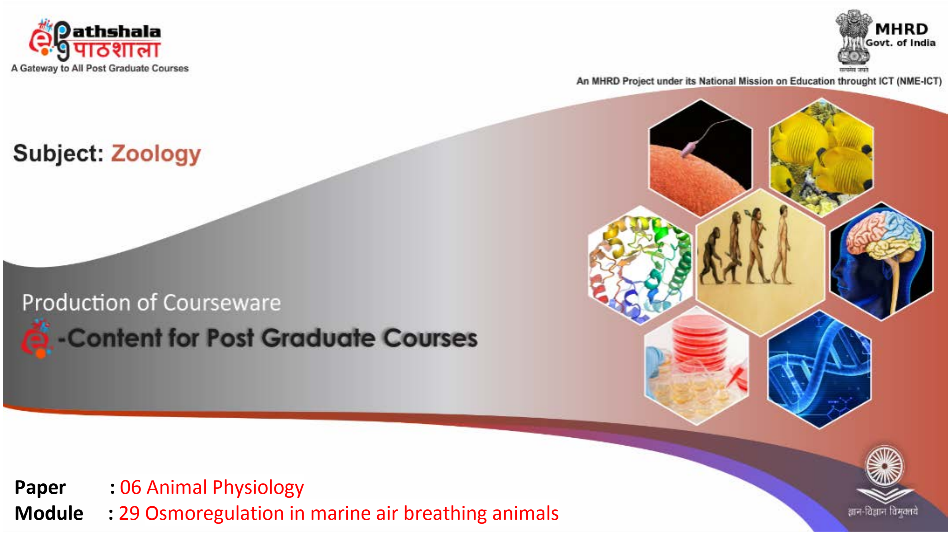

Development Team

Principal Investigator:	Prof. Neeta Sehgal Department of Zoology, University of Delhi
Co-Principal Investigator:	Prof. D.K. Singh Department of Zoology, University of Delhi
Paper Coordinator:	Prof. Rakesh Kumar Seth Department of Zoology, University of Delhi
Content Writer:	Dr. Kapinder and Dr Haren Ram Chiary Kirori Mal College, University of Delhi
Content Reviewer:	Prof. Neeta Sehgal Department of Zoology, University of Delhi

Description of Module	
Subject Name	ZOOLOGY
Paper Name	Zool 006 Animal Physiology
Module Name/Title	Osmoregulation
Module Id	M29: Osmoregulation in marine air breathing animals
Keywords	Osmoregulation, water balance, hyperosmotic urine, marine environment, salt gland, marine mammals.

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6. Summary

1. Learning Outcomes

After studying this module you shall be able to:

- Understand the concept of osmoregulation.
- Understand various factors which causes water and ion imbalance in marine air breathing animals.
- Learn mechanism of osmotic regulation in marine reptiles.
- Learn osmotic regulatory mechanisms in marine air breathing birds and mammals.

2. Introduction

The higher vertebrates such as reptiles, birds and mammals are typically terrestrial. However several vertebrates invaded secondarily in the sea and remained as air breather animals. With respect to problem of water and salt, they essentially remain as terrestrial animals and when compared to the fish, they remained physiologically isolated from surrounding sea water. In the fish, having gills for respiration, are relatively permeable to water, whereas higher marine vertebrates bear lungs and thus can escape the osmotic problem of close contact with the sea water. These marine vertebrates differ physiologically from their terrestrial relatives in the fact that they have only sea water to drink as well as most of their food contains high content of salt.

The sea water contains about 35 gm salts per liter and has osmotic concentration about 1000 mOsm. When Plant and invertebrate animals are eaten by other animals, they present roughly the same osmotic problem as drinking of sea water.

When a vertebrate intake sea water from the surroundings, the salts are absorbed in the body and causes increase in the concentration of salt in the body fluid. Unless the salts are eliminated with a smaller volume of water than that which was taken in, there can be no net gain of water. In other words, the salt must be excreted in a solution at least as concentrated as sea water, otherwise the body will become more and more dehydrated.

