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Review Article

Breaking the cold-blooded rule: Opah's secret to whole-body endothermy

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Abstract: Endothermy represents a significant evolutionary advancement that improves physiological efficiency and ecological adaptability; yet, among fishes, it is typically limited to regional heat retention. The opah (*Lampris* spp.) is exceptional as the only known teleost to exhibit true whole-body endothermy, sustaining elevated body temperatures regardless of external conditions. This review synthesizes current knowledge on the anatomical, physiological, and molecular mechanisms underlying this rare adaptation. At the core of opah endothermy is a unique counter-current heat-exchange system within the gill arches, where retia mirabilia retain metabolically produced heat that would otherwise be lost during respiration. The continuous movement of the pectoral fins generates significant metabolic heat, which is effectively conserved and distributed via insulated circulatory pathways, thereby maintaining higher temperatures in cardiac, neural, and visceral tissues. This systemic thermal elevation enhances aerobic performance, sensory function, and ecological competitiveness in cold, mesopelagic habitats. Comparative analyses indicate that this strategy is evolutionarily distinct from regional endothermy observed in lamnid sharks and scombrid fishes, highlighting a striking case of convergent thermal adaptation. Emerging genomic and mitochondrial evidence further suggests enhanced oxidative capacity and specialized muscle bioenergetics underlying sustained heat production. In summary, the opah challenges the conventional limits of fish physiology and serves as an intriguing model for exploring the evolutionary shifts between ectothermy and endothermy. Future comprehensive research integrating functional genomics, bioenergetics, and ecological modeling will be crucial to understanding the selective pressures and constraints that shape this rare and extraordinary characteristic.

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Introduction

Opah, often called moonfish and known by common names such as glittering fish or God's salmon (Quigley, 2001), belongs to the family Lampridae. It exhibits a cosmopolitan distribution and has been recorded in offshore regions of temperate, sub-tropical, and tropical waters, including the Mediterranean and Caribbean Seas (Heemstra, 1986; Collette, 2003; Dulčić et al., 2005; Polovina et al., 2008; Francour et al., 2010; Bego and Kashta, 2012; Sprem et al., 2014; Ergüden et al., 2019; Enajjar et al., 2020). This species inhabits waters ranging from the surface to the lower epipelagic-mesopelagic zone, with a depth range of 50-500 m and a temperature variation of 8-22°C (Nakano et al., 1997; Polovina et al., 2008). Reports indicate that opah exhibits diurnal variations in its vertical movement, with deeper depths during the day and shallower depths at night; specifically, the occupancy range at night is between 50-150 m, while during the day it extends from 100-400 m (Polovina et al., 2008; Francour et al., 2010). The shallow depth at which opah resides at night is believed to be a strategy to minimize encounters with predators by utilizing the surface layer (Polovina et al., 2008).

To date, opah has not been regarded as a target species for fishing; instead, it has been caught as bycatch while targeting large pelagic species such as sharks, tunas, and swordfish (Runcie et al., 2009; Huang and Liu, 2010; Hawn and Collette, 2012; Underkoffler et al., 2018). However, due to the tenderness, delicate flavor, and delightful taste of its

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flesh, opah is recognized as an excellent table fish (Hawn and Collette, 2012; Meida et al., 2020). It is available in both fresh and frozen forms (Collette, 1978), and the demand for frozen opah products is rising in countries such as America, Malaysia, Mauritius, Japan, and Taiwan (Barokah et al., 2020). Nevertheless, the production of endogenous formaldehyde in stored opah and its potential health risks are currently under discussion (Putri et al., 2018; Anissah et al., 2019; Barokah et al., 2020; Meida et al., 2020). In the markets of California, Hawaii, Japan, and New Zealand, opah is considered one of the most valuable commercial fish species (Vlieg et al., 1993; Collette, 2003; Polovina et al., 2008; Underkoffler et al., 2018). The flesh of opah comprises 21-34% protein, 1-13% lipid, 1-2% ash, and 0.21-0.28% soluble carbohydrates, along with 71% moisture content (Vlieg et al., 1993; Meida et al., 2020).

