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REVIEW, CONCEPT, AND SYNTHESIS

Drinking behaviors and water balance in marine vertebrates

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Abstract

Acquisition of fresh water is important to animals, and is both difficult and critical for species residing in marine environments. Adaptive radiations to fully marine habitats were constrained by the need for fresh water and the capacity of various taxa to adapt physiology to reliance on sources of water other than free drinking water. Here, we review the water relations of marine vertebrates, with an emphasis on drinking and the need to procure fresh water. Numerous marine teleost fishes drink seawater, but some do not, and drinking is more variable and complex than suggested by textbooks. The mechanisms by which fishes and other vertebrates regulate water balance involve the renin–angiotensin and aldosterone endocrine systems, but plasma osmotic and ionic concentrations as well as other chemical signals can also be involved. Multiple mechanisms for stimulation of drinking are operative and diverse among species. Clearly, evolutionary adaptations to environmental salinities can alter drinking behaviors. Marine elasmobranchs do not characteristically drink seawater, but euryhaline species drink upon returning to more concentrated seawater, as with teleosts. Hagfish are osmoconformers, and there is no evidence for drinking. In general, marine reptiles and most marine mammals and seabirds do not drink seawater. Exceptions include sea turtles, cetaceans, and some pinnipeds. Some marine species (e.g., sea snakes) require fresh water that can be acquired from ephemeral rainwater lenses, while others are adapted to utilize dietary and metabolic water. Regardless of drinking behaviors, numerous forms have evolved varied strategies for conserving water while reducing its losses to the surrounding sea.

Introduction

All life is dependent on water. In more complex organisms, the appropriate internal environment for physiological homeostasis is dependent on the regulation of volume, distribution, and ionic composition of water (Hochachka and Somero 2002). These attributes of organismal and cellular water are, in turn, dependent on an appropriate balance of input and output involving fluxes of water between the organism and its environment (Fig. 1). The influx of water is dependent on a combination of four sources: (i) inward fluxes across membranes having some degree of permeability to water; (ii) dietary free water that might be contained within ingested food; (iii) metabolic water that is a byproduct of cellular metabolism; and (iv) discretionary water that is voluntarily acquired from the environment by drinking (Fig. 1).

Acquisition of adequate amounts of water is challenging in three environments: (i) low latitude deserts; (ii) high-latitude or high-altitude environments where water is largely in a frozen state; and (iii) marine habitats where concentrations of salts in water are high. In spite of problems related to a dearth of fresh water and 'loading' of salt, animals live successfully in the world's oceans, and these include numerous species that are secondarily marine. The evolutionary transition from terrestrial to marine habitats has involved at least 30 independent lineages of vertebrates excluding fish (Zimmer 1998; Lillywhite et al. 2008a; Kelley and Pyenson 2015). The majority of these taxa overcame challenges that were physical, biotic, and physiological (Lillywhite et al. 2008a). Adaptation to saltwater and obtaining fresh water were key problems.

Few animals can maintain water balance relying on dietary and metabolic water alone. Most require sources of fresh water for drinking. The evolutionary transitions from terrestrial or freshwater to marine systems frequently

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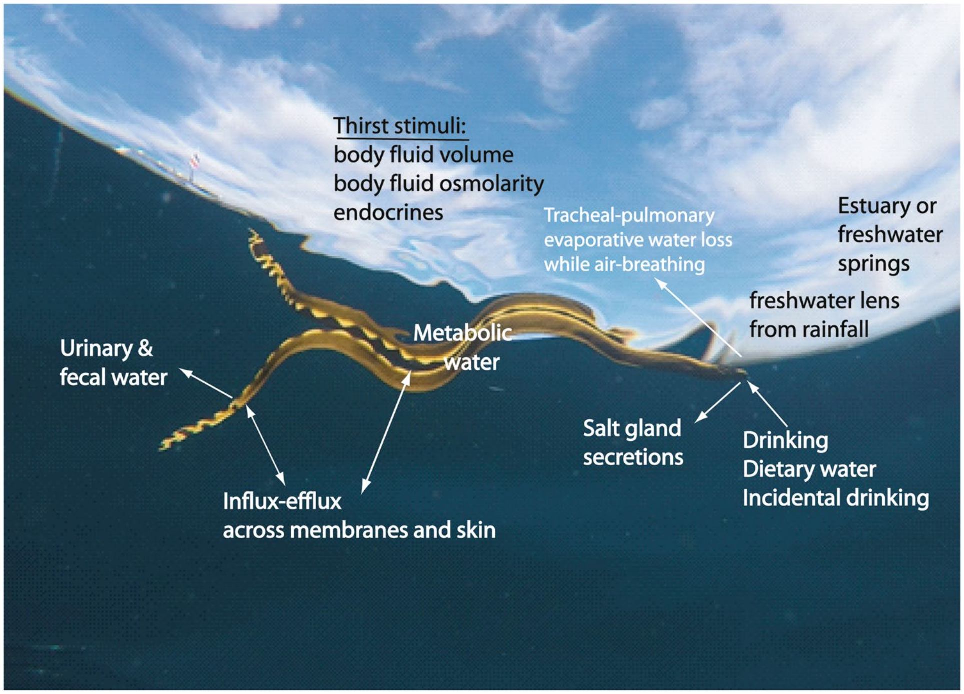

Fig. 1 Pathways of water exchange between a yellow-bellied sea snake (*Hydrophis platurus*) and surrounding ocean. The snake is seen from below and is floating on the surface of the ocean in the Golfo de Papagayo, Costa Rica, shown here to represent a generalized marine vertebrate. Routes of water exchange are shown in white font in the lower half of the illustration, whereas black font above indicates the stimuli for thirst and the potential sources of fresh drinking water. Photograph by Mark Sandfoss

involved forms that were associated with estuarine habitats, and thus, ancestral marine vertebrates had access to fresh water (Kelley and Pyenson 2015; Takei 2015; Cooper et al. 2016; Houssaye and Fish 2016; Lillywhite et al. 2017). Hence, the adaptive radiations to a fully marine existence were constrained by the need for fresh water and the capacity of various taxa to adapt their physiology to reliance on sources of water other than free drinking water. Drinking seawater or freshwater can influence the distribution and phenotypic characteristics of animals (Wolcott and Wolcott 2001).

While there is a robust literature concerning the physiological elements of osmoregulation in animals, relatively little information is available related to drinking behaviors and ecology associated with acquisition of free water in the environment, especially for marine species. Here, we review what is known concerning this subject, with an emphasis on behavioral acquisition of fresh water, largely in marine vertebrates. Although our focus is on marine forms, we include some information from other species that seems important for understanding the evolutionary transition from terrestrial, freshwater, or estuarine environments to the realm of the ocean.

Dehydration and thirst

The total body water of vertebrates expressed as a percentage of body mass ranges generally from 65 to 70% in endothermic mammals and birds, from 70 to > 80% in amphibians and reptiles, and from 63 to > 75% in fishes (Thorson 1961, 1964, 1968; Takei 2000). The responses to dehydration vary among different taxa, but generally the responses are quicker in endotherms than in ectotherms. Dehydration is actually a complicated process that can be evaluated in terms of changes in total body water, extracellular compartments including blood volume, and intracellular dehydration. Changes in each compartment may involve different signaling mechanisms that induce thirst and drinking. These include, but are not limited to: volume receptors generally localized within the cardiovascular system (heart atrium and veins) or, in birds, the extravascular extracellular compartment; plasma sodium concentration or osmolarity affecting osmoreceptors in the hypothalamus and possibly other sites; Angiotensin II (AII) and atrial natriuretic peptide (ANP)—released in response to hypovolemia and increased plasma osmolarity—stimulating thirst centers in the forebrain or, in fishes, the medulla oblongata; and actions of antidiuretic hormones that variously affect water balance and indirectly thirst and drinking (Takei 2000).

The route of ingesting water, or drinking, differs among species and habitats. Characteristically, we are accustomed to regard drinking to involve an oral mechanism that incorporates conscious regulation of the esophageal sphincter in terrestrial tetrapods. However, amphibians do not drink by mouth but cutaneously, absorbing water across the skin. This usually involves a specialized thin patch of pelvic integument in anurans (Fig. 2) (Bentley and Yorio 1979; Hillyard et al. 1998). In fishes, the surrounding water enters the esophagus by relaxation of the esophageal sphincter, and

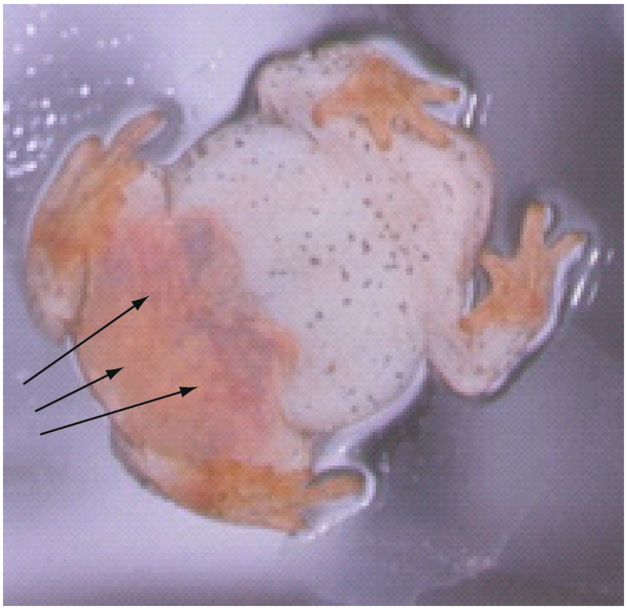

Fig. 2 Underside of the desert anuran *Bufo punctatus*, with arrows pointing to the reddened pelvic skin that is termed 'seat patch.' The reddened skin in this animal illustrates a 'water absorption response' in which blood flow to the thin ventral seat patch increases under hormonal influence to enhance uptake of water from a wet substrate, against which the animal presses the abdominal and pelvic skin. Photograph by Stanley Hillyard

stenohaline marine fish do not seem to consciously regulate the actions of the sphincter. In many aquatic animals, the source of water is a *fait accompli,* because the medium surrounds them. Terrestrial animals have specialized morphology and behaviors in various species that assist the acquisition of water in the environment. Examples include condensation of water onto the skin (Lasiewski and Bartholomew 1969) and collection of rain water that moves across the skin toward the mouth by capillary action in some desert lizards (Comanns et al. 2017).

Fishes

Teleosts

Marine fishes face the problem of losing water to the surrounding sea while gaining salts across permeable membranes, especially the gills that are irrigated by a buccopharyngeal pump and constantly exposed to seawater (Krogh 1939; Evans 2008, 2010). Marine teleosts face a hyperosmotic environment as their blood and extracellular fluids are ~ 30% of osmolarity found in seawater. Thus, without regulation of water input, marine teleosts tend to be dehydrated and salt-loaded, depending on the water and ionic permeabilities of gill epithelia. Freshwater teleosts have it the other way around.

Homer Smith first proposed that marine teleosts drink seawater to replace water that is lost osmotically, and the excess salts ingested with seawater as well as acquired by diffusion were excreted (Smith 1930). Evidence for drinking was based on use of the volume marker phenol red, which became concentrated in the gut, indicating that much of the water was absorbed across the gut epithelium. These and pioneering studies by August Krogh and Ancel Keys led to the basic model of osmoregulation in teleost fishes that is accepted today. The fundamental summary of the model is that teleost fishes are hypo-osmotic to seawater; oral ingestion of seawater balances osmotic water losses; uptake of water and NaCl in the gut provides the required water; renal and rectal excretion removes divalent ions; and branchial excretion removes excess NaCl (Smith 1932; Evans 2008). It was further shown that sodium chloride secretion by the gills is an active process and dilutes the internal medium.

Water balance has been investigated for numerous species of fish including eels, anglerfish, sculpin, goosefish, trout, flounder, lungfish, killifish, salmon, and numerous others. Although fewer than 0.5% of more than 26,000 species of teleosts have been investigated, we have some knowledge of water balance for both stenohaline and euryhaline species. The fundamental assumption that currently appears in many textbooks is that marine fishes (usually implied as teleosts) drink surrounding seawater to maintain water balance. In contrast, freshwater fishes are constantly invaded by osmotic influx of water and have no need to drink fresh water. Euryhaline species that migrate between fresh water and seawater are stimulated to drink only in seawater. They scarcely drink in fresh water and constantly drink in seawater (Takei 2000). Stenohaline fish that remain in either environment do not have need to regulate drinking.

Kobayashi et al. (1983) studied drinking in 20 species of freshwater fishes and found that seven species drank water like marine species of fish, and the remaining species did not drink. Hence, some freshwater fishes drink fresh water, although the reason is not clear. Moreover, these same authors found that of 17 species of marine fishes tested, 11 drank seawater, but three species did not, and in another three species, drinking of seawater was minor and equivalent to freshwater drinking by fishes in fresh water. Thus, drinking by fishes, including marine species, is more variable and complex than one might have supposed based on textbook information (see also Perrott et al. 1992).