The reptilian kidney is not as efficient to produce urine which is more concentrated than the body fluids, and the bird kidney can usually produce urine no more than twice as concentrated as the blood. Because the concentration of their body fluid is about 300 to 400 mOsm per liter, the urine cannot reach the concentration of sea water. The kidney therefore does not have a sufficient concentrating ability to permit these animals to drink sea water or eat food with a high salt content, and if they do, they must have other mechanisms for salt excretion.

3. Marine Reptiles

Three orders of reptiles -turtles, lizards and snakes have marine representatives. Some of the sea snakes are completely independent of land, even in their reproduction, for they bear live young, never leave the sea, and would in fact be quite helpless on land. Sea turtles spend most of their lives in the open sea, but they return to tropical sandy beach for reproduction. Only female turtles go on land to lay their eggs, the males never set foot on land. The marine lizards are more tied to land. An example is the Galapagos marine iguana, *Amblyrhynchus cristatus*. It lives in the surf of the Galapagos Island, where it climbs on the rocks and feeds exclusively on seaweed. The crocodiles, has no truly marine representative. The salt water crocodile, *Crocodylus porosus*, is primarily estuarine in its habits.

3.1 Physiological mechanisms for osmoregulation

3.1.1 Skin

Skin forms an important potential route for the exchange of water and, in aquatic reptiles, ions with the external environment. In aquatic reptiles, the integument is highly permeable to water. The permeability of the skin to water, determined as the rate of evaporative water loss under identical conditions, decreases with increasing aridity of the habitat (also often reported as increasing resistance to water loss with increasing aridity), a pattern observed across orders and across species in a single order. The permeability of the integument of aquatic species to water decreases as the salinity of their normal habitat increases and this holds across orders and across species.

The skin of aquatic reptiles also has a substantial permeability to sodium, and, at least among snakes, it is significantly greater in freshwater species than in estuarine or marine species. The high rate of sodium influx that this permits in freshwater species may explain their intolerance to seawater. Within reptilian skin, the epidermis forms the limiting barrier for water exchange and, in aquatic species, for ion exchange with the environment. Within the epidermis, lipids form the major barrier for the diffusion of water.

3.1.2 Salt Glands

The excretion of excess salt, which the reptilian kidney is unable to handle, is carried out by specialized extra renal glands capable of excreting hyperosmotic salt solutions, thereby contributing to the elimination of excess electrolytes (primarily sodium or potassium) while conserving free water (figure 1). These glands may be external nasal glands, lachrymal glands or premaxillary, sublingual or lingual glands, depending on the species. Although salt glands are present in many species, they have not been found in terrestrial snakes, alligators (*Alligator mississippiensis*), geckoes and the one species of pygopodid lizard. The primary cation secreted by reptilian salt glands is clearly related to diet and habitat. The salt gland produces a highly concentrated fluid that contains primarily sodium and chloride in concentration substantially higher than in sea water that can vary with the salinity of the water to which they are adapted, whereas the salt glands of terrestrial tortoises and lizards generally secrete potassium as the primary cation, reflecting their herbivorous diet. There are some exceptions. The salt glands of two terrestrial varanid lizards (*Varanus semiremex* and *V. salvator*), which eat crustaceans and other animals in marine mangrove swamps and take in much salt water, secrete primarily sodium. The salt gland does not function continuously but they secrete intermittently in response to a salt load that increases the plasma salt concentration. Similar salt glands are also found in marine birds.

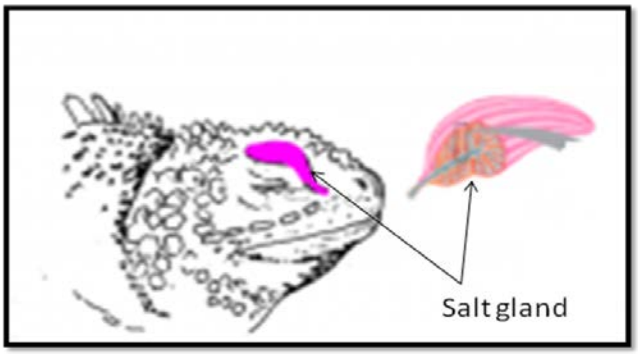

Figure.1: Location of Reptile salt gland.

