Introduction to elasmobranch physiology

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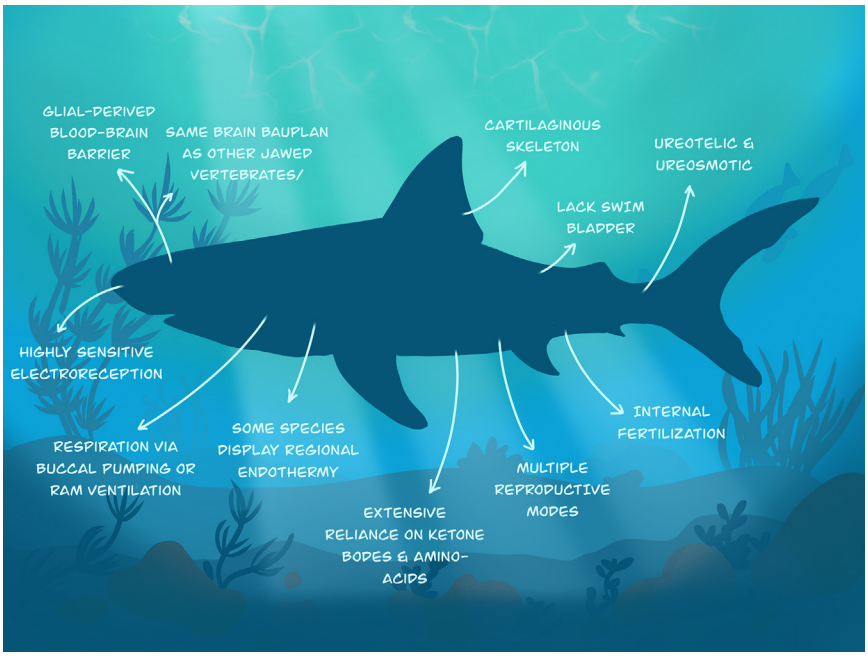
Key points

- Elasmobranchs have a cartilaginous skeleton, which is different from the bony skeletons of other fishes.
- Elasmobranchs have a unique reproductive system with nearly a dozen different types of reproductive modes.
- Elasmobranchs have a relatively slow growth rate and late sexual maturity, which makes them vulnerable to overfishing.
- Elasmobranchs lack gas-inflated swim bladders.
- The primary nitrogenous waste in elasmobranchs is urea, which is retained in body fluids to elevate internal osmolality.
- Depending on their environment, elasmobranchs employ osmoconformation and osmoregulation strategies.
- Some elasmobranch species can maintain certain body parts at temperatures above the ambient water temperatures, a phenomenon known as regional endothermy.
- Two main respiratory modes are observed in elasmobranchs: ram-ventilation and buccal pumping.
- The stress response in elasmobranchs involves the secretion of catecholamines and corticosteroids, including the exclusive 1-alpha-hydroxycorticosterone.
- Elasmobranch metabolism relies extensively on lipid-derived ketone bodies and amino acids. Notably, certain tissues like cardiac and skeletal muscle lack the capacity for long-chain fatty acid oxidation.
- Tonic immobility in elasmobranchs is a common but poorly understood behavior, often used in research, that varies across species and requires further study.
- Beyond their keen olfactory and visual senses, elasmobranchs also possess specialized electroreceptive organs called ampullae of Lorenzini.
- The brain structure of elasmobranchs aligns with the general bauplan of jawed vertebrates and features compact myelin as well as a glial-derived blood–brain barrier.

Abstract

The long evolutionary history of the elasmobranchs (sharks, skates, and rays) has shaped many of their defining physiological processes. Elasmobranchs are ureotelic and ureosmotic, and display both osmoconformation and osmoregulation strategies. Stress responses involve the secretion of catecholamines and corticosteroids, and metabolism relies extensively on lipid-derived ketone bodies and amino acids. Most are ectothermic; yet some species show regional endothermy associated with vascular countercurrent heat exchangers. Elasmobranchs possess electroreceptive organs extremely sensitive to the electrical fields, among other exquisite features. This article discusses these aspects of elasmobranchs' excretion, osmoregulation, buoyancy, metabolism, respiration, endocrinology, neurophysiology, and related topics.

Teaching slide



Introduction

Cartilaginous fishes (class Chondrichthyes) have inhabited the oceans for approximately 450 million years, surviving all five major mass extinctions, which makes them one of the most successful groups of marine organisms (Kriwet et al., 2008; Whitenack et al., 2022). Extant members of this class can be split into two subclasses: the Elasmobranchii (sharks, skates, and rays) and the Holocephali (chimaeras). While the latter currently comprises around 60 species, the former comprises more than a thousand species that are found in quite different aquatic habitats where they perform distinct functional roles. Elasmobranchs are mostly marine, but some are estuarine (~10%), while others are euryhaline (~2%) or obligate freshwater species (~1%) (Martin, 2005; Ebert et al., 2021). The subclass Elasmobranchii includes the longest-living vertebrates (i.e., the Greenland sharks, *Somniosus microcephalus*), the largest fish in the world (i.e., the whale shark, *Rhincodon typus*), warm-bodied fast-swimming predators (e.g., shortfin mako shark, *Isurus oxyrinchus*), parasitic species (e.g., the cookie cutter shark, *Isistius brasiliensis*), trowel-shaped deep-sea goblin sharks (*Mitsukurina owstoni*), flattened benthic dwellers (e.g., catsharks, skates), and freshwater species (e.g., stingrays of the family Potamotrygonidae). Many occupy the top of the marine food webs, where they regulate prey abundance and contribute to the health of ecosystems. Further, given the ability of elasmobranchs to modulate resource use and promote carbon sinking, they indirectly contribute to the mitigation of climate change (Hammerschlag et al., 2019; Nowicki et al., 2019).