Drinking also varies across life stages. Salmon smolt drinks seawater, while younger life stages cannot survive in seawater (Talbot et al. 1982; Potts et al. 1970). Brown trout late alevins and fry also could not survive in seawater (Talbot et al. 1982), although rainbow trout have been shown to adapt to seawater (Bath and Eddy 1979), and this difference may vary between species of trout. Another teleost, the Atlantic cod (*Gadus morhua*), is stenohaline, and its larvae have been found to increase drinking beyond that of adult fish, while their yolk sac is absorbed until leveling off to adult levels (Mangor-Jensen and Adoff 1987).

The rate of water uptake in adult marine teleosts is about 9.5% of body weight/h, yet this varies considerably depending on species (Smith 1930; Mangor-Jensen and Adoff 1987). One study from Bath and Eddy (1979) discovered that freshwater-adapted euryhaline rainbow trout (*Salmo gairdneri*) increased drinking response immediately after rapid placement in seawater, which then decreased after 6–8 h. The upper limit for trout was described as 2 days of survival in full-strength seawater, but most fish were able to adapt within a week and a half in two-thirds strength seawater. Salmon smolt, however, a related euryhaline fish, could adapt to rapid transfer (Potts et al. 1970). Salmon alevins also survived transfer to salty water longer than did trout (Talbot et al. 1982). These differences even among closely related species suggest a wide diversity of tolerances to salinity.

The mechanisms by which fishes and other vertebrates internally regulate water and ionic balance involve the renin-angiotensin system (RAS). Marine-dwelling teleosts have a renin system remarkably like that found in mammals; however, fish do not respond to an activation of thirst in the forebrain, like mammals, but to a hindbrain-stimulated swallowing reflex (Takei 2000). The sensitivity of this system varies interspecifically, even within clades. The RAS frequently regulates blood pressure and thirst, with the angiotensin hormone being dipsogenic and inducing drinking in multiple species.

Whether the RAS system stimulates drinking behavior and has other roles in osmoregulation has been explored extensively. AII induces drinking in both seawater-adapted and freshwater-adapted killifish (*Fundulus heteroclitus*), whereas its competitive inhibitor P-113 suppresses drinking in saltwater-adapted or exposed killifish (Malvin et al. 1980). While the subsequent body of research supports the conclusions of an active RAS system, the exact mechanisms remain unclear. A study by Beasley et al. (1986) tested two stenohaline marine species, the winter flounder (*Pseudopleuronectes americanus*) and long-horned sculpin (*Myoxocephalus octodecemspinosus*), and they found that AII and hemorrhage stimulated drinking; however, unlike the previous study by Malvin et al. (1980), exogenous enzyme inhibitors did not suppress drinking. Balment and Carrick (1985) found that flounder (*Platichthys flesus*) increased drinking with increasing plasma osmotic and chloride concentrations, although the seawater-adapted fish increased drinking moreso than those that were adapted to fresh water. The data suggested that plasma osmotic conditions may contribute to drinking behavior. An antidipsogenic agent was successful in suppressing some drinking response (Balment and Carrick 1985). Although there are variations in results of these studies, strong evidence of an RAS system persists. The environment of each population of fish, the type of AII, sample size, and even technique may influence the results, as each of the mentioned studies used varying species, populations, and techniques. The drinking mechanism in marine and other fishes needs to be further explored in different populations of the same species as well as a larger breadth of species in context of ecology.

In the study by Kobayashi et al. (1983) mentioned earlier, it was found that AII stimulated drinking in euryhaline species but not in stenohaline freshwater or marine species. The conclusion from these studies was that AII does not stimulate drinking in species that live permanently in seawater or freshwater habitats where osmotic changes rarely occur, but, in contrast, AII induces drinking in species that encounter dehydration by virtue of entering waters of higher osmotic concentration than those in which they typically reside (Kobayashi et al. 1983).

The exact stimulus that induces drinking in teleosts is not clear, and multiple mechanisms may be operative with diversity among species. Some studies cite blood volume, or a barometric sensor, as the stimulus (Beasley et al. 1986), whereas a study on seawater-adapted eels (*Anguilla japonica*) by Ando and Nagashima (1996) hypothesized that intestinal Cl^- directly depresses drinking, and intestinal Na^+ stimulates drinking when Cl^- levels diminish. Therefore, sensing of blood volume would be unlikely as the drinking mechanism is faster than changes in blood volume. This is in direct contrast to the results from Beasley et al. (1986), who found that hemorrhaging can stimulate drinking in the stenohaline winter flounder (*Pseudopleuronectes americanus*) and longhorn sculpin (*Myoxocephalus octodecemspinosus*). Hemorrhaging did not affect drinking rates in three freshwater fish (Beasley et al. 1986), which suggests that evolutionary adaptations to varying environmental salinities could alter drinking behavior. Another study by Ando et al. (2000) supported the hypotheses that hemorrhage and plasma hyperosmolarity depress drinking, in contrast to the Ando and Nagashima (1996) study. The Ando et al.'s (2000) study also supported the dipsogenic effects of AII of eel, as well as histamine, serotonin, isoproterenol, acetylcholine, carbachol, and a mammalian substance P. When the eels were treated with captopril, a blocking agent for AI, hemorrhage did not alter drinking rates (Ando et al. 2000), suggesting that hypovolemia affects drinking rates through the RAS system.

Thirst in response to hypovolemia is closely related to AII in plasma. Renin is secreted in response to hypovolemia, and inhibitors of the RAS system inhibit drinking that is normally induced by hypovolemia (Takei 2000). An intestinal antidipsogenic, eel intestinal pentapeptide (EIPP), may be the link between these contrasting studies, as this antidipsogenic peptide could explain the reduction of drinking via the intestinal Cl^- content. ANP also is an important hormone involved in various pathways that promote seawater adaptation in the eel where it also acts to inhibit drinking (Takei 2000). In some species, it is unclear whether drinking of seawater is induced by thirst or sodium (Takei et al. 1979). Eels start drinking in seawater before any increases of internal osmotic pressure and are thought to sense Cl^- ions by receptors in the buccal region that possibly stimulate drinking (Hirano 1974).

Finally, buccal drying has been shown to motivate drinking in the amphibious mudskipper, a response that is similar to 'dry mouth' that can be involved in regulation of thirst in terrestrial mammals. Losses of buccal water on land by AngII-induced swallowing, by piercing holes in the opercula, or by water-absorptive gel placed in the buccopharyngeal cavity motivated mudskippers to move to water for refilling (Katayama et al. 2018). Hence, local sensation has an important role in the drinking behavior of the mudskipper. The role of local stimuli in drinking behaviors of fishes and other vertebrates has often been overlooked because of a paradigm of more 'general thirst' involving the potent effects of hormones. In summary, the exact mechanisms for drinking behavior in teleosts remain unclear, despite the discoveries of the RAS, osmotic/ionic, and other stimuli.

Elasmobranchs

Elasmobranchs are largely marine and generally considered to be relatively stenohaline, with euryhaline and freshwater species being the exceptions. Out of ~ 1100 known species, ~ 170 (belonging to 34 families) are reported to occur in either fresh water or estuarine waters (Martin 2005). Osmoregulation by sharks in seawater differs from that of teleosts. They use organic osmolytes (urea and trimethylamine oxide) to elevate plasma osmolality to values usually slightly above seawater, and sodium and chloride have a lesser role as the principal extracellular osmolytes. Thus, elasmobranch fishes are typically isosmotic or slightly hyperosmotic to surrounding seawater, primarily attributable to retention of urea (Hammerschlag 2006; Ballantyne 2016). Only the coelacanth among other fishes accumulates urea and TMAO to maintain isosmotic plasma similarly to elasmobranchs (Takei 2000).

As a consequence of this manner of osmoregulation, it was thought that elasmobranch fishes had no requirement for drinking insofar as osmotic water loss was absent or minimal. However, marine elasmobranchs do have the propensity to drink in response to changing conditions of the environment (Hazon et al. 1989, 1997), and physiological actions of the RAS are similar to that in other fishes. The administration of homologous angiotensin II produces a dose-dependent response in drinking rate, and the smooth muscle relaxant papaverine has a potent dipsogenic effect, increasing basal drinking levels almost 20-fold (Anderson et al. 2001). The effect of papaverine is almost certainly secondarily attributable to a reduction of blood pressure and subsequent stimulation of the endogenous RAS.

Although marine elasmobranchs are not characteristically regarded to drink seawater (and the same could be assumed for coelacanths), euryhaline species drink upon returning to more concentrated seawater as with teleosts (Anderson et al. 2007; Evans and Claiborne 2009). In all sharks, the rectal gland is the principal site of NaCl secretion (Epstein and Silva 2005), the kidneys retain urea, and TMAO (Cohen et al. 1958; Janech et al. 2006), and the gills are the site of acid–base regulation as well as salt uptake in dilute seawater or fresh water (Hammerschlag 2006; Evans and Claiborne 2009; Reilly et al. 2011).

Cyclostomes

The hagfish, representing the most primitive extant vertebrate, is unique in maintaining the ionic concentration of its plasma nearly identical to that of seawater. Hence, these animals osmoconform, and their internal osmolarity matches that of surrounding seawater. There appears to be no need to drink, and early studies were equivocal whether hagfish drank or not. Glover et al. (2017) concluded that hagfish do not drink based on the studies of markers. These authors also documented hagfish having high water permeability which confers rapid osmotic equilibration when exposed to osmotic perturbations.

Amphibians

No amphibian has permanently adapted to a marine environment, but several species of anurans inhabit coastal areas where they are exposed to bodies of water having moderate salinity. These include the Green toad (*Bufo viridis*) of Europe and the Middle East and several species of frogs in tropical southeast Asia (Shoemaker et al. 1992). Perhaps, the better known example is the Crab-eating frog (*Fejervarya cancrivora*) that inhabits mangroves and was first studied physiologically by Gordon et al. (1961). These frogs accumulate urea somewhat like elasmobranchs, so they are isosmotic or hyperosmotic to water which they might encounter. The skin is quite permeable, similar to that of many other frogs, so water balance is most likely achieved by avoiding dehydration (staying out of direct sunlight, etc.) and absorbing hypo-osmotic water when available from rainfall. However, nothing is known concerning deliberate cutaneous 'drinking' per se in terms of either patterns or strategy.

These and other frogs (e.g., Indian rice frog, *Fejervarya limnocharis*) produce tadpoles that develop in brackish coastal rock pools and osmoregulate using features similar to those of marine teleosts (Wu and Kam 2009), perhaps including drinking of hypersaline water (Shoemaker et al. 1992). Several studies have shown that tadpoles that are tolerant of brackish water have limited osmoregulatory ability in hyperosmotic environments, and acclimation enhances responses that enable tadpoles to complete development to metamorphosis (Wu et al. 2013). It is noteworthy that tadpoles of *F. cancrivora* can tolerate up to full-strength seawater and regulate internal osmolarity below that of the medium at salinity ≥ 40% sea water (Gordon and Tucker 1965; Shoemaker et al. 1992). The ability to maintain body fluids slightly hyperosmotic to the environment appears to mitigate the dehydration of tadpoles in high salinity (Wu et al. 2013).

Because amphibians typically ‘drink’ by absorbing water across the skin (Fig. 2), it is difficult to separate either reflexive or conscious drinking from passive movements of water across the skin of frogs or tadpoles living in contact with coastal brackish waters. Other contexts for drinking in amphibians include uptake of water from moist soils in desert species, and drinking from rainfall by some arboreal species of ‘waterproof’ frogs living in arid habitats (Shoemaker et al. 1992).

Non-avian reptiles

Crocodilians

There are three major lineages of extant crocodilians, and the large majority of species associate with freshwater systems. However, several species enter estuarine or marine habitats and possess lingual salt glands. *Crocodylus porosus* of the Indo-Pacific region and *C. acutus* of the Caribbean, Central, and South America have been found in the open ocean. *Caiman latirostris* occurs in estuaries in southern Brazil. The American alligator, *Alligator mississippiensis*, also enters coastal brackish waters and may enter the ocean to forage (Fig. 3) (Nifong and Silliman 2017). Whatever might be the habitat, crocodilians maintain body fluid concentrations at about 1/3 seawater, similar to that in most other vertebrates.