(Source: http://ketheridge.sites.gettysburg.edu/BIO206/wp-content/uploads/2017/02/Screen-Shot-2017-02-16-at-11.47.50-PM-300x191.png)

In marine lizard the salt glands empty their secretion into the anterior portion of the nasasl cavity and a ridge keeps the fluid from draining back and being swallowed. A sudden exhalation occasionally forces the liquid as a fine spray of droplets out through the nostrils. A marine turtle, whether plant eating or carnivores, has a large salt excreting gland in the orbit of each eye. The duct from the gland opens into the posterior corner of the orbit and a turtle that has been salt loaded cries salty tears.

Sea snakes also excrete salty fluid in response to salt load have salt gland that opens into into the oral cavity from which the fluid is expelled (figure 2). The Australian salt water crocodiles *Crocodylus porosus* and North American *Corocodylus acutus* possess salt glands that are distributed over the surface of the tongue.

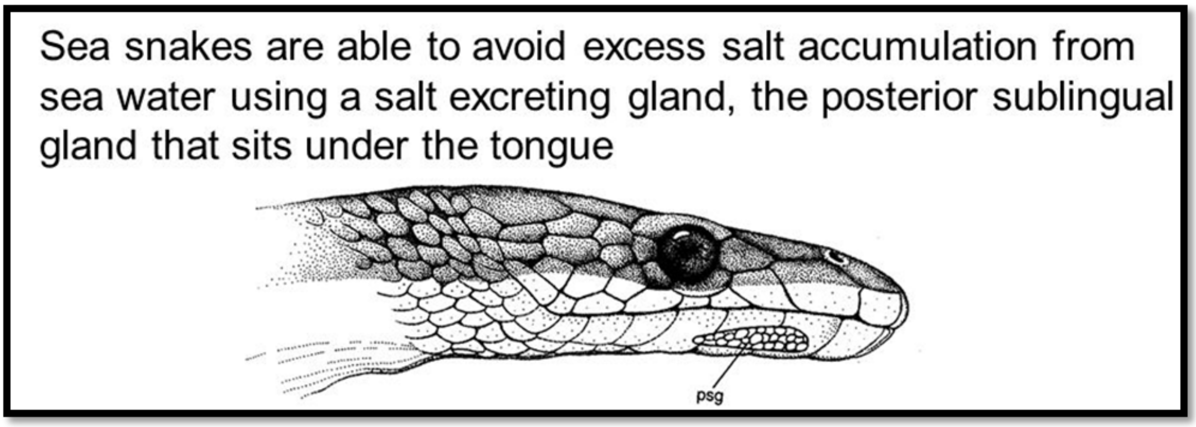

Figure 2: Salt removal gland in sea snakes.
(Source: http://images.slideplayer.com/28/9270288/slides/slide_24.jpg)

4. Marine Birds

Many birds are marine, but most of them live on and above rather than in the ocean. Many are coastal but some are truly pelagic. Birds that can adapt to a marine habitat, the need to excrete sodium chloride and generate free water far exceeds the capabilities of their kidneys. This requirement is met by secretion of a highly concentrated sodium chloride solution by paired supraorbital nasal salt glands, through a duct; connect with the nasal cavity (figure 3 and 4).