Globally, six species of opah have been identified based on their geographical distribution, morphology, and genetic analysis. These include *Lampris guttatus* (Brünnich, 1788), commonly known as opah; *L. incognitus* (Underkoffler et al., 2018), referred to as small-eye Pacific opah; southern spotted opah, *L. australensis* (Underkoffler et al., 2018); big-eye Pacific opah, *L. megalopsis* (Underkoffler et al., 2018); southern opah, *L. immaculatus* (Gilchrist 1904); east Atlantic opah, *L. lauta* (Lowe, 1838) (Hyde et al., 2014; Underkoffler et al., 2018; Terlecki et al., 2022). Recently, Kukuev (2021) proposed a revision of the genus *Lampris*, placing the spotless species, *L. immaculatus*, within the subgenus *Paralampris*, while the five-spotted species are placed in the subgenus *Lampris*.

Endothermy is defined as the ability to generate and retain metabolic heat, enabling an organism to maintain a body temperature that is higher than that of its surrounding environment (Franck et al., 2019; Legendre and Davesne, 2019). Due to water's high thermal conductivity, fish have significant difficulty regulating their body temperature. The species that demonstrate endothermy, referred to as regional endothermers, constitute merely 0.1% of all fish (Bernal et al., 2001; Dickson and Graham, 2004). These species possess exceptional swimming abilities, a high tolerance for cold temperatures, and enhanced visual acuity for vertical migration and niche expansion, thereby gaining an advantage as dominant predators (Wegner et al., 2015). Previously, regional endothermy has been documented in billfishes, butterfly mackerel, lamnid sharks, and tunas (Linthicum and Carey, 1972; Carey, 1982; Block and Carey, 1985; Block et al., 1993; Sepulveda et al., 2007). The purpose of this review is to analyze the facts regarding whole-body endothermy in opah, as well as the genetic associations related to this distinctive phenomenon. Furthermore, it highlights current research trends, identifies information gaps regarding this species, and suggests avenues for future research initiatives.

Literature review

The published literature related to opah has been searched from different sources like Google Scholar, ResearchGate, Science Direct, Academia, JStore and Mendeley.

Regional endothermy in fishes

Earlier studies have documented regional endothermy in fish (Carey et al., 1971, 1985; Block and Finnerty, 1994; Dickson and Graham, 2004), where vascular counter-current heat exchangers enable these fish to retain metabolically generated heat in specific areas such as the pectoral muscles, viscera, and cranial region, thereby maintaining the temperature of these areas significantly above that of the surrounding water. Among the various forms of regional endothermy in fish, cranial endothermy is the most prevalent (Linthicum and Carey, 1972; Carey, 1982; Block and Carey, 1985; Block et al., 1993; Sepulveda et al., 2007). It has been observed that cranial endothermy enhances the foraging efficiency of predatory fish in cold, dark waters by assisting their central nervous system in adapting to rapidly fluctuating water temperatures during vertical migrations and by improving their ability to pursue fast-moving prey through increased flicker fusion frequency, which keeps cranial temperatures elevated above the surrounding water (Carey, 1982; Block, 1987, 1993; Block and Finnerty, 1994; Fritsches et al.,

2005).

In most fish exhibiting cranial endothermy, heat is generated by specialized heater tissues, which are modified ocular muscles, including the superior, medial, inferior, and lateral rectus extraocular muscles (Block, 1987; Wolf et al., 1988; Finnerty and Block, 1992; Sepulveda et al., 2007). These muscles possess a high density of mitochondria, extensive sarcoplasmic reticulum, and significant oxidative capacity (Block, 1991). In these fishes, the heat produced by the heater tissues is retained through two mechanisms: the existence of an insulating layer of adipose tissue that envelops the eyes and brain (Carey, 1982; Fritsches et al., 2005; Sepulveda et al., 2007), and the presence of retia mirabilia, which serve as vascular counter-current heat exchangers in the cranial area (Linthicum and Carey, 1972; Carey, 1982; Block and Carey, 1985; Carey et al., 1985; Block, 1991; Sepulveda et al., 2007). These adaptations are crucial for reducing both conductive and convective heat loss.