As long-lived and K-selected species, most elasmobranchs exhibit slow growth, late sexual maturity, long gestation periods, and reduced fecundity. Some argue that the evolutionary success of this group is due, in part, to their diverse female reproductive modes (e.g., lecithotrophy vs. matrotrophy, oviparity, lecithotrophic viviparity, viviparity with histotrophy, placentotrophy, oophagy, among others) and mating strategies, with sperm storage and multiple paternity being commonly reported (Wheeler et al., 2020). These animals are also known to have particularly slow rates of genetic evolution and, thus, maintain many primitive features (Venkatesh et al., 2014; Hara et al., 2018). Indeed, elasmobranchs have a more limited genetic repertoire when compared to teleost fishes and other subsequent vertebrates, due to having only one genome duplication separating them from the jawless fishes. This limitation restricts the ability of elasmobranchs to evolve new protein isoforms without affecting existing pathways (Ballantyne, 2015). On the other hand, representing one of the oldest extant branches of the vertebrate tree of life, they present a long line of physiological innovations that have allowed them to stand the test of time.

This article will briefly discuss key aspects of elasmobranch physiology, including buoyancy and locomotion, excretion, osmoregulation, metabolism, respiration, neurophysiology, and related topics (see more comprehensive reviews in Carlson et al., 2004; Evans et al., 2004; Hammerschlag, 2006; Gardiner et al., 2012; Anderson, 2015; Ballantyne, 2015; Bucking, 2015; Milsom and Taylor, 2015; Morrison et al., 2015; Wright and Wood, 2015; Yancey, 2015; Ballantyne, 2016; Gleiss et al., 2022; Meredith et al., 2022; Yopak, 2022).

Buoyancy and locomotion

Buoyancy presents a physical challenge for aquatic animals that are mobile and traverse the water column. Elasmobranchs exhibit a wide range of buoyancy across species, ranging from almost neutral to negative buoyancies (Bone and Roberts, 1969; Baldridge,

1970; Pinte et al., 2019; Priede et al., 2020), with some species even exhibiting positive buoyancy (e.g., Nakamura et al., 2015). Unlike most teleost fishes that have gas-inflated swim bladders, elasmobranchs lack this feature and have evolved various strategies to reduce the energetic costs associated with negative buoyancy in the water column. First, their skeletons are comprised of cartilage rather than bone, which significantly reduces their overall density. To counteract their general negative buoyancy, they employ their wing-like fins to generate hydrodynamic lift during continuous swimming, thereby preventing sinking (Iosilevskii and Papastamatiou, 2016). Elasmobranchs also rely on oil-filled livers containing mostly triacylglycerols (TAG), diacylglycerol ethers (DAGE), sterols, and squalene for hydrostatic lift (Bakes and Nichols, 1995; Bordier et al., 1996; Wetherbee and Nichols, 2000; Jayasinghe et al., 2003; Priede et al., 2020). Deep-sea sharks have especially large livers (>20% of body mass), containing high volumes of these low-density lipids (>80% of liver mass), including DAGE (up to ~90%) or squalene (up to ~80%). Their large livers allow them to swim at slow speeds without sinking; although, this comes at the cost of increased drag due to reduced streamlining. Deep sea sharks also have less red muscle tissue and smaller fins than shallow-living sharks because hydrodynamic lift is less relevant for deep sea species (Corner et al., 1969; Iosilevskii and Papastamatiou, 2016; Gleiss et al., 2017). Elasmobranchs also use high concentrations of nitrogen compounds, namely urea and methylamines (e.g., trimethylamine oxide; TMAO, sarcosine, and betaine) that reduce body density (**Fig. 1**) (Ballantyne et al., 1987; Withers et al., 1994a,b; Yancey et al., 2002, 2004; Yancey, 2005; Treberg et al., 2006).

TMAO is an important osmolyte and a key counteracting solute that safeguards protein structure and function against environmental stressors, such as urea and ammonia toxicity (Yancey and Somero, 1979, 1980). Urea, TMAO, and other methylamines have opposite effects on elasmobranch protein structural stability and enzyme kinetics (Yancey and Somero, 1979, 1980). Such effects cancel each other out most effectively at about a 2:1 urea:TMAO ratio, which is roughly ~400:200 mM at cellular levels in marine elasmobranchs (**Fig. 2**). Salt-methylamine counteraction is not yet known in elasmobranchs. TMAO levels have also been shown to increase with depth in skates and both mid-water and deep-sea teleost fishes (Kelly and Yancey, 1999; Bockus and Seibel, 2016) to balance the adverse effects of elevated pressure on protein structure (Yancey and Siebenaller, 1999; Yancey et al., 2001, 2004).

Excretion

Most fish species are ammoniotelic, meaning that they produce ammonia as their major nitrogenous waste product. Yet, most elasmobranchs are prominent exceptions, since they are ureotelic and ureosmotic. Urea, a considerably less toxic molecule, serves as their primary nitrogenous waste. It is also retained in body fluids (**Fig. 2**) to increase internal osmolality. For instance, in the spiny dogfish (*Squalus acanthias*), urea accounts for up to 49% of the total osmolytes in the plasma, with TMAO and inorganic ions, such as sodium and chloride, accounting for the remainder (Kajimura et al., 2006). Additionally, metabolic ammonia is stored as glutamine and subsequently converted to urea through the ornithine-urea cycle (OUC; Kirschner, 1993; Ballantyne, 1997). This pathway is the primary means for urea production in the liver of elasmobranchs (**Fig. 3**), with the exception of freshwater potamytrygonid rays (Schooler et al., 1966; Walsh and Mommsen, 2001). Some evidence suggests that urea synthesis may also occur in extrahepatic tissues, namely in skeletal muscle (Steele et al., 2005) and the stomach (Tam et al., 2003), although this area remains a subject of ongoing research.