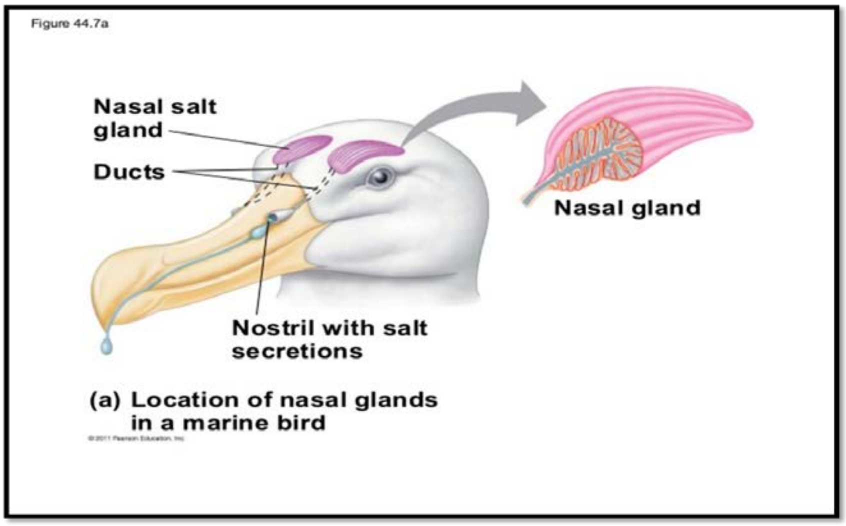

Figure 3: Location of salt gland in marine birds.

(Source: https://www.indiawilds.com/forums/attachment.php?attachmentid=18684&stc=1&d=1495613767)

Nasal glands are also found in most terrestrial birds which are very small as compare to marine birds. They are generally located on top of the skull above the orbit of each eye, in shallow depressions in the bone. In birds that are fed a diet high in salt concentration, the glands increase in size and become even larger than normal.

Figure 4: Skull of seabird has a pair of salt glands located over the eyes that excrete salty fluid from the nostrils which runs down grooves in the bill.

(Source: https://www.birdnote.org/show/seabirds-drink-salt-water)

However, as noted with regard to reptiles, the glands consist of secretary tubules (figure 5). Groups of these tubules form lobules in which all of the tubules empty into a common central ductule. A number of these ductules empty into primary ducts, which in turn empty into two main ducts, one for each gland. These ducts carry the secreted fluid to the nasal cavity where it is removed by passive dripping or shaking of the head.

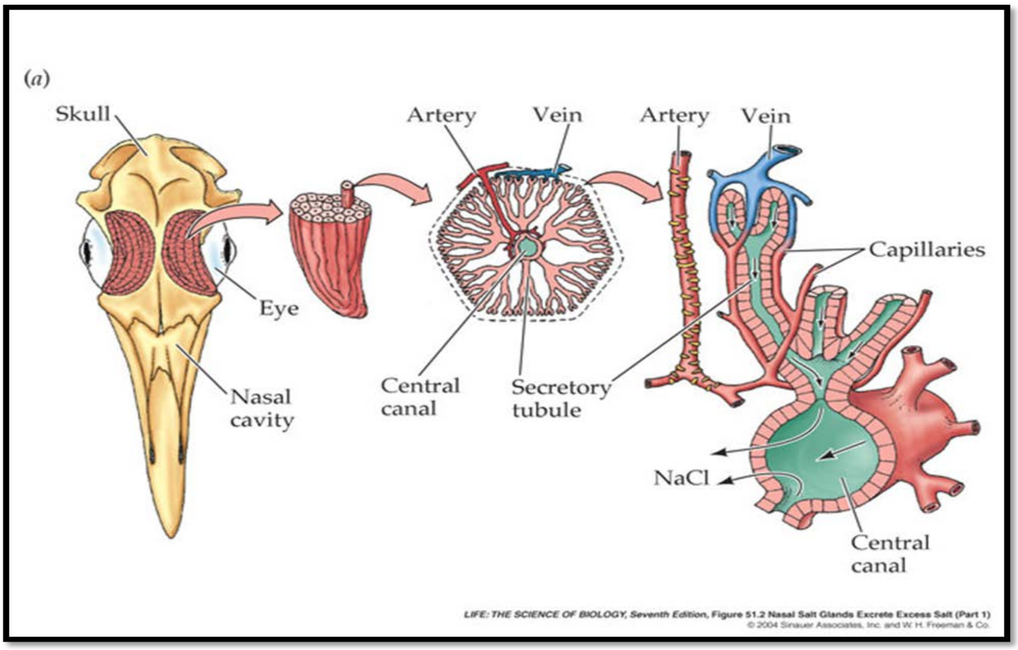

Figure 5: Structure of salt gland in marine birds.
(Source: http://www.blc.arizona.edu/courses/schaffer/182/Saltgland.JPG)