Whole-body endothermy in opah

The presence of cranial endothermy has previously been documented in opah (Block, 1987; Runcie et al., 2009), which is believed to help them adapt to the wide temperature variations encountered during vertical migration and to hunt fast-moving prey in cold, deep waters (Runcie et al., 2009). Wegner et al. (2015) were the first to identify opah as the only fish species that demonstrates the phenomenon of whole-body endothermy, which allows opah to uphold superior physiological functions in frigid, deep habitats, including heightened muscle strength, greater endurance, improved temporal resolution, and better neural conduction for the eye and brain. Furthermore, it accelerates food digestion and assimilation while reducing the adverse effects of cold temperatures on cardiac and other organ functions, without requiring a return to the surface to warm the heart.

Physiology related to whole-body endothermy

Opah employs two distinct strategies for generating and conserving heat. By continuously propelling their pectoral fins and utilizing specialized intracranial thermogenic tissue, they can produce heat. The presence of retia mirabilia in the gills (an additional feature compared to other regional endotherms) and the cranium, along with a thick layer of adipose tissue covering, aids in heat conservation (Runcie et al., 2009; Wegner et al., 2015; Franck et al., 2019).

Metabolic heat production: Opah generates metabolic heat through the constant movement of their large pectoral fins (Wegner et al., 2015; Bo et al., 2022). The dark red aerobic muscles in the pectoral fins, which contain elevated levels of sarcoplasmic reticulum calcium ATPase (SERCA) and the regulatory protein sarcolipin (SLN), assist opah in their continuous swimming and heat generation via futile calcium cycling (Franck et al., 2019), following the process of excitation-thermogenic coupling (Morrissette et al., 2003). The pectoral muscle mass constitutes 16% of the total weight of opah, the highest percentage recorded among all known fish species (Wegner et al., 2015). Due to ongoing metabolic processes, the temperature of the pectoral muscles has been observed to be approximately 5°C higher than that of the surrounding water (Wegner et al., 2015; Bo et al., 2022).

Intracranial thermogenesis: Runcie et al. (2009) have provided a detailed account of the function of cranial endothermy in opah. They noted the absence of specialized cranial heater tissues in opah, which are typically found in other fish species that exhibit cranial endothermy. The contraction of the proximal lateral rectus extraocular muscle (PLRM) and the proximal superior rectus extraocular muscle (PSRM) generate heat in opah; among these, PLRM is identified as the primary source of heat production due to its status as the largest extraocular muscle, possessing a greater capacity for aerobic heat generation compared to other muscles. Additionally, the positioning of PLRM within the cranial cavity helps warm the brain by conducting heat through the thin layer of bone that separates the PLRM from the brain.

Heat conservation by retia mirabilia: Within the opah, two proposed counter-current heat exchangers (retia mirabilia) are located in the cranium, specifically on the medial surfaces of the PLRM and

PSRM. These heat exchangers are composed of complex networks of tightly arranged arterioles and venules that function in opposite directions. The aim is to reduce convective heat loss from the gills by facilitating the transfer of heat from the warm venous blood leaving these muscles to the cooler arterial blood returning from the gills (Runcie et al., 2009; Stevens, 2011). As a result, the cold oxygen-rich blood from each efferent arteriole takes in heat from the warm deoxygenated blood of the afferent arteriole, thus becoming heated before it is distributed throughout the body. In addition to cranial retia mirabilia, opah possesses additional counter-current retia mirabilia within each thick, fat-insulated gill arch, where heat loss is greatest. These retia mirabilia are created by closely packed afferent arterioles (which deliver blood to the gills) and efferent arterioles (which collect blood from the gills), arranged in an alternating pattern within each arch. Consequently, the cold, oxygenated blood from each efferent arteriole absorbs heat from the warm, deoxygenated blood of the afferent arteriole, warming it before it is circulated throughout the body.