Crocodilians are especially prone to expose epithelial areas of the mouth to external water when feeding, and ‘incidental drinking’ is thought to be a major source of salt and water intake (Dunson 1985; Mazzotti and Dunson 1989). True drinking (without food intake), however, is an important part of osmoregulation in semi-marine crocodilians. Laurence E. Taplin (1984) first investigated the drinking behavior of the saltwater crocodile (*Crocodylus porosus*). The name of this animal can be misleading, for it largely frequents estuarine habitats, and periodically ventures into fresh or saltwater. Taplin found that *C. porosus* drinks fresh water, but does not drink saltwater. He also concluded that this species drinks facultatively in fresh water to remain in water balance, largely because of low skin permeability and inadequate cutaneous influx to offset urinary losses related to excretion of waste products. In marine habitats, saltwater crocodiles undergo losses of body water, largely attributable to cutaneous and buccal efflux, but they do not drink seawater.

Fig. 3 American alligator, *Alligator mississippiensis*, in coastal salt marsh and beach habitats on Sapelo Island, Georgia (typical salinity = 20–36 ppt). The lower inset shows an alligator in a den excavated in an upland freshwater wetland where the animal can access fresh water and seek thermal refuge. Photographs by James Nifong

Saltwater crocodiles are able to discriminate seawater from fresh water, and Taplin (1984) suggested that fine-tuned drinking behavior enables the species to inhabit a wide range of salinities in which it is known to occur. However, Mazzotti and Dunson (1989) concluded that access to fresh water is not necessary for relatively long periods in marine or brackish waters, although there is considerable anecdotal evidence for facultative drinking when saltwater crocodiles return to land following prolonged sojourns at sea. In American alligators, multiple abiotic factors (e.g., relative humidity, temperature, and precipitation) appear to be key variables that influence the duration of foraging trips between fresh and salt or brackish waters (Nifong and Silliman 2017). Although American alligators do not have functional salt glands, they also engage in relatively long forays into marine environments (Fig. 3).

Theoretically, it is more difficult for smaller animals, e.g., hatchlings, to conserve water or sodium than for an adult (Mazzotti and Dunson 1989). In laboratory studies, freshly hatched and unfed *C. porosus* lost weight and died more rapidly in salt water than in fresh water, suggesting that these hatchlings were dependent on fresh water for survival (Magnusson 1978). Older (> 30 days) hatchlings and size classes were thought to no longer need fresh water. Taplin (1984) noted that larger saltwater crocodiles stayed for long periods of time without access to freshwater or a reliable food source if overland and hatchlings were hypothesized to drink diluted water from rainfall (Mazzotti and Dunson 1989). Speculations about a freshwater requirement of young or hatchling crocodilians are, however, questionable. Hatchlings of *Crocodylus porosus* in salt water do not appear to use potentially accessible freshwater springs, even when the fresh water was within the apparent home range (Grigg et al. 1980). The authors of this study concluded that hatchlings of *C. porosus* can survive and grow in hyperosmotic saltwater without drinking freshwater.

The salt glands of crocodilians that inhabit brackish or saltwater have limited capabilities, and so drinking fresh water when available allows maintenance of homeostasis when in hyperosmotic habitats (Jackson et al. 1996). Estuarine crocodilians will not drink seawater, and the estuarine broad-snouted caiman (*Caiman latirostris)* will not drink hyperosmotic water (Grigg et al. 1998). Two species of freshwater alligatorids, the American alligator (*Alligator mississippiensis*) and caiman (*Caiman crocodilus*), were found to drink fresh water and hyperosmotic sea water indiscriminately, whereas an estuarine population of the former drank only fresh water (Jackson et al. 1996). It was concluded that discrimination of salinity is determined, at least in part, by habitat. However, three species of estuarine crocodiles (*C. porosus*, *C. acutus*, and estuarine populations of *C. johnstoni*) drink fresh water but not hyperosmotic sea water even when severely dehydrated (Mazzotti and Dunson 1984; Taplin 1984, 1988; Taplin et al. 1993). These observations suggest that, in crocodilians, the ability to discriminate fresh water from seawater is influenced by phylogeny as well as by ecology (Jackson et al. 1996).

There is limited information known about the endocrine control of thirst and drinking in crocodilians. Compensatory drinking behavior exhibited by the Nile crocodile appears to involve the RAS and interrenal steroidogenesis and thus may play an integrative role in the fluid homeostasis of crocodilians (Balment and Loveridge 1989). With respect to the sensory detection of salinity of water, Jackson and Brooks (2007) have proposed that sensory organs present on the post-cranial scales of crocodiles (but not alligatorids) flatten when exposed to increased osmotic pressure, and this is interpreted as a chemical stimulus that conveys information about the salinity of water in the animal's environment. When contact between the skin and a surrounding sea water solution was blocked, crocodiles (*C. porosus*) lost their ability to discriminate among salinities.

Turtles

Turtles are one of the older groups of reptiles, with earliest forms dating back some 220 million years (Li et al. 2008). There are more than 350 species living today, and of these, only seven species are entirely marine except for ovipositing eggs on beaches. Sea turtles constitute a single evolutionary radiation, with five lineages being traced back to 105 million years (Kear and Lee 2006). Thus, sea turtles have had a long association with seawater.

Sea turtles are highly migratory and their ranges span the globe. They are found in tropical and temperate waters throughout the world and migrate long distances between nesting and feeding grounds, some more than 2000 km. Sea turtles have varied diets, some being strictly or largely herbivorous, while others prey on marine invertebrates (e.g., leatherbacks, *Dermochelys coriacea*, feed on jellyfish). The foods of sea turtles all contain salts at concentrations similar to seawater, and these reptiles cannot produce a urine that is concentrated beyond the osmolarity of their blood plasma. Excess salts are secreted via paired lachrymal salt glands (Wyneken 2001). Leatherback sea turtles, *Dermochelys coriacea*, are obligate feeders on soft-bodied jellyfish and have larger salt glands than other species of sea turtles (Wyneken 2001; Davenport 2017). These turtles may feed almost continuously and take in large quantities of salt, both in prey and in incidental drinking during ingestion of prey (Davenport 2017). Excess salt is secreted by the salt glands.

Young sea turtles are hatched on beaches and are thus susceptible to dehydration in air as well as in seawater. Reina et al. (2002) studied salt and water regulation in hatchling leatherback sea turtles and found they dehydrated more rapidly on land than in seawater. Their experimental work with these hatchlings also demonstrated that turtles osmoregulated effectively by drinking seawater. Hatchlings tolerated significant changes in internal composition and achieved internal salt and water balance by drinking and subsequent function of salt glands when in seawater. Other studies have demonstrated that hatchling sea turtles gain mass rapidly in seawater, despite not eating during the same period (Bennett et al. 1986; Marshall and Cooper 1988).

Other sea turtles also drink seawater and osmoregulate in the ocean with gross similarity to marine fishes, but with excess ingested salts being eliminated by the salt glands. The possibility that sea turtles might drink seawater was proposed more than 50 years ago by Holmes and McBean (1964) who demonstrated substantial drinking in juvenile *Chelonia mydas* using the phenol red technique. Preliminary tests by Taplin (1984) also demonstrated that juvenile loggerhead turtles, *Caretta caretta*, will drink seawater, although earlier, it was generally thought that marine reptiles did not drink seawater, and this hampered the understanding of osmoregulation of sea turtles. Bennett et al. (1986) further showed that drinking seawater enabled hatchling sea turtles (*C. caretta*) to avoid and recover from dehydration. Hatchlings dehydrate rapidly between hatching and reaching the sea, and metabolism of yolk is insufficient to maintain water balance. Thus, drinking seawater to rehydrate after hatching suggests that incidental ingestion and drinking of seawater are important in marine turtles.

Sea turtles, including hatchlings, occasionally enter rivers or lagoons where they potentially might drink fresh water. Adult Kemp's ridley sea turtles (*Lepidochelys kempii*) adapted to seawater increased drinking when exposed to fresh water in the laboratory, and the freshwater consumption increased by about 50% (Ortiz et al. 2000). The increased consumption of fresh water resulted in hemodilution and a lowering of plasma osmotic and ionic concentrations, but did not change levels of adrenocorticoids. The latter observation was interpreted as a muted, delayed, or masked stimulation of the release of aldosterone and corticosterone. The stimulus or function of increased drinking is not clear, but prolonged exposure to fresh water without supplements of salts will diminish the osmoregulatory capacity of these turtles (Ortiz et al. 2000).

Because sea turtles can acquire water by drinking seawater, there seems to be no need for turtles to drink fresh water (with exception of terrestrial hatchlings) and, therefore, migrate to estuaries for reasons related to water balance. There is no information concerning the possibility of sea turtles drinking from freshwater lenses formed by rainfall on the ocean (Fig. 4; see section on sea snakes). Estuarine and euryhaline turtles are of interest in these contexts. There are some studies of blood chemistry that suggest adult sea turtles can become dehydrated during the nesting period, and that the requirement for depositing water in eggs limits the inter-nesting interval of females (Price et al. 2019).

Fig. 4 A pair of sea turtles, *Chelonia mydas*, floating on the surface of the ocean in the Golfo Papagayo, Costa Rica. Sea turtles spend variable periods of time at the ocean's surface and obviously could drink from freshwater lenses formed by intense rainfall, as do sea snakes. No one evidently has observed the behavior, and the possibility that sea turtles drink fresh water in the open ocean remains unknown. Photograph by H.B.L.

There are about eight species of turtles that occur in brackish waters, including mangrove and painted terrapins (*Batagur* spp.), pig-nosed turtles (*Carettochelys* spp.), and the giant softshell (*Pelochelys cantori*)—all with largely coastal ranges in parts of southern Asia (Rasmussen et al. 2011). While some ranges of these turtles include freshwater habitats, they will enter brackish waters of estuaries and even full seawater temporarily.

The diamondback terrapin, *Malaclemys terrapin*, is the only exclusively brackish water turtle in the world. It is a species of emydid turtle that inhabits saltmarsh, tidal creeks, and estuarine habitats along the eastern coastline of the United States. At various times, this turtle can be found in marine habitats and full-strength seawater which it tolerates quite well. It is adapted to seawater in having low permeability to salt and water, and a lachrymal salt gland (Dunson 1970, 1985). Nonetheless, diamondback terrapins cannot survive indefinitely in seawater without access to fresh or low-salinity water to maintain hydration. It was shown by Davenport and Macedo (1990) that terrapins can detect vibrations related to rainfall and leave seawater to drink from thin films of water on nearby substrata, ingesting as much as 14% of body mass during drinking bouts of 10–12 min. These turtles can arch the neck in such a manner that facilitates drinking stretching the neck downwards to drink from thin films or pools (Fig. 5) (Davenport and Macedo 1990), or stretching the neck upwards to collect rainfall directly (Bels et al. 1995). The structure of the lower jaw and mouth

Fig. 5 A hatchling diamondback terrapin, *Malaclemys terrapin*, drinking from a dish of fresh water in the laboratory. The dish of fresh water is elevated at one end of an aquarium that is filled with 5 L of saline water. The terrapin is able to access the fresh water by leaving the saline water and crawling up a ramp to the suspended platform and dish. Photograph by Elizabeth A. Ashley

Fig. 6 A Mojave Desert tortoise, *Gopherus agassizii*, drinking from a small rock pool following a rainstorm. USGS photograph by J.S. Mack

permits the animal to drink from films of water as thin as 1–2 mm. Similarly, specialized postures involving an arched neck, elevated posterior carapace, and forelimbs direct water toward the mouth in some species of tortoises living in xeric terrestrial habitats (Fig. 6) (Auffenberg 1963).

Hatchling or smaller terrapins are less tolerant of seawater than adults. If there is no access to fresh water, terrapins lose appetite (Davenport and Ward 1993) and cannot grow well in 100% seawater (Dunson 1985). Yet, adult terrapins will nest and oviposit in locations that are adjacent to full seawater. Terrapins occur in marshes where hatchlings and juveniles are routinely exposed to high salinities (Dunson 1985). The hatchlings can discriminate fresh water from salt water, and they may cease feeding and exploit rainfall as a periodic source of fresh water (Dunson 1985; Davenport and Macedo 1990; Davenport and Ward 1993; Davenport and Magill 1996; Holliday et al. 2009). The hatchlings have a higher water content than adults (77% vs. 64.5%), but nonetheless dehydrate in full seawater where salt is ingested largely by means of 'incidental drinking' (Dunson 1985). Terrapins rely on drinking fresh or brackish water to remain in water balance, unlike sea turtles. This seems at least partly related to the fact that the salt gland of terrapins secretes sodium at rates that are lower than those of sea turtles (Dunson 1976). Recent studies by Ashley et al. (unpublished) have demonstrated that (i) exposure of hatchling terrapins to environments of high salinity promotes learning by terrapins to utilize periodically available sources of fresh water (Fig. 5), and (ii) limited access to fresh water can reduce growth and possibly increase mortality.