While marine elasmobranchs have mechanisms for retaining urea, they still experience urea loss to the external environment (Wood et al., 1995, 2007b; Fines et al., 2001). Given their need for nitrogen (N) for both growth and osmoregulation, coupled

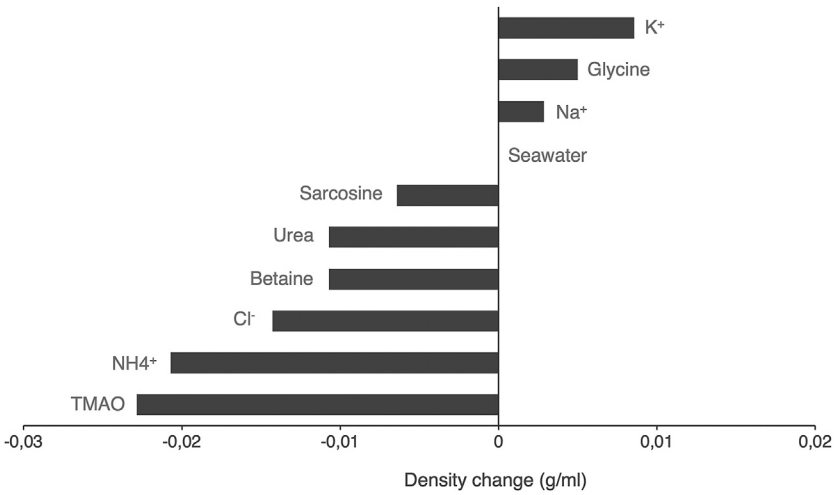


Fig. 1 Difference in density (g/mL) between seawater (1.024 g/mL; set as zero) and 1 M solutions of different solutes — urea, ammonia, methylamines, inorganic ions, and amino acids. Adapted from Yancey (2015).

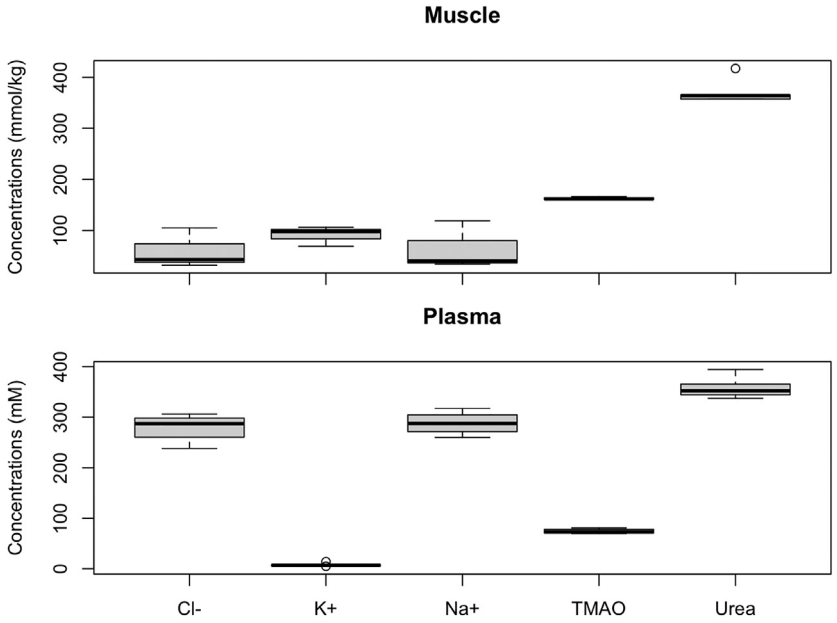


Fig. 2 Concentrations of selected osmolytes in the muscle (mmol kg^{-1}) and plasma (mM) of marine elasmobranchs. Data from Burger and Hess (1960), Pillans and Franklin (2004), Yancey (2015).

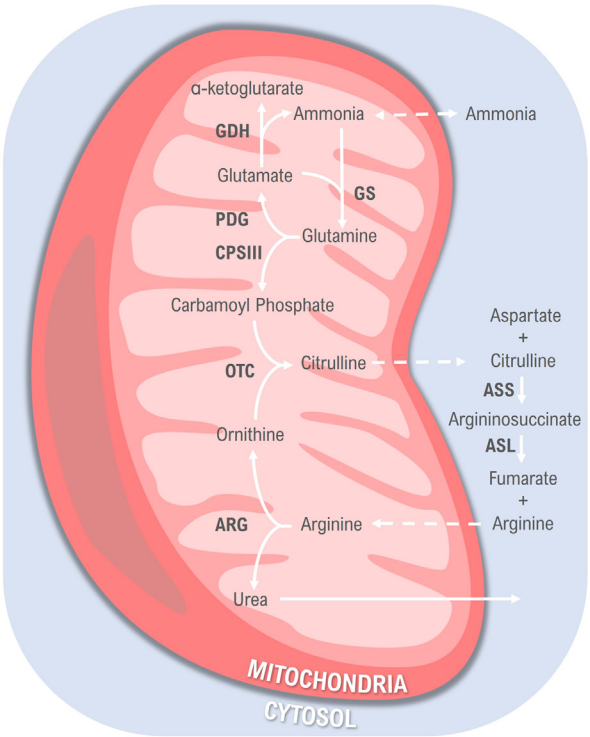


Fig. 3 Ornithine-urea cycle (OUC) in an elasmobranch mitochondrion. Abbreviations: GDH — glutamate dehydrogenase; GS — glutamine synthetase; PDG — phosphate-dependent glutaminase; CPS III — carbamoyl phosphate synthetase III, OTC — ornithine transcarbamoylase; ASS — argininosuccinate synthetase; ASL - argininosuccinate lyase; ARG - arginase; UT — urea transporter. Adapted from Wright and Wood (2015).

with high rates of urea-N loss across the gills (usually 400–600 μmol N kg^{-1} h^{-1}) and irregular feeding patterns, these elasmobranchs are likely to be N limited in their natural habitats (Kajimura et al., 2006, 2008; Wood et al., 2007a). Yet, there is some evidence that they may actively take up ammonia from the surrounding environment to synthesize urea (Nawata et al., 2015; Wood and Giacomin, 2016).