Regulation of the avian salt glands involves (1) progressive adaptation upon exposure to a salt load and (2) rapid activation of the secretary process in the already salt-adapted gland. The salt gland generally remains inactive and starts secreting only in response to an osmotic stress. The secreted fluid has a simple composition; it contains mostly sodium and chloride in` rather concentration. The salt gland differs drastically from the kidney which changes the concentration and the relative proportions of the secreted components over a very wide range.

The Cormorant is a coastal bird and a fish eater, which secretes a fluid with a relatively low salt content, about 500 to 600 mmol Na/liter. The Herring gulls which eats more invertebrate food and consequently ingest more salt, has a concentration of 600 to 800 mmol Na per liter. The Petrel is a highly oceanic bird that feeds on planktonic crustaceans has sodium concentration in the nasal fluid upto 1100 mmol per liter.

The fluid secreted from the salt gland of a marine bird always contains mostly sodium and very little potassium. The ratio between these two ions remains at about 30:1 and if the amount of potassium in the diet of gull is increased, the Na/K ratio does not change much.

Sea turtles and sea snakes have similarly high Na/K ratio, but in the marine iguana have lower ratio and the relative amount of potassium excreted by the salt gland is higher. The diet of the marine iguana is primarily marine algae and in general plants contains large quantities of potassium (figure 6). The marine iguana therefore lives on a diet with relatively high potassium content, and its need for potassium excretion is correspondingly high.

Figure 6: Marine Iguana.
(Source: https://www.santacruzgalapagoscruise.com/wp-content/uploads/2017/05/GPS90243-GPS-Generales-B15_Marine-Iguana.jpg)

A typical land lizard from a dry habitat, the false iguana (*Ctenosaura)* `has a nasal secretion with a very high potassium concentrations and a low sodium concentration, giving a Na/K ratio of 0.15.

5. Marine mammals

Marine mammals are well adapted to their hyperosmotic environment. To osmoregulate properly in a marine habitat, physiological mechanisms intended to conserve fresh water and thus avoid dehydration are required. However, as challenging as enduring life in a high-salt environment may be, aquatic mammals also diverged and inhabited freshwater niches. Although adapting to freshwater habitats may appear beneficial because conserving fresh water no longer poses a problem, those aquatic mammals that adopted such habitats are confronted with a different osmotic challenge. Living in a salt-‘free’ environment requires the appropriate physiological mechanisms to conserve electrolytes. However, some marine mammals have adapted to yet a third, and potentially greater, osmotic challenge, prolonged fasting in an arid terrestrial environment (i.e. Ortiz et al., 1978). The ability to maintain water balance and electrolyte homeostasis during extended periods of complete abstinence from food and water requires even more robust mechanisms designed to conserve both salts and water while maintaining internal homeostasis.

The seals, whales, and sea cows are exclusively marine mammals which spend their entire life in the sea. Seals return briefly to land to bear and nurse their young, but whales and sea cow (manatee and dugong) even bear their young in water. Seals and whales are carnivores and feed on fish, certain large invertebrates and marine plankton organisms. Those that feed on fish obtain food with a rather low salt content (less than 1%), but with a relatively high protein content. The crab eating seal of the Antarctic and the walrus (which feed on clams and other bottom organisms) live on food organisms that are isosmotic with sea water. The baleen whales feed on crustacean plankton organisms with the high salt content characteristic of marine invertebrates.

The kidney of whales and seals can produce urine more concentrated than sea water. The highest chloride concentration in whale urine is 820 mmol per liter. This is well above the concentration of sea water (about 535 mmol Cl per liter) and a whale that takes food with a high salt content or even sea water, should be able to eliminate the salt without difficulty.