Lizards

Various species of lizards, and especially those inhabiting islands, live in intertidal habitats where they may feed on salty prey and experience dry conditions of habitat with limited rainfall (Fig. 7). For example, intertidal species of the lizard *Uta* feed on intertidal isopods that may have salt concentrations higher than seawater, and this has been interpreted as causally related to hypertrophy of salt glands in these lizards (Grismer 1994). A number of lizards use resources from estuaries, intertidal or marine habitats, and they forage in the intertidal zone. Evidently, this is a behavior that is driven by pressures for resources or unsuitable inland habitat (Grismer 1994; Lillywhite et al. 2008a). However, only one saurian species has made a successful evolutionary transition to directly utilize resources in the ocean.

The marine iguana (*Amblyrhynchus cristatus*) of the Galapagos Islands is the most marine of lizards, but reproduces and basks on land where it is susceptible to terrestrial predators. Marine iguanas feed exclusively on marine plants, and they spend considerable time foraging in the ocean. They ingest considerable quantities of salt, largely by means of incidental intake of seawater and isosmotic algae. Excess salts are excreted via salt glands (Shoemaker and Nagy 1984). Seawater has been estimated to account for about 40% of the water intake of iguanas. However, dehydrated

Fig. 7 A marine iguana, *Amblyrhynchus cristatus*, shown perched in dehydrating conditions on a Galapagos island. Marine iguanas feed on marine plants and ingest considerable incidental seawater in the process. A smaller, insectivorous lava lizard, *Microlophus albemarlensis,* is perched atop the head of this individual. Drinking behaviors of both species are not known. Photograph by Dan Costa

animals without food or water for 8 days of fasting did not drink seawater, and the water ingested when animals fed on marine plants in the wild exceeded the content of the food. Thus, Shoemaker and Nagy (1984) concluded that marine iguanas acquire water from incidental ingestion during feeding and do not drink in the conventional sense. Marine iguanas perch on lava rocks where they are exposed to wind and tropical sun (Fig. 7). We are not aware of any observations to indicate that these lizards drink fresh water during periods of rainfall, but such behavior seems likely.

Marine snakes

All extant species of marine snakes are secondarily marine and represent multiple evolutionary transitions from terrestrial, freshwater, or amphibious species (Sanders et al. 2010, 2013). There are more than 100 species of marine snakes if estuarine species are included. These are represented by three species of file snakes (Acrochordidae), about 18 species of largely estuarine colubrids (Colubridae), more than 15 species of homalopsids (Homalopsidae), eight species of amphibious sea kraits (Elapidae: *Laticauda* spp.), and about 60 species of viviparous, entirely marine 'true' sea snakes (Elapidae: Hydrophiinae) (Pyron et al. 2013). The two lineages of sea snakes (*Laticauda* + Hydrophiinae) evolved from different terrestrial ancestors and adapted independently to marine life (Sanders et al. 2013). The hydrophiine sea snakes represent the most speciose group of marine reptiles and originated relatively recently, approximately 8–6 mya (Sanders et al. 2008; Lee et al. 2016). They range widely in coastal and reef ecosystems in tropical and subtropical waters, and the pelagic species *Hydrophis platurus* (yellow-bellied sea snake; see Fig. 1) ranges from the tip of southern Africa across the Indo-Pacific to the western coastline of Central America (Rasmussen et al. 2011).

It was formerly believed that sea snakes drank seawater and eliminated excess salts via sublingual salt glands ('like other marine reptiles'). However, recent studies have demonstrated that (1) sea snakes do not drink seawater; (2) when dehydrated they drink fresh water to maintain water balance (Fig. 8); and (3) they dehydrate at sea during periods of drought (Lillywhite et al. 2008b, 2012, 2014a, b, 2015, 2019). Yellow-bellied sea snakes in offshore waters near Guanacaste, Costa Rica, potentially withstand as long as 6 months of drought and drink from freshwater lenses that form on the surface of the ocean when heavy rains begin after the end of the dry season (Lillywhite et al. 2014b, 2019). Following drought, these snakes were also shown to be in a low state of body condition and to have significantly lower total body water than conspecifics captured during the wet season (Lillywhite et al. 2014b). Logically, free-ranging snakes would not be in a dehydrated condition if they drank seawater.

Sea snakes have relatively high levels of body water, dehydrate slowly when in seawater, and have a relatively high tolerance of dehydration (Lillywhite et al. 2009, 2012, 2014a, b, 2015). File snakes, sea kraits, and sea snakes do not drink fresh water until they experience considerable loss of body water, and in some species, this deficit exceeds 20% of body mass (Lillywhite et al. 2015). Nonetheless, the requirement for fresh water influences the geographic distribution and abundance of marine snakes (Lillywhite and Ellis 1994; Lillywhite et al. 2008b; Lillywhite and Tu 2011; Brischoux et al. 2012; Udyawer et al. 2016).

Sources of fresh water available to marine snakes include precipitation on land, where amphibious sea kraits ingest water that is dripping from vegetation (Fig. 9) or accumulated in rock pools (Guinea 1991; Bonnet and Brischoux 2008), estuaries (Udyawer et al. 2016), freshwater springs (Lillywhite et al. 2008b), and freshwater lenses that form on the surface of the ocean during heavy rainfall (Lillywhite 1996; Lillywhite et al. 2014b, 2019). In the case of pelagic sea snakes, freshwater lenses may be the only source of fresh water in most circumstances (Fig. 1). Of course, some of these sources might involve water that is brackish to varying degrees. Laboratory studies of drinking in sea kraits demonstrate that they will consume dilute brackish water, but do not drink water that is more than 30% seawater (Lillywhite et al. 2008b), whereas the hydrophiine sea snake *Hydrophis platurus* will drink up to 50% seawater (Lillywhite et al. 2012). Across the various investigations cited herein, testing of hundreds of sea snakes revealed not a single one to drink full seawater. These findings imply that marine snakes have the ability to discriminate among waters of varying

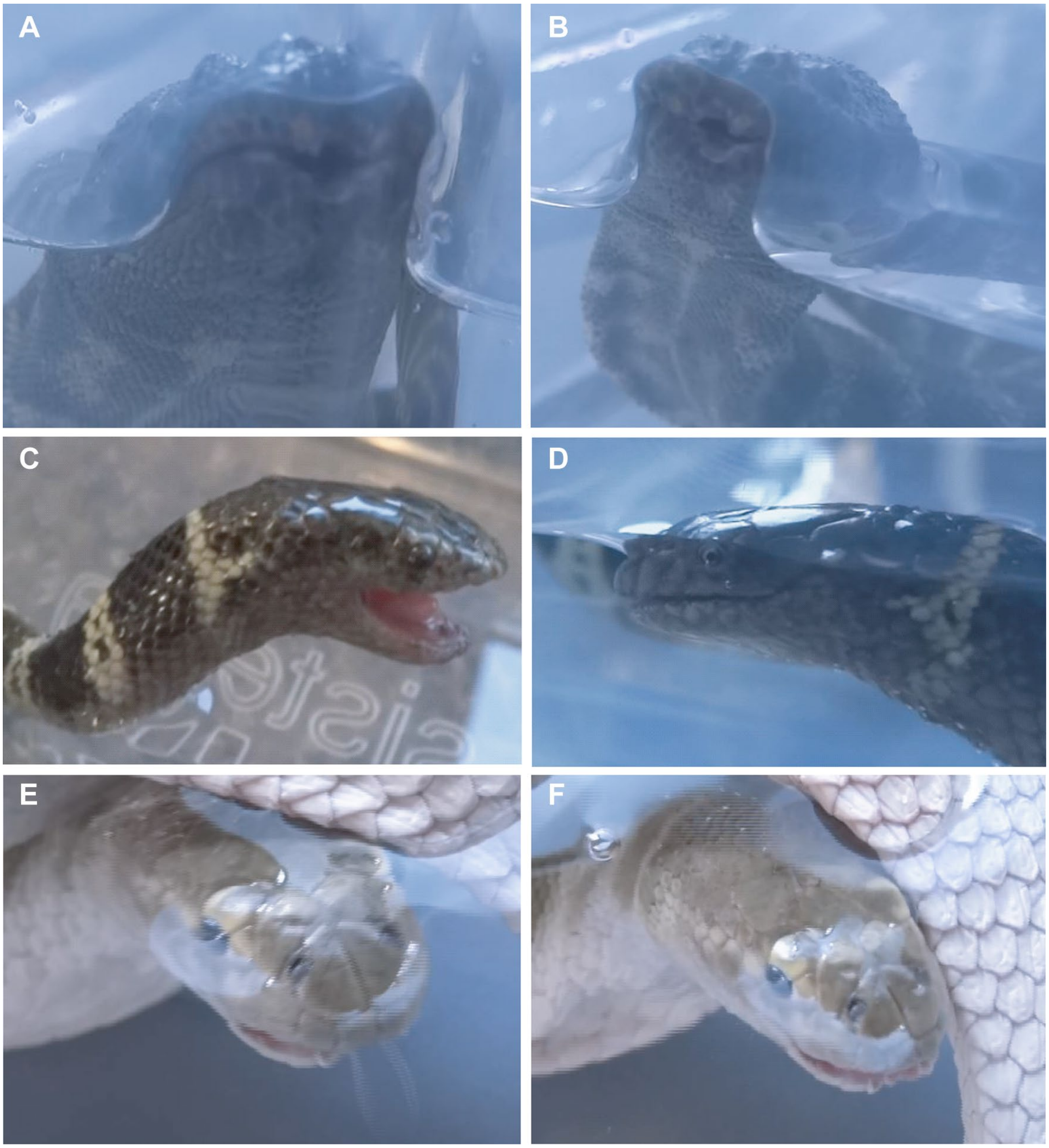

Fig. 8 Marine snakes drinking from surfaces of fresh water in the laboratory. **a**, **b** Little file snake, *Acrochordus granulatus*, from a marine population in mangroves near Cebu, central Visayas, Philippines. **c**, **d** Elegant sea snake, *Hydrophis elegans*, from a population near Weipa, Queensland, Australia. **e**, **f** Shaw's sea snake, *Hydrophis curtus*, from a population near Weipa, Queensland, Australia. Note that in most cases, the snake's head is elevated to drink from the very surface of the water. In photo **e**, note that the tynes of the tongue are protruded, which occurs between each act of swallowing, presumably as a sensory 'test' of water quality/salinity. Photographs by H.B.L.

salinity (Lillywhite et al. 2008b; Kidera et al. 2013). Coastal estuarine species of colubrid snakes do not ingest seawater, whereas 'freshwater' species ingest seawater and die as a result (Dunson 1980).

The question arises whether free water and metabolic water from prey can satisfy the water requirements of marine snakes. Theoretical considerations as well as data from studies of both desert and marine reptiles suggest that feeding alone without drinking does not contribute a net gain of water (Lillywhite et al., 2008b, 2014a, b; Wright et al., 2013; Murphy and DeNardo 2019). With respect to sea snakes, it appears that the requirements of water for digestion, excretion, and defecation outweigh the net water gains from digestion and metabolism of prey, which, in these snakes, are almost exclusively fish and impose an excretory nitrogen load. Hence, eating prey could actually exacerbate the dehydration associated with drought, instead of providing a benefit. This likely explains why

Fig. 9 Sea kraits drinking water following rainfall at New Caledonia. **a** *Laticauda saintgironsi* drinking rainwater from wetted vegetation. **b** *Laticauda colubrina* will drink fresh water similarly from a pipette. Photographs by Xavier Bonnet

some marine snakes (*Acrochordus granulatus*) in captivity cease feeding once they become partially but not critically dehydrated (Lillywhite et al. 2014a); pelagic sea snakes (*Hydrophis platurus*) captured during seasonal drought are thirsty and dehydrated in spite of feeding (Lillywhite et al. 2014a, b); and several species of snake increase consumption of fresh water following ingestion of food (Lillywhite 2017). Further research is needed to better understand the interplay of feeding and drinking in context of homeostasis of body water.

Previous assumptions concerning sea snakes drinking seawater were likely based in the fact that sea snakes possess salt glands. However, Dunson and Dunson (1974) described the sublingual salt gland of sea snakes as being small with comparatively low rates of secretion. Thus, it seems that while salt glands of sea snakes might assist water and ion balance, they evidently cannot by themselves enable sea snakes to avoid dehydration by drinking seawater (see Lillywhite et al. 2008b). While having at least a limited role in maintaining water balance, it seems likely that the salt glands of sea snakes are more important for ionic regulation compared with fluid homeostasis.

Almost nothing is known concerning the neuroendocrine control of drinking in marine snakes, but dehydration thresholds for drinking are greater than generally known in terrestrial snakes. The adrenocorticoid response appears to be delayed or absent insofar as sea snakes exposed to a hypo-osmotic environment did not show an increase in aldosterone (Duggan and Lofts 1978). The RAS does seem to be active in terrestrial snakes (Kobayashi et al. 1979).

Understanding the freshwater requirements of marine snakes is important for understanding their global distribution and association with habitats where fresh water is abundant (Brischoux et al. 2012; Lillywhite et al. 2008b; Lillywhite and Tu 2011). Attributes related to drinking and water balance are also important for assessing the probable causes and extent of recent declines and extinctions of marine snakes at multiple global hotspots (Goiran and Shine 2013; Guinea 2013; Lukoschek et al. 2013).