Osmoconformation and osmoregulation

Elasmobranchs employ both osmotic strategies, osmoconformation and osmoregulation, depending on their environment. As previously noted, marine and euryhaline elasmobranchs have the ability to reabsorb and retain urea and other solutes, thus maintaining a hyper-osmotic internal environment when in seawater. While extracellular fluids have high NaCl, available from seawater, cellular osmolality is raised mainly by organic osmolytes (**Fig. 2**). As a result, there is almost no osmotic loss of water and no need to drink seawater. In contrast, marine teleost fishes remain slightly hypo-osmotic, experience water loss, and maintain osmotic balance by actively drinking seawater and secreting excess salts via the gills and kidney (Evans et al., 2005).

While marine elasmobranchs are osmoconformers, they also act as ionoregulators by maintaining plasma ion concentrations below those found in seawater. Plasma Na^+ and Cl^- concentrations are around 250–300 mmol/kg (**Fig. 2**), which is half the concentrations found in seawater. Thus, the constant inward diffusion of Na^+ and Cl^- from the surrounding environment is balanced by salt excretory mechanisms found mainly in the rectal gland (RG)—a small organ in the colon—and the gills (Piermarini and Evans, 2000; Pillans et al., 2008; Wright and Wood, 2015). Briefly, salt excretion in the rectal gland entails: (i) a drop in intracellular Na^+ by the action of Na^+/K^+-ATPase, (ii) the entering of Na^+, K^+, and Cl^- via a Na^+/K^+2Cl^- cotransporter, (iii) K^+ out-diffusion to the extracellular fluid through a K^+ channel and Cl^- diffusion to the lumen through a Cl^- channel traveling along concentration and charge gradients, and (iv) Na^+ diffusion between the epithelial cells directly to the lumen along concentration and charge gradients.

Euryhaline elasmobranchs in freshwater environments (e.g., bull shark, *Carcharhinus leucas*; Atlantic stingray, *Hypanus sabinus*) become osmoregulators (i.e., hyperosmotic) and, to reduce internal osmolality, they decrease urea synthesis and the retention of urea, TMAO, and ions (**Fig. 4**). Stenohaline species in freshwater environments (family Potamotrygonidae) have lost the ability to produce urea via the OUC, retain almost no urea or TMAO, and therefore the RG is non-functional. These species are osmo- and ion-regulators, like freshwater teleost fishes (Piermarini and Evans, 1998; Pillans and Franklin, 2004; Pillans et al., 2008).

Metabolism

Having maintained a generally high trophic ranking throughout their long evolutionary history, sharks and their relatives exhibit diverse and often unusual strategies for energy storage and utilization (Speers-Roesch and Treberg, 2010). The uniqueness of their intermediate metabolism is significantly influenced by their dependence on urea for osmoregulation. This shifts the focus of their

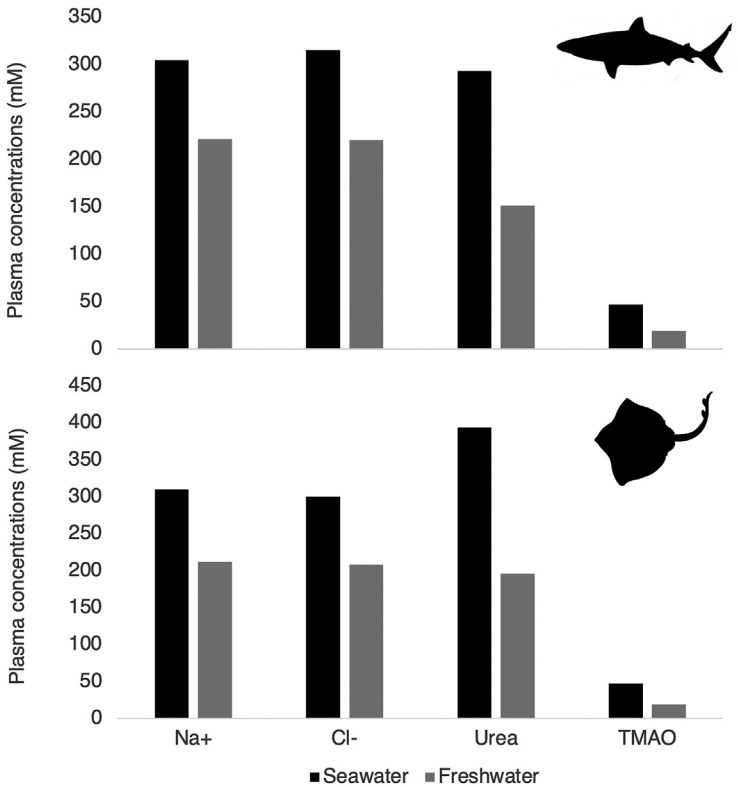


Fig. 4 Osmolyte concentrations in plasma (mM) of bull shark (*Carcharhinus leucas*; upper panel) and Atlantic stingray (*Hypanus sabina*; lower panel) in seawater and freshwater environments. Data from Piermarini and Evans (1998), Pillans and Franklin (2004).

nitrogen metabolism toward glutamine production, thereby increasing their protein intake requirements and modulating its allocation (Speers-Roesch and Treberg, 2010; Ballantyne, 2015; Gleiss et al., 2022). In this context, their urea-driven high protein demand likely contributes to their predominantly carnivorous diet and generally elevated trophic level (Ballantyne, 2015). Similarly, the metabolic physiology of these organisms has adapted to fulfill the energy requirements of a predator in fluctuating and resource-scarce ecosystems, enabling them to handle an especially unpredictable influx of energy (Jorgensen et al., 2015; Gleiss et al., 2022).

