. Leips, and J.W. Snodgrass. 2011. Road salt stress induces novel food web structure and interactions. Wetlands 31: 843–851.

Vences, M., D.R. Vieites, F. Glaw, H. Brinkmann, J. Kosuch, M. Veith, and A. Meyer. 2003. Multiple overseas dispersal in amphibians. Proceedings of the Royal Society B 270: 2435–2442.

Viertel, B. 1999. Salt tolerance of *Rana temporaria*: Spawning site selection and survival during embryonic development (Amphibia, Anura). Amphibia-Reptilia 20: 161–171.

Viosca, P., and Jr. 1923. An ecological study of the cold blooded vertebrates of southeastern Louisiana. Copeia 115: 35–44.

Weick, D.L. 1980. Osmotic regulation and salinity tolerance in the Pacific tree frog *Hyla regilla*. M.A. thesis [unpublished], California State University, USA.

Werner, F. 1909. Reptilien, Batrachier und Fische von Tripolis und Barka. Zoologische Jahrbücher Abteilung für Systematik 27: 595–646.

Whitfield, P.H., and N.L. Wade. 1992. Monitoring transient water quality events electronically. Water Resources Bulletin 28: 703–711.

Whitfield, P.H., and N.L. Wade. 1996. Transient water quality events in British Columbia coastal streams. Water Science and Technology 33: 151–161.

Williams, W.D. 2001. Anthropogenic salinisation of inland waters. Hydrobiologia 466: 329–337.

Wittig, K.P., and S.C. Brown. 1977. Sodium balance in the newt, *Notophthalmus viridescens*. Comparative and Biochemical Physiology 58A: 49–52.

Wogan, G.O.U., J.V. Vindum, J.A. Wilkinson, and A.K. Shein. 2008. New country records and range extensions for Myanmar amphibians and reptiles. Hamadryad 33: 83–96.

Wright, A.H., and A.A. Wright. 1938. Amphibians of Texas. Transactions of the Texas Academy of Sciences 21: 5–35.

Wu, C.-S., and Y.-C. Kam. 2009. Effects of salinity on the survival, growth, development, and metamorphosis of *Fejervarya limnocharis* tadpoles living in brackish water. Zoological Science 26: 476–482.

Wu, C.-S., I. Gomez-Mestre, and Y.-C. Kam. 2012. Irreversibility of a bad start: Early exposure to osmotic stress limits growth and adaptive developmental plasticity. Oecologia 169: 15–22.

Wu, C.-S., W.-K. Yang, T.-H. Lee, I. Gomez-Mestre, and Y.-C. Kam. 2014. Salinity acclimation enhances salinity tolerance in tadpoles living in brackish water through increased Na^+, K^+-ATPase expression. Journal of Experimental Zoology 321: 57–64.

Wygoda, M.L., T.F. Dabruzzi, and W.A. Bennett. 2011. Cutaneous resistance to evaporative water loss in the crab-eating frog (*Fejervarya cancrivora*). Journal of Herpetology 45: 417–420.

Young, R.T. 1924. The life of Devils Lake, North Dakota. Publication of the North Dakota Biological Station, USA.

Published on 28 May 2015