Mammals have in their water balance an item that does not apply to birds and reptiles: The female nurses her young and large quantities of water are required for production of milk. One way of reducing this loss of water would be to produce more concentrated milk. It has long been known that seal and whale milk has very high fat content and higher protein content than cow’s milk. This has usually been interpreted as necessary for the rapid growth of the young and particularly as a means of` transferring a large amount of fat to be deposited as blubber and serve as insulation.

The high fat content of seal milk can also be viewed in light of the limited water resources of the mother. In the Weddell seal, the fat content of the milk gradually increases during the lactation period, while the water content decreases correspondingly.

Indeed, seal provide nutrients for their young with a minimal expenditure of water. For each gram of water used, seal transfer nourishment more than 10 times as effectively as land mammals.

5.1 Urine concentration in marine mammals

In marine mammals, drinking of sea water is not a common behavior and these animals can produce more concentrated urine as compare to sea water. The maximum osmolality of urine found in any marine mammal is recorded 2658 mosmol per liter. Moreover, mammals inhabiting in freshwater can also concentrate their urine when provided a hyperosmotic stimulus, suggesting that marine mammals which are present in freshwater rather than marine condition can maintained their urine-concentrating abilities. An analysis of the cortical and medullary thickness of the kidney in West Indian manatees suggests that these mammals are able to make their urine more concentrated than that of sea water. When manatees, kept in fresh water, were exposed to marine water for four days, the concentration of the urine produced by them was only 217 mosmol that is 29% lower in concentration than the animal's plasma osmolality. Although the manatees was in hypertonic water, it continued to feed on lettuce which is its normal diet and has a high water content, therefore fresh water source was maintained in the animal and there was no need to concentration of its urine.

Originally, it was thought that marine mammals used to drink sea water because their urine concentration was usually greater than the marine water and it was also assumed that the composition of their urine was basically composed of Na^+ and Cl^-. However, for marine mammals to get solute-free water after consuming marine water having more salt concentration, they have to excrete high concentration of Na^+ and Cl^- as compared to the sea water which they drink. Except for few marine mammals, most of the mammals do not regularly concentrate the level of Na^+ and Cl^- above the sea water, further suggesting that these animals are not actually rely on the consumption of sea water to maintain their fluid balance.

5.2 Hormonal regulation

In mammals, the primary hormones responsible for osmoregulation are angiotensin (angiotensin I, II or III), atrial natriuretic peptide (ANP), aldosterone and vasopressin (AVP).

Angiotensinogen is converted into angiotensin I by renin and which is further converted into angiotensin II and finally angiotensin converting enzyme convert it into angiotensin III. Consequently, angiotensin II stimulates adrenal gland to release aldosterone from the adrenal gland. Release of aldosterone stimulates the resorption of sodium ions into the distal tubule of nephron and causes decrease in the excreted sodium ions. Increased cardiac pressure (volume) induces atrial distention that is the primary mechanism for ANP (atrial natriuretic peptide) release. The ANP function by inhibiting the actions of aldosterone and angiotensin II by inhibiting the synthesis and release of renin. The inhibition of renin therefore causes excretion of more sodium ions. The angiotensin II and aldosterone also have the water retention abilities, however, vasopressin is found to be most potent antidiuretic agent which stimulates the water channels (aquaporins) synthesis in the collecting duct of nephrons. These four major hormones which are actively involved in osmoregulation have been found in a variety of pinnipeds.

The activity of plasma renin and aldosterone levels exhibit positive correlation in the fasting northern elephant seal pups and California sea lions which suggest that under normonatremic conditions, regulation of electrolyte balance is done through the renin–angiotensin–aldosterone system (RAAS) (figure 7).