A major peculiarity of elasmobranch energy metabolism is the relative importance of different energy sources, namely their extensive reliance on lipid-derived ketone bodies and amino acids in tissues that generally rely on the oxidation of long-chain fatty acids (Ballantyne, 1997; Speers-Roesch and Treberg, 2010). Elasmobranchs are known to accumulate large quantities of lipids in their livers. However, while some of these lipids represent an efficient form of energy storing, such as triacylglycerides and diacylglycerol ethers, a considerable portion of the lipids accumulated (e.g., squalene) are rendered unavailable as an energy source and are instead dedicated toward buoyancy (Ballantyne, 1997; Gleiss et al., 2022). Given the lack of long-chain fatty acid oxidation capacity in certain tissues, namely in the cardiac and skeletal muscle, elasmobranchs mobilize liver lipid reserves by releasing ketone bodies for use as oxidative fuel, alongside amino acids. While the ability to carry out long-chain fatty acid oxidation is present in other tissues, elasmobranchs ubiquitously rely on ketone bodies and amino acids. Fittingly, and in contrast with other vertebrates, high levels of circulating ketone bodies (e.g., especially β-HB) are observed in elasmobranchs, even in the absence of fasting—in other words, these animals are in a permanent state of ketosis (Ballantyne, 1997; Gleiss et al., 2022). Additionally, unlike fatty acids that require protein carriers such as albumin—largely absent in elasmobranchs (Metcalf and Gemmell, 2005)—ketone bodies are water-soluble and can therefore circulate through the bloodstream without the need for such protein carriers (Ballantyne, 1997; Speers-Roesch and Treberg, 2010) (**Fig. 5**).

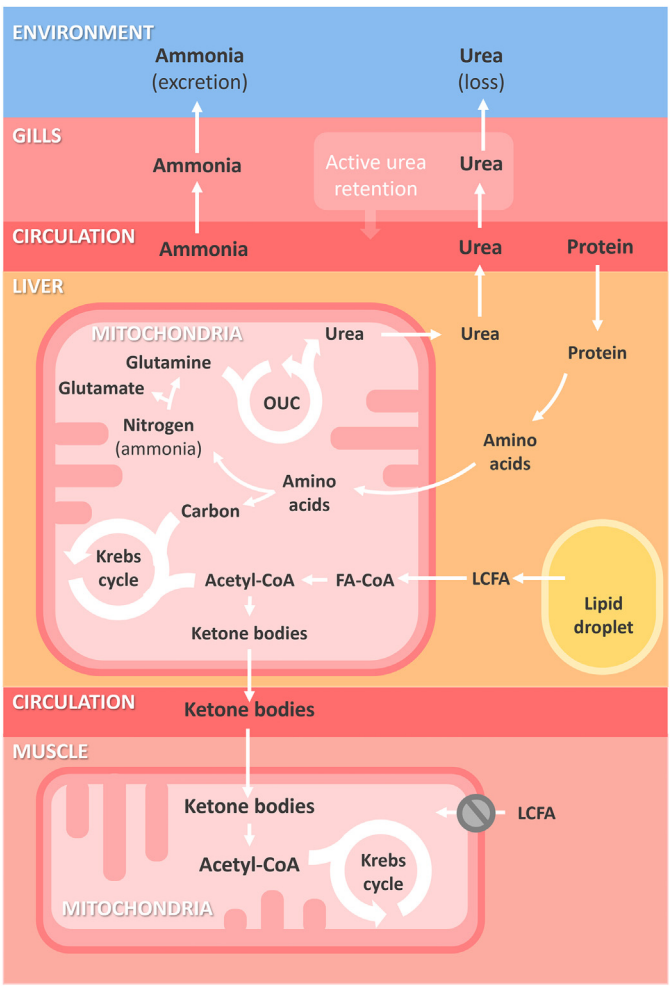


Fig. 5 Summary of key pathways relevant for elasmobranch energy metabolism, highlighting the nitrogen allocation and subsequent loss in the ornithine-urea cycle (OUC) to urea production and lipid mobilization. The ketone bodies are a key substrate in skeletal muscle due to the absence of long-chain fatty acid (LCFA) oxidation capacity. Adapted from Gleiss et al. (2022).

While elasmobranchs do utilize carbohydrates as an energy source, their significance and relative contribution to aerobic metabolism remain poorly understood. Despite a diet low in carbohydrates, glucose may actually serve as an important fuel for specific tissues, such as the heart, red muscle, brain, and rectal gland (Moon and Mommsen, 1987; Sidell et al., 1987; Moyes et al., 1990; Ballantyne et al., 1992; Walsh et al., 2006). Indeed, glycogen is the primary source of anaerobic ATP generation, leading to muscle lactate accumulation during exercise, which is reconverted to glycogen *in situ* (Richards et al., 2003; Speers-Roesch and Treberg, 2010). In conclusion, the metabolic profile of elasmobranchs seems largely modulated by their urea-dependent osmoregulation and is characterized by a considerable reliance on amino-acids and ketone bodies as aerobic fuel. Further investigation is warranted to elucidate these complex metabolic pathways.

Digestion

As the oldest extant members of the Gnathostomata infraphylum, sharks and their relatives have developed a diverse array of feeding strategies alongside the evolution of a functional jaw. Despite having a simpler gastrointestinal tract than other vertebrates and exhibiting less anatomical and physiological diversity compared to teleost fishes, elasmobranchs have evolved several important digestive adaptations. These adaptations enable them to effectively break down protein-rich food and absorb the necessary nutrients to meet their energetic requirements (Ballantyne, 2015; Bucking, 2015). Namely, elasmobranchs represent the first known group to produce acidic secretions in their stomachs (Koelz, 1992; Johnsen et al., 1997). Their stomachs achieve lower pH levels compared to those of teleost fishes, owing to the higher osmolarity of their body fluids, which raises the potential for HCl production (Cortés et al., 2008). These gastric secretions contain acid proteases (e.g., pepsinogen/pepsin), as well as a protective mucous layer (Bucking, 2015). Additionally, this group introduced several other proteins important for protein digestion, such as carboxypeptidase B and elastase (Ballantyne, 2015). Conversely, elasmobranchs exhibit relatively slow bile secretion and lipid digestion (Ballantyne, 2015).