Marine birds

Recent opinions now estimate that there are some 19,000 species of birds living at present (Barrowclough et al. 2016). Of these, roughly 500 species are marine, belonging to families that are considered to be "seabirds." Seabirds associate with the oceans in various ways, and many roam far out to sea. They can be found hundreds of miles from land and may spend years at sea without returning to land. Some marine birds, such as penguins, have become highly capable swimmers and spend all or most of their non-breeding time in seawater. The earliest seabirds evolved in the Cretaceous period, and modern families of seabirds evolved within the last 60 million years. Seabirds generally forage for food over long distances and they often migrate. Some seabirds such as albatross and petrels spend much of their lives at sea, while others venture into freshwater areas (Fig. 10). Long-distance migratory shorebirds (charadriiforms) are considered 'osmotic generalists', because they utilize wetlands and freshwater habitats during the breeding season and switch to marine habitats during winter or migration (Blakey et al. 2006; Gutiérrez et al. 2011).

Seabirds generally feed on marine prey—primarily fish, squid, and crustaceans—and they ingest incidental seawater; hence, there is need to handle large quantities of ingested salt, especially from crustaceans and other invertebrates. Discrimination of prey during feeding has been shown to be an important behavioral aspect of osmoregulation in some species (Troup and Dutka 2014). Like marine reptiles, the kidney of seabirds has limited capacity to excrete salts (up to about 1/2 the concentration of seawater) and cannot maintain water balance if seawater is ingested. Hence, a major part of ingested salt is excreted extrarenally by means of nasal salt glands that aid in the maintenance of water balance.

Fig. 10 Waved albatrosses (*Phoebastria irrorata*) in flight (top) and nesting in the Galapagos Islands (bottom). These birds will forage up to 100 km distance from where the chicks are hatched and feed largely on fish, squid, and crustaceans. Albatrosses consume salt in their food and excrete excess salts by nasal salt glands. Whether albatrosses drink seawater is unclear, but some species might not (Costa and Prince 1987). The waved albatross is a spectacular flyer and can soar over the sea for hours. Photographs by Dan Costa

The salt glands of birds are well studied, and they occur in terrestrial, non-marine birds as well as seabirds. In the former group, the salt glands are often inactive when supplies of fresh water are sufficient, yet they show remarkable phenotypic plasticity morphologically and physiologically, and they become active as a consequence of drinking saline water (Shuttleworth and Hildebrandt 1999; El-Gohary et al. 2013). The salt glands enlarge if exposure to hyperosmotic water is prolonged (Holmes 1975). The size of salt glands in seabirds is comparatively large and may also vary with ingestion of salt loads (Schmidt-Nielsen 1960). The Black beaked gull (*Larus marinus*) was demonstrated to process seawater equivalent to one-tenth of its body mass after just about 3 h (Schmidt-Nielsen 1960).

Ingestion of seawater increases plasma osmolality which, in turn, activates the secretion of excess salt through the salt glands (Holmes 1975). As in fish and mammals, the RAS has a key role in the osmoregulation of seabirds (Taylor 1977), but the exact pathways have not been studied in birds to the extent of some other vertebrates. Other hormones are linked to osmoregulation as well. Ingestion of salt water in birds stimulates the hypothalamo–hypophyseal adrenal system, and adrenocorticotropic hormone (ACTH) is released from the anterior pituitary as a result (Sturkie 1976). ACTH triggers the secretion of both aldosterone and corticosterone from the adrenal cortex. A comparative analysis of marine vs. terrestrial birds with and without salt glands demonstrated that corticosterone levels were significantly higher in wintering marine birds and birds with salt glands than in terrestrial birds or birds without salt glands (Brischoux et al. 2015). Melatonin increases sodium concentration in the plasma as well as urine flow rate and urine sodium concentration, but decreases plasma osmolality and potassium concentration in the urine (Hughes et al. 2007). Hughes et al. (2007) posited that melatonin acts directly on osmoregulatory mechanisms. The varying hormonal controls outside of the RAS tie osmoregulation to seasonal environmental cues.

It seems clear judging largely from laboratory investigations related to functioning of the salt glands that marine and some terrestrial birds can withstand drinking seawater and are able to maintain water balance by virtue of having robust salt glands that can excrete the excess salt. However, the question of whether marine birds drink seawater in the wild remains unresolved at the time of this writing (see Schmidt-Nielsen and Fange 1958; Schmidt-Nielsen et al. 1958; Bicudo et al. 2010). Certainly one cannot make any textbook generalization, but there seem to be numerous anecdotal observations of drinking behaviors in wild seabirds. Very few of these are published, however. Certainly, many coastal marine species go to freshwater streams to drink and bathe. Because all marine birds are carnivores, they likely get sufficient water from food, especially if they are ingesting teleost fishes. When drinking occurs, it seems to be not common and not a large quantity—nothing like what one sees in terrestrial seed-eaters, for example. In penguins (*Pygoscelis papua*), the intake of water from drinking seawater is usually less than 5% of water influx (Robertson et al. 1988). Costa and Prince (1987) and some others concluded that gray-headed albatrosses, *Diomedea chrysostoma*, likely do not drink seawater. Species that have been seen drinking seawater (or at least, behaving like they were drinking) include: adelie penguin, western and California gulls, giant petrels, wandering albatross, and silver gulls (Mark Chappell, Harold Heatwole, personal communications). Seabirds are more likely to take occasional drinks while incubating at solar-exposed sites and active during midday (Simmons 1970; Hulsman 1975; Buttemer and Astheimer 1990).

Marine mammals

By recent estimates, there are about 6400 species of extant mammals, of which 124 are marine (Burgin et al. 2018). These include sirenians, cetaceans, pinnipeds, three species of mustelids, and polar bear (*Ursus maritimus*). Marine mammals are polyphyletic, diverse, and broadly distributed with dependence on oceans for feeding. The majority of species evolved ≤ 50 mya and are secondarily marine (Uhen 2007). The five principal lineages of marine mammals include both entirely marine and semi-aquatic species.

Although there are exceptions, marine mammals, and marine birds generally do not commonly drink salt water (Ortiz 2001). Voluntary drinking of seawater is situational and varies among taxa of marine mammals. In common dolphins (*Delphinus delphis*), for example, up to 16% of the water flux is from drinking (Hui 1981), while some pinnipeds do not drink seawater at all. Mammals are well known for the concentrating abilities of the kidney, and some marine species can produce urine having an osmolality greater than that of seawater (Bester 1975; Costa 1982; Maluf 1989). In general, the osmolality of urine varies with that of blood plasma and the habitat of the mammal (Beuchat 1996; Ortiz 2001). However, with few exceptions, marine mammals are not able to concentrate salts to levels exceeding that in sea water, suggesting that they do not rely on drinking seawater to maintain fluid balance (Ortiz 2001). In general, water balance in fully marine mammals is attributable to metabolic and dietary water, and electrolyte balance is maintained by the incidental ingestion of salt water. It is worth noting that marine mammals occurring in freshwater habitats have retained the renal capacity to concentrate urine in response to a hyperosmotic stimulus (Ortiz 2001).

Pinnipeds

Generalizations about water balance in marine mammals are based largely on studies of pinnipeds. While the data are limited, there is more information available pertaining to these animals than for other groups of marine mammals. Several studies have confirmed that pinnipeds can maintain water balance solely from dietary and metabolic water (Ortiz et al. 1978; Ortiz 2001). Nonetheless, some pinnipeds will drink either fresh water or seawater depending on environmental conditions and life stages. Incidental drinking related to feeding under water apparently accounts for significant ingestion of water in the harbor seal (*Phoca vitulina*, Fig. 11) (Depocas et al. 1971). Voluntary drinking of seawater has been documented in several species of pinnipeds, and in otariids, it appears to be related to environmental temperature and thermoregulation as a means of mitigating heat stress (Gentry 1981; Costa and Gentry 1986; Costa and Trillmich 1988; Skalstad and Nordoy 2000; Storeheier and Nordoy 2001). It has also been suggested that ingestion of salt water, whether incidental or not, could be important for balance of electrolytes (Ortiz 2001). Amphibious or partly terrestrial pinnipeds minimize water that is lost through the lungs via apneic (periodic) ventilation and having a nasal countercurrent heat exchanger and complex nasal turbinates. Moreover, these mammals evidently do not sweat.

Fig. 11 Harbor seals, *Phoca vitulina*, resting near shore at Año Nuevo, California. This species is the most widely distributed pinniped, and occurs in coastal waters of the northern Atlantic and Pacific Oceans and the Baltic and North Seas. Harbor seals may circumstantially drink fresh water, but likely do not drink seawater except for incidental ingestion during feeding under water. Photograph by Dan Costa

Fasting is an important component in the life histories of pinnipeds, and prolonged periods of fasting (1.5–3 months in pups of elephant and gray seals) can lead to dehydration and imbalance of electrolytes (Ortiz 2001). Fasting seals have comparatively low turnover rates of water and are able to maintain water balance during prolonged fasting as a result. However, the ability to maintain osmotic and ionic homeostasis is variable among fasting pups of different species. In general, fasting seals rely on water that is derived from the catabolism of fat stores as their sole or principal source of water (Ortiz et al. 1978; Castellini et al. 1987), in addition to conserving water that is lost in urine because of a reduced need to excrete nitrogen (urea) as a result of reduction in metabolism of protein. Pups of northern elephant seals (*Mirounga angustirostris*) undergo a 10–12 week postweaning fast on land after a suckling period of about 4 weeks (Le Boeuf et al. 1972; Reiter et al. 1978). Studies of postweaning pups demonstrate that protein catabolism and urea production decrease during these natural fasts, which occur without an exogenous source of water (Adams and Costa 1993). In addition, terrestrial apnea reduces respiratory evaporative water loss to levels that permit water balance attributable principally to production of metabolic water (Lester and Costa 2006). The ability of pups of northern elephant seals to conserve water during prolonged fasts has been well documented and is an integral part of their natural history (Ortiz et al. 1978; Costa and Ortiz 1982; Huntley et al. 1984; Castellini et al. 1990). On the other hand, protein provides a substantial amount of energy during the first 2 weeks of a 4–6 week postweaning fast of pups of harp seals, which is based on ice or in cold water, and is important for thermoregulation (Worthy and Lavigne 1983). A study by Stewart et al. (2014) on lactating gray seals (*Halichoerus grypus*) hypothesized that the seals choose weaning pools based on salinity and access to freshwater. These hypotheses were based on study and personal observation, and a direct correlation was not established. Ingestion of fresh water has been observed in harp seals and in harbor seals, but its importance to fluid balance is not known (Irving et al. 1935; Renouf et al. 1990).

Most pinnipeds probably do not drink seawater, and drinking is not essential in maintaining water balance; it may be important in particular circumstances and requires further study to gain a clearer picture of its occurrence and significance. Circulating concentrations of the four primary hormones involved in osmoregulation—angiotensin (angiotensin I, II, or III), atrial natriuretic peptide (ANP), aldosterone, and vasopressin (AVP)—have been reported for a variety of pinnipeds (e.g., Aubin and Geraci 1986; Zenteno-Savin and Castellini 1998), and the RAS is active in these and other marine mammals. Pinnipeds as well as other marine mammals regulate water flux via the RAS–aldosterone system (Ortiz 2001).

Cetaceans

Most data on the drinking behavior and water balance of cetaceans are from studies of dolphins and porpoises. Because of logistical reasons, little is known concerning drinking behaviors. Studies of dolphin species using isotopic dilution techniques have demonstrated that during fasting, these animals consumed sea water at rates ranging between 4.5 and 13 ml kg^{-1} day^{-1} (Telfer et al. 1970; Hui 1981). However, it was subsequently shown that the skin is a major avenue for water flux, and that delphinids may experience net gains of fresh water in hypo-osmotic habitats (Andersen and Nielsen 1983). Unlike pinnipeds, fasting cetaceans produce a dilute urine and potentially become dehydrated. However, production of metabolic water (resulting from stimulated oxidation of fat) is sufficient to mitigate a necessity for drinking seawater or producing a highly concentrated urine (Hui 1981). Therefore, the question of whether cetaceans drink in the wild is intriguing and requires further study. The RAS and aldosterone are present and active in bottlenose dolphins (Malvin et al. 1978).

Relatively little is known concerning osmoregulation in whales. Kjeld (2003) calculated an estimated seawater ingestion of 1–2% of ingestion volumes for large baleen whales (i.e., fin whales and sei whales). Despite the salt content of the ingested food, the urine has relatively low osmolality (~1100 mOsm) related to the large water content of the krill and the absence of water losses through the skin. The kidneys excrete more water and salts than is characteristic of most terrestrial mammals, and there seems no need for these whales to drink seawater in excess of what is ingested incidentally with feeding.