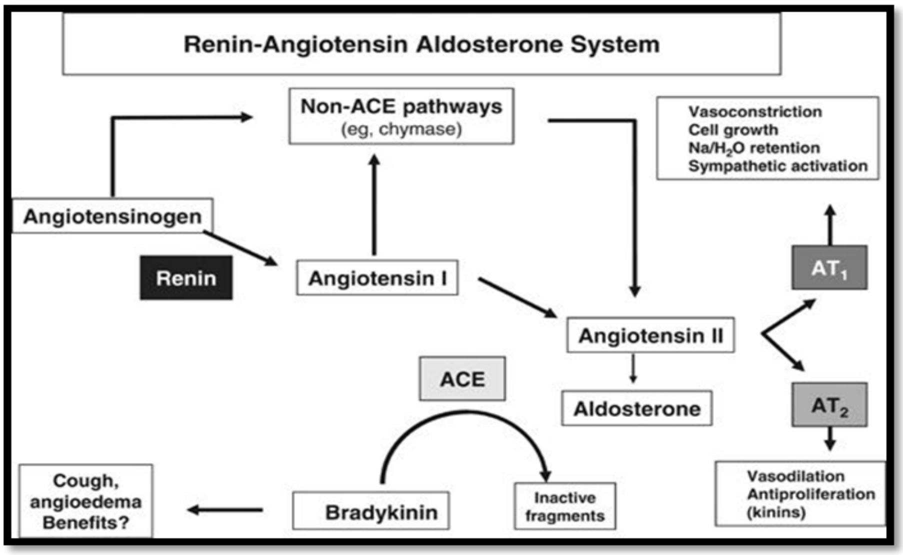

Figure 7: The renin–angiotensin–aldosterone system (RAAS).

(Source: https://media.nature.com/full/nature-ssets/jhh/journal/v20/n2/images/1001960f1.jpg)

There are number of studies that provide various evidences to suggest that tubular water resorption is mediated through AVP in seals, as in terrestrial mammals. The intravenous infusion of pitressin, a synthetic AVP, in a water-loaded harbor seal causes decrease in the urine flow rate along with increases in the concentration of urinary electrolyte. When Baikal and ringed seals were kept in force-fasted conditions, they exhibited an increase in excreted AVP that is associated with increase in urine osmolality and decreased urine flow rate. Under force-fasted conditions in grey seals, there is an increase in urine osmolality in combination with increased plasma osmolality as well as AVP. Whereas, in naturally fasting postweaned elephant seal pups exhibits increased urine osmolality in spite of a decrease in plasma AVP.

Collectively, electrolyte as well as water resorption are mediated by RAAS and AVP system, respectively, in pinnipeds. During hyponatremic conditions, mediation through pituitary–adrenal axis is also required to replete the concentration of salts.

6. Summary

- The higher marine vertebrates differ physiologically from terrestrial animals primarily in that they drink sea water as well as their food also contains high content of salts.
- Three orders of reptile viz. turtles, snakes and lizards have marine representatives.
- Reptile skin forms an important possible route for the water and ion exchange with the external environment.
- The permeability of integument of aquatic reptiles to water decreases with increase in salinity of their normal habitat and this holds across orders and across species.
- In reptiles, the salt gland produces concentrated fluid that primarily consists of sodium and chloride which is substantially higher in concentration than in sea water.
- The salt gland does not function continuously in reptiles but they secrete in response to a salt load that increases the plasma salt concentration.
- Birds that are adapted to a marine habitat have to excrete sodium chloride and generate free water that is far exceeds the capabilities of their kidneys.

- Regulation of avian salt glands involves progressive adaptation upon exposure to high salt load and activation of secretary process in the salt-adapted gland.
- Marine mammals are well adapted to their hyperosmotic environment.
- The ability to maintain water balance and electrolyte homeostasis is a stronger mechanisms designed to conserve both water and salts concentration while maintaining internal homeostasis.
- In marine mammal, the consumption of sea water is not a common behavior and these animals can produce more concentrated urine than that of sea water.
- In mammals, the primary hormones responsible for osmoregulation are angiotensin, atrial natriuretic peptide, aldosterone and vasopressin. These hormones have been reported for a variety of pinnipeds.
- Collectively, water and electrolyte resorption in marine mammals are mediated by AVP (aldosterone and vasopressin) and the RAAS (renin–angiotensin–aldosterone system), respectively as they are in terrestrial mammals.