Another key anatomical adaptation with significant physiological implications is the presence of a spiral valve in the elasmobranch intestine. This feature is notable, especially given that elasmobranchs have a shorter intestine compared to teleost fishes with similar diets. This structure slows the passage of food through the gut and increases the surface area for absorption of nutrients (Bucking, 2015). Conversely, similar to teleost fishes, the stomach of elasmobranchs may also have an absorptive function (Sims et al., 2006; Liew et al., 2013). Additionally, although the rectal gland is primarily involved with osmoregulation, it may also play a role in digestion. Feeding has been shown to increase NaCl secretion in this gland (Wood et al., 2008) and other transcriptomic responses have been observed as well (Deck et al., 2013).

The cost of turning food into fuel, including the processes of digestion, absorption, and breakdown of nutrients, is known as specific dynamic action (SDA) and is associated with a postprandial increase in oxygen uptake rates (Secor, 2009). This metric is difficult to assess and particularly challenging but can represent a considerable energy burden. The carnivorous diet of elasmobranchs leads to extended postprandial processes and, thus, extended SDA effects, with a gut retention that can exceed 200 h (Gleiss et al., 2022). As increased temperatures are known to increase the rate of enzymatic reactions—including those performed by digestive enzymes—some sharks are thought to behaviorally modulate the rate of their postprandial processes by pursuing waters of best-suited temperatures (Sims et al., 2006; Di Santo and Bennett, 2011).

Endothermy

Most fishes, including elasmobranchs, are ectothermic, meaning that their body temperature closely matches the ambient water temperature. That is because the metabolically produced heat is rapidly lost to the water by: (i) convective transfer via the blood at the gills, and (ii) thermal conduction across the body surface (Brill et al., 1994). Yet, lamnid sharks (e.g., the longfin and shortfin mako sharks, *Isurus paucus* and *Isurus oxyrinchus*, respectively; the great white shark, *Carcharodon carcharias*; salmon shark, *Lamna ditropis*; and the common thresher shark, *Alopias vulpinus*) can maintain parts of their bodies above ambient temperature by retaining metabolic heat generated by the continuous activity of the aerobic swimming muscles, as well as through digestion and assimilation (Bernal et al., 2001a,b; Goldman et al., 2004; Sepulveda et al., 2005; Perry et al., 2007; Watanabe et al., 2019). The ability of lamnid sharks to elevate red muscle (RM) temperature above ambient water temperature—known as regional endothermy—is linked to the RM's more anterior and medial position within the body myotome, closer to the vertebral column. This contrasts with the more peripheral location of RM observed in ectothermic sharks (Bernal et al., 2001a, 2003; Graham and Dickson, 2001; Gardiner et al., 2012). The associated metabolic heat is conserved through vascular countercurrent heat exchangers called *retia mirabilia* (rete is Latin for "net or network", and mirabile for "wonderful") (Stevens, 2011). Lamnid sharks also display (i) blood vessels that carry blood from the warm RM to a venous sinus near the brain and eyes, and (ii) visceral heat exchange *retia*. The former may elevate the brain temperature of the mako and salmon sharks from 3 °C to ~10 °C above ambient water temperatures, respectively (Block and Carey, 1985; Anderson and Goldman, 2001; Gardiner et al., 2012). The salmon shark is the only elasmobranch species with a separate *rete* aiding the kidney. Moreover, two species of myliobatoid rays (*Mobula tarapacana* and *Manta birostris*) possess cranial *retia* (Alexander, 1995, 1996), but the respective body temperatures and eventual thermoregulatory abilities have yet to be tested.

Respiration and ventilation

Elasmobranchs display two main respiratory modes: ram-ventilation and buccal pumping. The former is observed in pelagic, active species that move forward to pass oxygen-rich seawater over their gills. Most elasmobranchs are facultative ram-ventilators, but some are obligate ram ventilators (e.g., lamnid sharks), having to swim continuously (Bernal et al., 2001a; Milsom and Taylor, 2015). Buccal pumping is mostly found in demersal sharks, skates, and rays that use buccal movements to suction water into the mouth and then across the gills for oxygenation. This type of ventilation allows these species to remain motionless for extended periods of time (Carlson et al., 2004; Milsom and Taylor, 2015); yet, it is still unclear how temporally consistent these periods of sustained immobility are and if they reflect a form of sleep (Kelly et al., 2019, 2020).

Endocrinology

Elasmobranchs have a functional hypothalamic–pituitary–interrenal (HPI) axis. The pituitary gland is associated with the release of key hormone families, including: (i) growth hormone, that targets the liver to stimulate the synthesis and release of insulin-like factors I and II (IGF-I and II) and prolactin (PRL) that, besides osmoregulation, may be involved in the regulation of color and luminescence in some sharks, through the expansion of melanophores in photogenic cells (Claes and Mallefet, 2009; Claes et al., 2011); (ii) glycoproteins, including thyroid stimulating hormone (TSH); (iii) proopiomelanocortin (POMC), the precursor of melanocortins and endorphins; and (iv) neurohypophysial hormones, including oxytocin- and vasotocin-like hormones (Anderson, 2015).