Sirenians

Species of this taxon are strictly herbivorous and inhabit a full range of salinities, ranging from freshwater habitats (Amazonian manatee, *Trichechus inunguis*) to full seawater (marine dugong, *Dugong dugon*). The West African (*T. senagalensis*) and West Indian (*T. manatus*) manatees move between fresh and marine waters, and most understanding of osmoregulation comes from studies of the latter euryhaline species (Fig. 12; Ortiz et al. 1998). Manatees are able to concentrate their urine, and this ability led to speculation that consumption of seawater was a means of maintaining water balance (Irvine et al. 1980). However, studies using isotopic water demonstrated that manatees do not voluntarily drink seawater, but rather, during periods of fasting, derive the water they need from metabolic water as in pinnipeds

Fig. 12 A Florida manatee, *Trichechus manatus latirostris*, subspecies of the West Indian manatee and the largest living sirenian, moves freely between fresh water and seawater. West Indian manatees do not drink seawater under natural conditions, but they will drink fresh water when it is available. Photograph by Dan Costa

and cetaceans (Ortiz et al. 1999). West Indian manatees will drink fresh water when it is available, and water turnover studies demonstrate higher turnover rates in animals residing in fresh water (Ortiz et al. 1998, 1999; Ortiz 2001; Ortiz and Worthy 2006). Recent studies of captive dugongs (*Dugong dugong*) indicate very high water turnover rates for a marine mammal, and data suggest that dugongs may consume seawater either by voluntary drinking or incidental drinking (Lanyon et al. 2006). Structure of the kidney suggests that this species has a greater concentrating ability than does the manatee (Ortiz et al. 1998).

The consumption of incidental and dietary water can be high in manatees, but concentrations of electrolytes and osmolality of blood plasma is similar in free-ranging freshwater and marine manatees, suggesting the likelihood that wild animals in freshwater environments have access to salts—either by moving occasionally to marine water or selectively consuming vegetation such as seagrasses with higher salt content (Ortiz et al. 1998, 1999; Irvine et al. 1980; Medway et al. 1982). Therefore, captive manatees held for long periods in fresh water may be susceptible to hyponatremia (as are seals).

Because manatees do not drink seawater (Ortiz et al. 1998) and are commonly found in sodium-depleted environments (Best 1981), imbalances of sodium and electrolytes are expected. Little is known concerning the endocrinology of water balance in manatees, but the RAS–aldosterone system is present and appears to regulate sodium balance (Ortiz et al. 1998). Responses of these endocrine systems decrease when freshwater manatees are exposed to salt water and increase when returned to fresh water. The sensitivity seems to be greater than in pinnipeds and dolphins (Ortiz et al. 1998; Ortiz 2001).

Mustelids

Thirteen species of otters occur in both freshwater and marine habitats. Roughly half of the species are entirely or partially marine, and there is relatively little known concerning the drinking and water balance of these animals. Sea otters (*Enhydra lutris*) are entirely marine and have the ability to concentrate their urine somewhat greater than do river otters (*Lutra canadensis*), and can excrete Na^+ and Cl^- at concentrations that are greater than that in their environment (Costa 1982). Like manatees, the river otter has retained the capacity to concentrate urine, even though adapted to a freshwater habitat. Importantly, sea otters actively drink seawater as a means of excreting nitrogen (urea) and are the only marine mammals reported to actively consume sea water (Costa 1982). The fluxes of water in sea otters are reported to be quite high (269 ml kg^{-1} day^{-1}) compared with data for pinnipeds (Costa 1982).

Polar bears

The water requirements and intake of water are not well understood and are complicated by the availability of water in the form of cold snow and ice from which the salt has been leached. If polar bears ate much protein, as in captivity, the acquisition of sufficient water to eliminate the metabolic end products would be energetically demanding or stressful. Wild polar bears do not need much water in winter, because they eat mostly fat in the form of blubber (Perry 1966; Nelson et al. 1983). The metabolic water produced from the catabolism of fat evidently maintains normal hydration, as it does in denning black bears (Nelson et al. 1973).

During summer, polar bears roam around freely and utilize a variety of food sources including waterfowl, berries, grass, and seaweed (e.g., Russell 1971). It is reported, however, that bears can undergo metabolic adjustments that do not require them to feed and drink daily (Nelson et al. 1973, 1983). This involves utilization of body fat while protecting lean body mass. Blubber and some skin of seals also provide a store of other nutrients, so metabolism of largely fat from these prey may not require other sources of nutrients. The requirements of non-denning, lactating, and growing bears are different. Protein is required for growth and production of milk. This may have little influence on water balance; however, because protein is used for requirements of growth or milk rather than being catabolized (Manchester 1970).

Thus, polar bears have evolved a strategy of metabolic adaptation that involves feeding primarily on fat, and this minimizes the need for consuming water. Further studies are required, however, to understand the drinking behaviors of these unusual carnivores.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflicts of interest.

References

Adams SH, Costa DP (1993) Water conservation and protein metabolism in northern elephant seal pups during the postweaning fast. J Comp Physiol B 163:367–373

Andersen SH, Nielsen E (1983) Exchange of water between the harbor porpoise, *Phocoena phocoena* and the environment. Experientia 39:52–53

Anderson WG, Takei Y, Hazon N (2001) The dipsogenic effect of the renin-angiotensin system in elasmobranch fish. Gen Comp Endocrinol 124:300–307. https://doi.org/10.1006/gcen.2001.7712

Anderson WG, Taylor JR, Good JP, Hazon N, Grosell M (2007) Body fluid volume regulation in elasmobranch fish. Comp Biochem Physiol 148A:3–13

Ando M, Nagashima K (1996) Intestinal Na and Cl- levels control drinking behavior in the seawater-adapted eel *Anguilla japonica*. J Exp Biol 199:711–716

Ando M, Fujii Y, Kadota T, Kozaka T, Mukuda T, Takase I, Kawahara A (2000) Some factors affecting drinking behavior and their interactions in seawater acclimated eel, *Anguilla japonica*. Zool Sci 17:171–178

Auffenberg W (1963) A note on the drinking habits of some land tortoises. Anim Behav 11:72–73

Ballantyne JS (2016) Some of the most interesting things we know, and don't know, about the biochemistry and physiology of elasmobranch fishes (sharks, skates and rays). Comp Biochem Physiol B 199:21–28

Balment RJ, Carrick S (1985) Endogenous renin-angiotensin system and drinking behavior in flounder. Am J Physiol Regul Integr Comp Physiol 248:R157–R160. https://doi.org/10.1152/ajpregu.1985.248.2.R157

Balment RJ, Loveridge JP (1989) Endocrines and osmoregulatory mechanisms in the Nile crocodile, *Crocodylus niloticus*. Gen Comp Endocrinol 73(3):361–367

Barrowclough GF, Cracraft J, Klicka J, Zink RM (2016) How many kinds of birds are there and why does it matter? PLoS One 11(11):e0166307. https://doi.org/10.1371/journal.pone.0166307

Bath RN, Eddy FB (1979) Salt and water balance in rainbow trout (*Salmo gairdneri*) rapidly transferred from fresh water to sea water. J Exp Biol 83:193–202

Beasley D, Schier DN, Malvin RL, Smith G (1986) Angiotensin-stimulated drinking in marine fish. Am J Physiol Regul Integr Comp Physiol 250:R1034–R1038. https://doi.org/10.1152/ajpregu.1986.250.6.R1034

Bels VL, Davenport J, Renous S (1995) Drinking and water expulsion in the diamondback turtle *Malaclemys terrapin*. J Zool (Lond) 236:483–497

Bennett JM, Taplin LE, Grigg GC (1986) Sea water drinking as a homeostatic response to dehydration in hatchling loggerhead turtles *Caretta caretta*. Comp Biochem Physiol A 83:507–513

Bentley PJ, Yorio T (1979) Do frogs drink? J Exp Biol 79:41–46

Best RC (1981) Foods and feeding habits of wild and captive Sirenia. Mamm Rev 11:3–29

Bester MN (1975) The functional morphology of the kidney of the Cape fur seal, *Arctocephalus pusillus* (Schreber). Modoqua Ser II 4:69–92

Beuchat CA (1996) Structure and concentrating ability of the mammalian kidney: correlations with habitat. Am J Physiol Regul Integr Comp Physiol 40:157–179

Bicudo JEPW, Buttemer WA, Chappell MA, Pearson JT, Bech C (2010) Ecological and environmental physiology of birds. Oxford University Press, New York

Blakey R, Zharikov Y, Skilleter GA (2006) Lack of an osmotic constraint on intake rate of the eastern curlew (*Numenius madagascariensis*). J Avian Biol 37:299–305

Bonnet X, Brischoux F (2008) Thirsty sea snakes forsake refuge during rainfall. Austral Ecol 33:911–921

Brischoux F, Tingley R, Shine R, Lillywhite HB (2012) Salinity influences the distribution of marine snakes: implications for evolutionary transitions to marine life. Ecography 35:994–1003

Brischoux F, Lendvai ÁZ, Bókony V, Chastel O, Angelier F (2015) Marine lifestyle is associated with higher baseline corticosterone levels in birds. Biol J Linn Soc 115(1):154–161. https://doi.org/10.1111/bij.12493

Burgin CJ, Colella JP, Kahn PL, Upham NS (2018) How many species of mammals are there? J Mamm 99(1):1–14

Buttemer WA, Astheimer LB (1990) Thermal and behavioural correlates of nest site location in black noddies. Emu 90:114–118

Castellini MA, Costa DP, Huntley AC (1987) Fatty acid metabolism in fasting northern elephant seal pups. J Comp Physiol B 157:445–449

Castellini JA, Castellini MA, Kretzmann M (1990) Circulatory water concentration in suckling and fasting northern elephant seals. J Comp Physiol B 160:537–542

Cohen JJ, Krupp MA, Chidsey CA (1958) Renal conservation of trimethylamine oxide by the spiny dogfish, *Squalus acanthias*. Am J Physiol 194:R229–R235

Comanns P, Falk JE, Kappel PH, Baumgartner W, Shaw J, Withers PC (2017) Adsorption and movement of water by skin of the Australian thorny devil (Agamidae: *Moloch horridus*). R Soc Open Sci 4:170591. https://doi.org/10.1098/rsos.170591

Cooper LN, Clementz MT, Usip S, Bajpai S, Hussain ST, Hieronymu TL (2016) Aquatic habits of cetacean ancestors: integrating bone microanatomy and stable isotopes. Integr Comp Biol 56:1370–1384

Costa DP (1982) Energy, nitrogen, electrolyte flux and sea water drinking in the sea otter *Enhydra lutris*. Physiol Zool 55:35–44

Costa DP, Gentry RL (1986) Reproductive energetics of the northern fur seal. In: Gentry RL, Kooyman GL (eds) Fur seals: maternal strategies at land and sea. Princeton University Press, Princeton, pp 79–101

Costa DP, Ortiz CL (1982) Blood chemistry homeostasis during prolonged fasting in the northern elephant seal. Am J Physiol Regul Integr Comp Physiol 242:R591–R595

Costa DP, Prince PA (1987) Foraging energetics of grey-headed albatrosses *Diomedea chrysostoma* at Bird Island, South Georgia. Ibis 129:149–158

Costa DP, Trillmich F (1988) Mass changes and metabolism during the perinatal fast: a comparison between Antarctic (*Arctocephalus gazella*) and Galápagos fur seals (*Arctocephalus galapagoensis*). Physiol Zool 61:160–169

Davenport J (2017) Crying a river: how much salt-laden jelly can a leatherback turtle really eat? J Exp Biol 220:1737–1744. https://doi.org/10.1242/jeb.155150

Davenport J, Macedo E-A (1990) Behavioural osmotic control in the euryhaline diamondback terrapin *Malaclemys terrapin*: responses to low salinity and rainfall. J Zool (Lond) 220:487–496

Davenport J, Magill SH (1996) Thermoregulation or osmotic control? Some preliminary observations on the function of emersion in the diamondback terrapin *Malaclemys terrapin* (Latrielle). Herpetol J 6:26–29

Davenport J, Ward JF (1993) The effects of salinity and temperature on appetite in the diamondback terrapin *Malaclemys terrapin* (Latreille). Herpetol J 3:95–98

Depocas F, Hart J, Fisher HD (1971) Seawater drinking and water flux in starved and fed harbor seals, *Phoca vitulina*. Can J Physiol Pharmacol 49:53–62

Duggan RT, Lofts B (1978) Adaptation to fresh water in the sea snake *Hydrophis cyanocinctus*: tissue electrolytes and peripheral corticosteroids. Gen Comp Endocrinol 36:510–520

Dunson WA (1970) Some aspects of electrolyte and water balance in three estuarine reptiles, the diamondback terrapin, American and "saltwater" crocodiles. Comp Biochem Physiol 32:161–174