The elasmobranch interrenal gland is a steroidogenic organ situated along the midline of the paired kidney. An exclusive characteristic of this organ is the production of a unique stress-related hormone, 1-alpha-hydroxycorticosterone (1α-OH-B) (Truscott and Idler, 1972). The biosynthetic pathway for 1α-OH-B entails the following: (i) translocation of cholesterol from the outer to the inner mitochondrial membrane through a regulatory protein (StAR), (ii) hydrolyzation of cholesterol to yield pregnenolone, which is achieved by an enzyme of the P450 family (CYP11A), (iii) movement of pregnenolone out of the mitochondria to the endoplasmic reticulum, where it is then converted to progesterone by the action of the enzyme 3β-hydroxysteroid dehydrogenase (3βHSD), (iv) conversion of progesterone into 11-deoxycorticosterone (DOC) achieved by the enzyme P450c21, and (v) transfer of DOC to the inner mitochondrial membrane, where it is converted to corticosterone via the enzyme P450c11β. As yet, the enzymes responsible for the final steps in the synthesis of 1α-OH-B remain undescribed (Anderson, 2015). In elasmobranchs, corticosterone concentrations are significantly lower than those of 1α-OH-B, and levels of both hormones are known to rise substantially in response to stress. Nevertheless, the functional roles of these hormones, whether as mineralocorticoids or glucocorticoids, are still not clearly understood.

In response to stress, elasmobranchs also secrete catecholamines, such as epinephrine and norepinephrine. These catecholamines are synthesized from the amino acid tyrosine in chromaffin cells, which are primarily distributed along the dorsal surface of the kidney in bundles known as axillary bodies. Unlike in other vertebrate groups, norepinephrine concentrations in elasmobranchs are higher than those of epinephrine. The predominant function of these catecholamines is to enhance cardiorespiratory performance, specifically by increasing cardiac output and blood pressure, thereby improving blood flow and facilitating the removal of metabolic waste (Brill and Lai, 2015).

In elasmobranchs, as in all vertebrates, another crucial function of the endocrine system is the regulation of reproduction through the hypothalamic-pituitary-gonadal axis. The endocrine cascade initiates with activation of gonadotropin-releasing hormone (GnRH) neurons in the brain. This, in turn, triggers the pituitary gland to produce and release gonadotropin hormones (GTH) into the bloodstream, then traveling to the gonads to promote gametogenesis and steroidogenesis.

Tonic immobility

In elasmobranchs, tonic immobility, which is a temporary, innate state of immobility observed across various taxa (Hoagland, 1928), has been well-documented (Henningsen, 1994) and is frequently employed for animal husbandry and surgical research procedures (Kessel and Hussey, 2015). Dorsoventral inversion of elasmobranchs often triggers a "limp response", where the individual enters a trance-like state accompanied by heavy, rhythmic breathing (Henningsen, 1994). Researchers often induce tonic immobility as an alternative to sedatives, especially when placing satellite tags.

Although the physiological basis of tonic immobility in elasmobranchs is increasingly understood (Davie et al., 1993; Brooks et al., 2011), limited information exists in the literature about its potential adaptive functions and variations between species. Although some species have been suggested to use tonic immobility as a basic defense mechanism (Gallup, 1977), empirical evidence is lacking. Moreover, the question of whether observed instances of tonic immobility across vertebrate phylogeny are genuinely homologous remains open.

Contemporary studies have begun to explore the duration and induction times of tonic immobility in elasmobranchs (Mukharror et al., 2020), potentially enabling taxonomic comparisons. Some reports indicate that not all elasmobranchs exhibit tonic immobility (Henningsen, 1994; Rummer, personal communication). However, these studies collectively cover only a small fraction of the total diversity of extant elasmobranchs and entirely overlook their sister clade, the Holocephali. Further research is needed to

broaden the range of Chondrichthyan diversity studied in relation to tonic immobility. Such expansion would facilitate interspecific comparisons and ancestral state reconstruction, contributing to a more comprehensive understanding of the potential adaptive function and evolutionary history of tonic immobility within this clade.

Neurophysiology

From an evolutionary perspective, sharks and their relatives represent the emergence of the archetypal brain structure for jawed vertebrates, appearing to possess a similar cognitive toolbox (Yopak, 2012). The brain of elasmobranchs is subdivided into a forebrain (i.e., olfactory bulbs, telencephalon, and diencephalon), midbrain (i.e., mesencephalon), and hindbrain (i.e., cerebellum and medulla), each region being associated with specific functions such as the integration of sensory information, motor control, and the regulation of physiological processes (Yopak, 2012; Guttridge et al., 2018). Importantly, even though elasmobranchs occupy a basal position in the phylogenetic tree, the allometric scaling of their brain closely resembles that of birds and mammals (Yopak, 2012). This likely imposes a considerable energetic burden, given that the brain is one of the most metabolically active organs in vertebrates (Soengas and Aldegunde, 2002), suggesting an important adaptative trade-off.

In addition to a range of sensory modalities common to most vertebrates, such as vision, chemoreception (including olfaction and gustation), audition, and mechanoreception (via direct touch and the lateral line), elasmobranchs are uniquely equipped with highly sensitive electroreception (Collin, 2012; Gardiner et al., 2012; Guttridge et al., 2018; Meredith et al., 2022). Specifically, elasmobranchs are equipped with specialized electroreceptive organs known as ampullae of Lorenzini, which enable them to detect weak electrical fields emitted by other organisms. This capability is crucial for their prey detection, capture, and predator evasion (Newton et al., 2019). Furthermore, these animals exhibit magnetoreception, which is likely instrumental in their orientation and navigation across vast distances and complex migration routes (Newton and Kajiura, 2020; Keller et al., 2021). The prominence, sensitivity, and detection thresholds of these various sensory modalities vary among species to better align with their specific ecological niches (Gardiner et al., 2012; Meredith et al., 2022).