Dunson WA (1976) Salt glands in reptiles. In: Gans C, Dawson WR (eds) Biology of the reptilia, physiology A, vol 5. Academic Press, New York, pp 413–445

Dunson WA (1980) The relation of sodium and water balance to survival in sea water of estuarine and freshwater races of the snakes *Nerodia fasciata*, *N. sipedon* and *N. valida*. Copeia 1980:268–280

Dunson WA (1985) Effects of water salinity and food salt content on growth and sodium efflux of hatchling diamondback terrapins (*Malaclemys*). Physiol Zool 58(6):736–747

Dunson WA, Dunson MK (1974) Interspecific differences in fluid concentration and secretion rate of sea snake salt glands. Am J Physiol 227:430–438

El-Gohary ZM, El-Sayad FI, Hassan HA, Hamoda AM (2013) The functional alterations of the avian salt gland subsequent to osmotic stress. Egypt J Hosp Med 51:346–360. https://doi.org/10.12816/0000851

Epstein FH, Silva P (2005) Mechanisms of rectal gland secretion. Bull MDIBL 44:1–5

Evans DH (2008) Teleost fish osmoregulation: what have we learned since August Krogh, Homer Smith, and Ancel Keys. Am J Physiol Integr Comp Physiol 295:R704–R713

Evans DH (2010) A brief history of the study of fish osmoregulation: the central role of the Mt. Desert Island Biological Laboratory. Front Physiol. https://doi.org/10.3389/fphys.2010.00013

Evans DH, Claiborne JB (2009) Osmotic and ionic regulation in fishes. In: Evans DH (ed) Osmotic and ionic regulation. Cells and animals. CRC Press, Boca Raton, pp 295–366

Gentry RL (1981) Seawater drinking in eared seals. Comp Biochem Physiol A 68:81–86

Glover CN, Wood CM, Goss GG (2017) Drinking and water permeability in the Pacific hagfish, *Eptatretus stoutii*. J Comp Physiol B 187:1127–1135. https://doi.org/10.1007/s00360-017-1097-2

Goiran C, Shine R (2013) Decline in sea snake abundance on a protected coral reef system in the New Caledonian Lagoon. Coral Reefs 32:281–284. https://doi.org/10.1007/s00338-012-0977-x

Gordon MS, Tucker VA (1965) Osmotic regulation in the tadpoles of the crab-eating frog (*Rana cancrivora*). J Exp Biol 42:437–445

Gordon MS, Schmidt-Nielsen K, Kelly HM (1961) Osmotic regulation in the crab-eating frog (*Rana cancrivora*). J Exp Biol 38:659–678

Grigg GC, Taplin LE, Harlow P, Wright J (1980) Survival and 'growth of hatchling *Crocodylus porosus* in saltwater without access to fresh drinking water. Oecologia (Berl.) 47:264–266

Grigg GC, Beard LA, Moulton T, Melo MT, Taplin LE (1998) Osmoregulation by the broad-snouted caiman, *Caiman latirostris*, in estuarine habitat in southern Brazil. J Comp Physiol B Biochem Syst Environ Physiol 168:445–452. https://doi.org/10.1007/s003600050164

Grismer LL (1994) Three new species of intertidal side-blotched lizards (genus *Uta*) from the Gulf of California, Mexico. Herpetologica 50:451–474

Guinea ML (1991) Rainwater drinking by the sea krait *Laticauda colubrina*. Herpetofauna 21:13–14

Guinea ML (2013) Surveys of the sea snakes and sea turtles on reefs of the Sahul Shelf. Final Report 2012–2013. In: Proc Monitoring Program Montara Well Release Timor Sea, Drysdale, VIC (Australia)

Gutiérrez JS, Masero JA, Abad-Gómez JM, Villegas A, Sánchez-Guzmán JM (2011) Understanding the energetic costs of living in saline environments: effects of salinity on basal metabolic rate, body mass and daily energy consumption of a long-distance migratory shorebird. J Exp Biol 214:829–835

Hammerschlag N (2006) Osmoregulation in elasmobranchs: a review for fish biologists, behaviourists and ecologists. Mar Freshw Behav Physiol 39:209–228

Hazon N, Balment RJ, Perrott M, O'Toole LB (1989) The renin–angiotensin system and vascular and dipsogenic regulation in elasmobranchs. Gen Comp Endocrinol 74:230–236

Hazon N, Tierney ML, Anderson WG, Mackenzie S, Cutler C, Cramb G (1997) Ion and water balance in elasmobranch fish. In: Hazon N, Eddy FB, Flik G (eds) Ionic regulation in animals. Springer, Heidleberg, pp 70–86

Hillyard SD, Hoff KS, Propper C (1998) The water absorption response: a behavioral assay for physiological processes in terrestrial amphibians. Physiol Zool 71:127–138

Hirano T (1974) Some factors regulating water intake by the eel, *Anguilla japonica*. J Exp Biol 61:737–747

Hochachka PW, Somero GN (2002) Biochemical adaptation: mechanism and process in physiological evolution. Oxford University Press, Oxford

Holliday DK, Elskus AA, Roosenberg WM (2009) Impacts of multiple stressors on growth and metabolic rate of *Malaclemys terrapin*. Environ Toxicol Chem 28:338–345

Holmes WN (1975) Hormones and osmoregulation in marine birds. Gen Comp Endocrinol 25:249–258. https://doi.org/10.1016/0016-6480(75)90195-1

Holmes WN, McBean RL (1964) Some aspects of electrolyte excretion in the green turtle, *Chelonia mydas mydas*. J Exp Biol 41:81–90

Houssaye A, Fish FE (2016) Functional (secondary) adaptation to an aquatic life in vertebrates: an introduction to the symposium. Integr Comp Biol 56:1266–1270

Hughes MR, Kitamura N, Bennett DC, Gray DA, Sharp PJ, Poon AM (2007) Effect of melatonin on salt gland and kidney function of gulls, *Larus glaucescens*. Gen Comp Endocrinol 151:300–307. https://doi.org/10.1016/j.ygcen.2007.01.017

Hui C (1981) Seawater consumption and water flux in the common dolphin *Delphinus delphis*. Physiol Zool 54:430–440

Hulsman K (1975) The skimming behaviour of terns. Sunbird 6:41–43

Huntley AC, Costa DP, Rubin RD (1984) The contribution of nasal countercurrent heat exchange to water balance in the northern elephant seal, *Mirounga angustirostris*. J Exp Biol 113:447–454

Irvine AB, Neal RC, Cardeilhac RT, Popp JA, Whiter FH, Jenkins RC (1980) Clinical observations on captive and free-ranging West Indian manatees, *Trichechus manatus*. Aquat Mamm 8:2–10

Irving L, Fisher KC, McIntosh FC (1935) The water balance of a marine mammal, the seal. J Cell Comp Physiol 6:387–391

Jackson K, Brooks DR (2007) Do crocodiles co-opt their sense of "touch" to "taste"? A possible new type of vertebrate sensory organ. Amphib Reptil 28:277–285

Jackson K, Butler DG, Brooks DR (1996) Habitat and phylogeny influence salinity discrimination in crocodilians: implications for osmoregulatory physiology and historical biogeography. Biol J Linn Soc 58:371–383. https://doi.org/10.1111/j.1095-8312.1996.tb01441.x

Janech MG, Fitzgibbon WR, Nowak MW, Miller DH, Paul RV, Plot DW (2006) Cloning and functional characterization of a second urea transporter from the kidney of the Atlantic stingray, *Dasyatis sabina*. Am J Physiol 291:R844–R853

Katayama Y, Sakamoto T, Saito K, Tsuchimochi H, Kaiya H, Watanabe T, Pearson JT, Takei Y (2018) Drinking by amphibious fish: convergent evolution of thirst mechanisms during vertebrate terrestrialization. Sci Rep 8:625. https://doi.org/10.1038/s41598-017-18611-4

Kear BP, Lee MSY (2006) A primitive protostegid from Australia and early sea turtle evolution. Biol Lett 2:116–119

Kelley NP, Pyenson ND (2015) Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. Science. https://doi.org/10.1126/science.aaa3716

Kidera N, Mori A, Tu M-C (2013) Comparison of freshwater discrimination ability in three species of sea kraits (*Laticauda semifasciata*, *L. laticaudata* and *L. colubrina*). J Comp Physiol A 199:191–195

Kjeld M (2003) Salt and water balance of modern baleen whales: rate of urine production and food intake. Can J Zool 81:606–616. https://doi.org/10.1139/z03-041

Kobayashi H, Uemura H, Wada M, Takei Y (1979) Ecological adaptation of angiotensin-induced thirst mechanism in tetrapods. Gen Comp Endocrinol 38:93–104

Kobayashi H, Uemura H, Takei Y, Itatsu N, Ozawa M, Ichinohe K (1983) Drinking induced by angiotensin II in fishes. Gen Comp Endocrinol 49:295–306

Krogh A (1939) Osmotic regulation in aquatic animals. Cambridge University Press, Cambridge

Lanyon JM, Newgrain K, Alli TSS (2006) Estimation of water turnover rate in captive dugongs (*Dugong dugon*). Aquat Mamm 32:103–108

Lasiewski RC, Bartholomew GA (1969) Condensation as a mechanism for water gain in nocturnal desert poikilotherms. Copeia 2:405–407

Le Boeuf BJ, Whiting RJ, Gantt RF (1972) Perinatal behavior of northern elephant seal females and their young. Behaviour 43:121–156

Lee MSY, Sanders KL, King B, Palci A (2016) Diversification rates andphenotypic evolution in venomous snakes (Elapidae). R Soc Opensci 3:150277. https://doi.org/10.1098/rsos.150277

Lester CW, Costa DP (2006) Water conservation in fasting northern elephant seals (*Mirounga angustirostris*). J Exp Biol 209:4283–4294

Li C, Wu X-C, Rieppel O, Wang L-T, Zhao L-J (2008) An ancestral turtle from the Late Triassic of southwestern China. Nature 456:497–501

Lillywhite HB (1996) Husbandry of the little file snake, *Acrochordus granulatus*. Zoo Biol 15:315–327

Lillywhite HB (2017) Feeding begets drinking: insights from intermittent feeding in snakes. J Exp Biol 220:3565–3570

Lillywhite HB, Ellis TE (1994) Ecophysiological aspects of the coastal-estuarine distribution of acrochordid snakes. Estuaries 17:53–61

Lillywhite HB, Tu M-C (2011) Abundance of sea kraits correlates with precipitation. PLoS One. https://doi.org/10.1371/journal.pone.00228556

Lillywhite HB, Sheehy CM III, Zaidan F III (2008a) Pitviper scavenging at the intertidal zone: an evolutionary scenario for invasion of the sea. BioScience 58:947–955

Lillywhite HB, Babonis LS, Sheehy CM III, Tu M-C (2008b) Sea snakes (*Laticauda* spp.) require fresh drinking water: implication for the distribution and persistence of populations. Physiol Biochem Zool 81:785–796

Lillywhite HB, Menon JG, Menon GK, Sheehy CM III, Tu M-C (2009) Water exchange and permeability properties of the skin in three species of amphibious sea snakes (*Laticauda* spp.). J Exp Biol 212:1921–1929

Lillywhite HB, Brischoux F, Sheehy CM III, Pfaller JB (2012) Dehydration and drinking responses in a pelagic sea snake. Integr Comp Biol 52:227–234

Lillywhite HB, Heatwole H, Sheehy CM III (2014a) Dehydration and drinking behavior of the marine file snake, *Acrochordus granulatus*. Physiol Biochem Zool 87:46–55

Lillywhite HB, Sheehy CM III, Brischoux F, Grech A (2014b) Pelagic sea snakes dehydrate at sea. Proc R Soc B 281:20140119

Lillywhite HB, Heatwole H, Sheehy CM III (2015) Dehydration and drinking behavior in true sea snakes (Elapidae: Hydrophiinae: Hydrophiini). J Zool 296:261–269

Lillywhite HB, Sheehy CM III, Heatwole H, Brischoux F, Steadman DH (2017) Why are there no sea snakes in the Atlantic? BioScience 68:15–24

Lillywhite HB, Sheehy CM III, Sandfoss MR, Crowe-Riddell J, Grech A (2019) Drinking by sea snakes from oceanic freshwater lenses at first rainfall ending seasonal drought. PLoS One 14(2):e0212099. https://doi.org/10.1371/journal.pone.0212099

Lukoschek V, Beger M, Ceccarelli D, Richards Z, Pratchett M (2013) Enigmatic declines of Australia's sea snakes from a biodiversity hotspot. Biol Conserv 166:191–202. https://doi.org/10.1016/j.biocon.2013.07.004

Magnusson WE (1978) Nesting ecology of *Crocodylus porosus*, Schneider, in Arnhem Land, Australia. Unpubl. PhD Thesis, Univ. of Sydney