Additionally, elasmobranchs are notable for the appearance of compact myelin—a glial membrane that surrounds and insulates axons—along with the primary adhesive proteins present in vertebrates (de Bellard, 2016). Morphologically and molecularly, compact myelin shows minimal variation across the vertebrate lineage, with the ultrastructure in chondrichthyans being virtually indistinguishable from that of tetrapods (de Bellard, 2016). This group also represents the earliest known expression of true myelin basic protein and myelin protein zero, present in both their central and peripheral nervous systems. Further, although they lack a true proteolipid protein, their myelin does contain a DM-like protein (de Bellard, 2016). Given their basal position in the phylogenetic tree, studying their myelin could provide valuable insights into the evolution of vertebrate myelin, an area that warrants further research.

In elasmobranchs, as in other vertebrates, the blood–brain barrier (BBB) maintains the internal homeostasis of the central nervous system independently from the bloodstream. This barrier selectively permits the entry of key molecules, namely essential nutrients, and the removal of waste, while blocking pathogens and potentially harmful substances (Dunton et al., 2021). Unlike most vertebrates—ranging from the jawless fishes, teleost fishes, sarcopterygians, and even chimaeras—whose BBB is assured by tight junctions in the vascular endothelium, the BBB in elasmobranchs is formed by glial cells, a feature more commonly observed in invertebrates (Bundgaard and Abbott, 2008; Dunton et al., 2021). Therefore, although it has been hypothesized that a glial-based BBB may represent the ancestral state in the vertebrate brain, phylogenetic analyses rarely support this notion. Instead, the glial-based BBB in elasmobranchs is likely to have evolved secondarily (Dunton et al., 2021).

Reproduction

The reproductive strategies in elasmobranchs are both extensive and diverse, with immense implications for managing their energy budget and overall life strategies. One of their key advantages is the ability to produce particularly robust offspring that are functional miniatures of their adult counterparts, aligning with a K-selection strategy. This is facilitated by a major evolutionary innovation: internal fertilization. Male elasmobranchs possess claspers, specialized structures derived from pelvic fins, which are used to transfer sperm into the female reproductive tract. These claspers are a defining feature of elasmobranchs (Grogan et al., 2012) and enable internal conception, setting the stage for a variety of reproductive modes.

Elasmobranch females invest significant energy in producing fully developed offspring. The ability to carry the developing embryo following conception provides opportunities for various strategies that enable females to modulate energy allocation during embryogenesis. Indeed, in elasmobranchs, maternal investment can take multiple forms, from the one-time provision of a large yolk (i.e., lecitotrophy) and protecting the embryo with leathery capsules that are tied to the substrate (i.e., oviparity) to extensive internal gestation periods (i.e., viviparity) that can exceed 1 year (e.g., *Notorynchus cepedianus*; Awruch et al., 2014), during which an array of strategies can be applied to continue the maternal transfer of nutrients during embryonic development (i.e., matrotrophy). Indeed, while all oviparous species are lecitotrophic, viviparous species have developed an extensive array of strategies, from lecitotrophy, which is observed in most extant shark orders (Miller et al., 2022), to the formation of a placenta-like structure that connects the female with the developing embryos, allowing for the direct exchange of nutrients and waste products between the two (i.e., placental viviparity; e.g., *Carcharhinus limbatus*; Verkamp et al., 2022). Other forms of matrotrophy exist,

such as histotrophy, where species secrete a nutrient-rich substance known as "uterine milk" (e.g., myliobatiform stingrays and *Carcharodon carcharias*; Tomita et al., 2022). Additionally, some species produce a series of unfertilized eggs that serve as a food source for the developing animals once their yolk sac is depleted, known as oophagy (e.g., *Alopias vulpinus*; Malavasi-Bruno and Amorim, 2018). Finally, at least one shark species (i.e., *Carcharias taurus*) is known to exhibit intrauterine cannibalism, where the biggest of the embryos will consume all other developing embryos from the same litter prior to birth, which is known as adelphophagy (Gilmore et al., 2005). Additionally, several instances of parthenogenesis have been recorded in elasmobranchs, where females produce a litter—consisting entirely of clones—without the contribution of a male (Pratt, 1993; Chapman et al., 2007, 2008; Robinson et al., 2011; Dudgeon et al., 2017; Feldheim et al., 2023). The physiological significance of these various reproductive strategies and their energetic implications is a subject of extensive exploration in the scientific literature.

Conclusions

Despite their seemingly simple and unconventional physiology compared to other vertebrates, elasmobranchs are remarkably well-adapted for low natural mortality rates, embodying a "survivor" strategy that has sustained them through geological time (Dulvy and Kindsvater, 2017; Whitenack et al., 2022). Owing to their basal position within the vertebrate phylogenetic tree, studying elasmobranch physiology offers a valuable lens for understanding the evolutionary foundations that have shaped subsequent extant vertebrates.

Conversely, the factors contributing to the ongoing biodiversity crisis appear to disproportionally affect species that are slow-living and large-bodied (Dirzo and Raven, 2003). Elasmobranchs are now among the most threatened groups of animals (Dulvy et al., 2021) and face a disproportional risk of losing both functional and phylogenetic diversity (Stein et al., 2018; Pimiento et al., 2020). Indeed, this group has a limited resilience to the extremely high rates of individual removal (Dulvy and Kindsvater, 2017), and global populations have declined significantly due to overexploitation (Dulvy et al., 2021). Moreover, climate change is expected to exacerbate these challenges by shifting their geographical range and pushing the boundaries of their physiological adaptability (Rosa et al., 2014, 2016; Santos et al., 2021; Rummer et al., 2022). Given these circumstances, a sound understanding of elasmobranch physiology and its influence on their adaptability to changing environments is crucial for developing effective conservation and management strategies aimed at mitigating their risk of extinction.

See Also: Cartilaginous fish skeletal tissues; Conserving the next generation: Perspectives in elasmobranch reproductive research; Endocrine stress axis and regulation of energy metabolism in Chondrichthyes; Osmoregulation in chondrichthyan fishes; Physiology of ampullary electrosensory systems; Unique aspects of reproductive energetics and endocrinology among Chondrichthyes.

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