Maluf NSR (1989) Renal anatomy of the manatee, *Trichechus manatus* (Linnaeus). Am J Anat 184:269–286

Malvin RL, Ridgway S, Cornell L (1978) Renin and aldosterone levels in dolphins and sea lions. Proc Soc Exp Biol Med 157:665–668

Malvin RL, Schiff D, Eiger S (1980) Angiotensin and drinking rates in the euryhaline killifish. Am J Physiol Regul Integr Comp Physiol 239:R31–R34. https://doi.org/10.1152/ajpregu.1980.239.1.R31

Manchester KL (1970) Sites of hormonal regulation of protein metabolism. In: Munro HN (ed) Mammalian protein metabolism, vol 4. Academic Press, New York, pp 229–298

Mangor-Jensen A, Adoff GR (1987) Drinking activity of the newly hatched larvae of cod *Gadus morhua* L. Fish Physiol Biochem 3:99–103

Marshall AT, Cooper PD (1988) Secretory capacity of the lachrymal salt gland of hatchling sea turtles, *Chelonia mydas*. J. Comp Physiol B 157:821–827

Martin RA (2005) Conservation of freshwater and euryhaline elasmobranchs: a review. J Mar Biol Assoc UK 85:1049–1073

Mazzotti FJ, Dunson WA (1984) Adaptations of *Crocodylus acutus* and *Alligator* for life in saline water. Comp Biochem Physiol 79 A:641–646

Mazzotti FJ, Dunson WA (1989) Osmoregulation in crocodilians. Am Zool 29:903–920

Medway W, Bruss ML, Bengtson JL, Black DJ (1982) Blood chemistry of the West Indian manatee (*Trichechus manatus*). J Wildl Dis 18:229–234

Murphy MS, DeNardo DF (2019) Rattlesnakes must drink: meal consumption does not improve hydration state. Physiol Biochem Zool 92:381–385

Nelson RA, Wahner W, Jones JD, Ellefson RD, Zollman PE (1973) Metabolism of bears before, during, and after winter sleep. Am J Physiol 224:491–496

Nelson RA, Folk GE Jr, Pfeiffer EW, Craighead JJ, Jonkel CJ, Steiger DL (1983) Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. Int Conf Bear Res Manag 5:284–290

Nifong JC, Silliman B (2017) Abiotic factors influence the dynamics of marine habitat use by a highly mobile ''freshwater'' top predator. Hydrobiologia 802:155–174

Ortiz RM (2001) Osmoregulation in marine mammals. J Exp Biol 201:1831–1844

Ortiz RM, Worthy GAJ (2006) Body composition and water turnover rates of bottle-fed West Indian manatee (*Trichechus manatus*) calves. Aquat Mamm 32:41–45

Ortiz CL, Costa D, Le Boeuf BJ (1978) Water and energy flux in elephant seal pups fasting under natural conditions. Physiol Zool 51:166–178

Ortiz R, Worthy G, Mackenzie D (1998) Osmoregulation in wild and captive West Indian Manatees (*Trichechus manatus*). Physiol Zool 71:449–457. https://doi.org/10.1086/515427

Ortiz RM, Worthy GAJ, Byers FM (1999) Estimation of water turnover rates of captive West Indian manatees (*Trichechus manatus*) held in fresh and salt water. J Exp Biol 202:33–38

Ortiz RM, Patterson RM, Wade CE, Byers F (2000) Effects of acute fresh water exposure on water flux rates and osmotic responses in Kemp's ridley sea turtles (*Lepidochelys kempi*). Comp Biochem Physiol A Mol Integr Physiol 127:81–87. https://doi.org/10.1016/s1095-6433(00)00240-3

Perrott MN, Grierson CE, Hazon N, Balment RJ (1992) Drinking behaviour in sea water and fresh water teleosts, the role of the renin-angiotensin system. Fish Physiol Biochem 10(2):161–168

Perry R (1966) The world of the polar bear. Univ. Washington Press, Seattle

Potts WTW, Foster MA, Stather JW (1970) Salt and water balance in salmon smolts. J Exp Biol 52:553–564

Price ER, Sotherland PR, Wallace BP, Spotila JR, Dzialowski M (2019) Physiological determinants of the interesting interval in sea turtles: a novel 'water-limitation' hypothesis. Biol Lett 15:20190248. https://doi.org/10.1098/rsbl.2019.0248

Pyron RA, Burbrink FT, Wiens JJ (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evol Biol 13:93. https://doi.org/10.1186/1471-2148-13-93

Rasmussen AR, Murphy JC, Ompi M, Gibbons JW, Uetz P (2011) Marine Reptiles. PLoS ONE 6(11):e27373. https://doi.org/10.1371/journal.pone.0027373

Reilly BD, Cramp RL, Wilson JM, Campbell HA, Franklin CE (2011) Branchial osmoregulation in the euryhaline bull shark, *Carcharhinus leucas*: a molecular analysis of ion transporters. J Exp Biol 214:2883–2895

Reina RD, Jones TT, Spotila JR (2002) Salt and water regulation by the leatherback sea turtle *Dermochelys coriacea*. J Exp Biol 205:1853–1860

Reiter J, Stinson NL, Le Boeuf BJ (1978) Northern elephant seal development: the transition from weaning to nutritional independence. Behav Ecol Sociobiol 3:337–367

Renouf D, Noseworthy E, Scott MC (1990) Daily fresh water consumption by captive harp seals (*Phoca groenlandica*). Mar Mamm Sci 6:253–257

Robertson G, Green B, Newgrain K (1988) Estimated feeding rates and energy requirements of gentoo penguins, *Pygoscelis papua*, at Macquarie Island. Polar Biol 9:89–93

Russell RH (1971) Summer and autumn food habits of island and mainland populations of polar bears—a comparative study. Unpublished MSc thesis, University of Alberta, Edmonton

Sanders KL, Lee MSY, Leys R, Roster R, Keogh J (2008) Molecular phylogeny and divergence dates for Australasian elapids and sea snakes (Hydrophiinae): evidence from seven genes for rapid evolutionary radiations. J Evol Biol 21:682–695

Sanders KL, Mumpuni Hamidy A, Head JJ, Gower DJ (2010) Phylogeny and divergence times of filesnakes (Acrochordus): inferences from morphology, fossils and three molecular loci. Mol Phylogenet Evol 56:857–867. https://doi.org/10.1016/j.ympev.2010.04.031

Sanders KL, Lee MSY, Mumpuni Bertozzi T, Rasmussen AR (2013) Multilocus phylogeny and recent rapid radiation of the viviparous sea snakes (Elapidae: Hydrophiinae). Mol Phylogenet Evol 66:575–591. https://doi.org/10.1016/j.ympev.2012.09.021

Schmidt-Nielsen K (1960) The salt-secreting gland of marine birds. Circulation 21:955–967. https://doi.org/10.1161/01.cir.21.5.955

Schmidt-Nielsen K, Fange R (1958) The function of the salt gland in the brown pelican. Auk 75(3):282–289

Schmidt-Nielsen K, Jörgensen CB, Osaki H (1958) Extrarenal salt excretion in birds. Am J Physiol 193:101–107

Shoemaker VH, Nagy KA (1984) Osmoregulation in the Galápagos marine iguana, *Amblyrhynchus cristatus*. Physiol Zool 57(3):291–300

Shoemaker VH, Hillman SS, Hillyard SD, Jackson DC, McClanahan LL, Withers PC, Wygoda ML (1992) Exchange of water, ions, and respiratory gases in terrestrial amphibians. In: Feder ME, Burggren WW (eds) Environmental physiology of amphibians. The University of Chicago Press, Chicago, pp 125–150

Shuttleworth TJ, Hildebrandt JP (1999) Vertebrate salt glands: short- and long-term regulation of function. J Exp Zool 283:689–701

Simmons KEL (1970) Aerial drinking and bathing by some tropical seabirds. Brit Birds 63:212

Skalstad I, Nordoy ES (2000) Experimental evidence of seawater drinking in juvenile hooded (*Cystophora cristata*) and harp seals (*Phoca groenlandica*). J Comp Physiol B 170:395–401

Smith HW (1930) The absorption and excretion of water and salts by marine teleosts. Am J Physiol 93:480–505

Smith HW (1932) Water regulation and its origin in fishes. Quart Rev Biol 7:1–26

St. Aubin DJ, Geraci JR (1986) Adrenocortical function in pinniped hyponatremia. Mar Mamm Sci 2:243–250

Stewart JE, Pomeroy PP, Duck CD, Twiss SD (2014) Finescale ecological niche modeling provides evidence that lactating gray seals (*Halichoerus grypus*) prefer access to fresh water in order to drink. Mar Mamm Sci 30:1456–1472

Storeheier PV, Nordoy ES (2001) Physiological effects of seawater intake in adult harp seals during phase I of fasting. Comp Biochem Physiol A 128:307–315

Sturkie PD (1976) Kidneys, extrarenal salt excretion, and urine. In: Sturkie PD (ed) Avian Physiology. Springer, New York, pp 264–285

Takei Y (2000) Comparative physiology of body fluid regulation in vertebrates with special reference to thirst regulation. Jpn J Physiol 50:171–186. https://doi.org/10.2170/jjphysiol.50.171

Takei Y (2015) From aquatic to terrestrial life: evolution of the mechanisms for water acquisition. Zool Sci 32:1–7

Takei Y, Hirano T, Kobayashi H (1979) Angiotensin and water intake in the Japanese eel, *Anguilla japonica*. Gen Comp Endocrinol 38:446–475

Talbot C, Eddy FB, Johnston J (1982) Osmoregulation in salmon and sea trout alevins. J Exp Biol 101:61–70

Taplin LE (1984) Drinking of fresh water but not seawater by the estuarine crocodile (*Crocodylus porosus*). Comp Biochem Physiol A Physiol 77:763–767. https://doi.org/10.1016/0300-9629(84)90198-1

Taplin LE (1988) Osmoregulation in crocodilians. Biol Rev Camb Philos Soc 63:333–337

Taplin LE, Grigg GC, Beard L (1993) Osmoregulation of the Australian freshwater crocodile, *Crocodylus johnstoni*, in fresh and saline waters. J Comp Physiol B 163:70–73

Taylor AA (1977) Comparative physiology of the reninangiotensin system. Fed Proc 36:1776–1780

Telfer N, Cornell LH, Prescott JH (1970) Do dolphins drink water? J Am Vet Med Assoc 157:555–558

Thorson TB (1961) The partitioning of body water in osteichthyes: phylogenetic and ecological implications in aquatic vertebrates. Biol Bull 120:238–254

Thorson TB (1964) The partitioning of body water in amphibia. Physiol Zool 37:395–399

Thorson TB (1968) Body fluid partitioning in reptilia. Copeia 1968:592–601

Troup G, Dutka TL (2014) Osmotic concentration of prey affects food discrimination behaviour in the Australian pelican. J Zool 294:170–179. https://doi.org/10.1111/jzo.12172

Udyawer V, Simpfendorfer CA, Read M, Hamann M, Heupel MR (2016) Exploring habitat selection in sea snakes using passive acoustic monitoring and Bayesian hierarchical models. Mar Ecol Prog Ser 546:249–262

Uhen MD (2007) Evolution of marine mammals: back to the sea after 300 million years. Anat Rec 290:514–522. https://doi.org/10.1002/ar.20545

Wolcott TG, Wolcott DL (2001) Role of behavior in meeting osmotic challenges. Am Zool 41:795–806

Worthy GAJ, Lavigne DM (1983) Energetics of fasting and subsequent growth in weaned harp seal pups, *Phoca groenlandica*. Can J Zool 61(447–4):56

Wright CD, Jackson ML, DeNardo D (2013) Meal consumption is ineffective at maintaining or correcting water balance in a desert lizard, *Heloderma suspectum*. J Exp Biol 216:1439–1447

Wu CS, Kam YC (2009) Effects of salinity on survival, growth, development, and metamorphic traits of *Fejervarya limnocharis* tadpoles living in brackish water. Zool Sci 26:476–482

Wu C-S, Yang W-K, Lee T-H, Gomez-Mestre I, Kam Y-C (2013) Salinity acclimation enhances salinity tolerance in tadpoles living in brackish water through increased Na+, K+-ATPase expression. J Exp Zool 9999:1–8

Wyneken J (2001). The anatomy of sea turtles. NOAA Technical Memorandum NMFS-SEFSC-470. NOAA Southeast Fisheries Science Center, Miami, Florida (USA)

Zenteno-Savin T, Castellini MA (1998) Plasma angiotensin II, arginine vasopressin and atrial natriuretic peptide in free ranging and captive seals and sea lions. Comp Biochem Physiol 119C:1–6

Zimmer C (1998) At the water's edge: macroevolution and the transformation of life. Free Press, New York