***Heat conservation by adipose tissue covering*:** The significant role of thick adipose tissue in heat retention in opah has been documented (Runcie et al., 2009; Wegner et al., 2015). The thick layer of fat in heat-producing regions and gills acts as an insulator, reducing heat loss. A substantial adipose tissue layer has been noted over the opisthotic bone, which is situated above the proximal area of the lateral extraocular rectus muscle and between the proximal region of the lateral extraocular rectus muscle and the gill cavity (Runcie et al., 2009). Additionally, the adipose tissue layer encasing the rear of the eyeball offers extra insulation. A layer of fatty connective tissue (0.88±0.21 cm in thickness) has also been observed over the dark red aerobic pectoral muscle, functioning as an insulator (Rosenblatt and Jhonson, 1976; Wegner et al., 2015). Furthermore, opah possesses the capability to elevate the heart's temperature by absorbing warm blood from both the coronary arteries and the systemic venous return. Additionally, it can insulate the heart due to a substantial fat layer (Wegener et al., 2015).

Genetic association related to whole-body endothermy

Metabolic heat production: Several genes involved in muscle development and differentiation, such as Gli1, Dcn, Paxbp1, and Mef2c (Cheng et al., 2010; Sun et al., 2013), have been identified as undergoing positive selection and rapid evolution in opah (Bo et al., 2022). Conversely, seven genes, including Myom2, Myom3, M-protein, Tcap, Tmod4, Unc45a, and Unc45b, have been identified in opah and are associated with myofibril assembly (Bo et al., 2022).

The continuous contraction and relaxation of pectoral muscles require the regulation of contractile protein activity, which is controlled by calcium ions. Bo et al. (2022) documented the active involvement of three genes: Casq2 (a calcium storage protein in the sarcoplasmic reticulum), Pdgfra (which aids in muscle development and regeneration), and Phka_b, along with three gene families, Camk2, Htr2, and Igh that contribute to the relentless contraction of pectoral fin muscles in opah.

To sustain thermogenesis, an adequate energy supply is crucial. In this context, two genes, Dlat and Pgm2, have been noted in opah, facilitating gluconeogenesis and the tricarboxylic acid cycle (Bo et al., 2022). Additionally, Ldhm, the primary LDH (Lactate dehydrogenase) isoenzyme in skeletal muscle, has been found to exhibit significantly higher activity in opah (Bo et al., 2022).

Intracranial thermogenesis: Bo et al. (2022) corroborated the findings of Runcie et al. (2009) through genomic analysis. The Sln pathway primarily facilitates intracranial thermogenesis in fish (Franck et al., 2019), and in opah, the Ryr1 [facilitates the liberation of Ca^{2+} from the sarcoplasmic reticulum (Maurya and Periasamy, 2015)] and Serca [functions as a calcium pump and attaches to Sln, leading to the discharge of Ca^{2+} back into the cytoplasm (Franck et al., 2019)] genes have been identified as being subject to positive selection and rapid evolution, which contribute to an increased supply of calcium in circulation, resulting in the generation of additional heat (Bo et al., 2022).

***Heat conservation by retia mirabilia*:** The alignment of arterioles and venules in retia mirabilia is induced by apelin, whose expression is under the control of Ang-1 (Kidoya et al., 2015). In opah, expansion of the Ang-1 gene has been documented by Bo et al. (2022).

***Heat conservation by adipose tissue covering*:** Aact, Insig1, and Ebf2 are three genes involved in fatty acid metabolism; the positive selection and rapid evolution of these genes in opah have further reinforced the significance of fatty acids in heat-generating regions (Bo et al., 2022).

Evolution of endothermy in opah

To exemplify convergent evolution, the independent evolution of endothermy in fish has been noted to occur six times; occurring twice in sharks (the lamnid sharks and the common thresher, *Alopias vulpinus*) and four times in teleosts (such as billfish, butterfly mackerel, tuna, and opah) (Davesne et al., 2018; Frank et al., 2019). By analyzing the bone histology of *Lampris*, Davesne et al. (2018) proposed that opah has co-evolved alongside other regional endothermal fish that exhibit regional/red-muscle endothermy, and they predicted a relationship between bone histology and endothermy in fish.

Strong genomic evidence of convergent evolution of whole-body endothermy in the opah has been documented by Wang et al. (2021) through comparison of the opah with mammals, birds, and other regionally endothermic fishes. They have conducted a detailed study of the molecular foundations of endothermy evolution in the opah and reported that the opah genome has the highest proportion of long terminal repeat (LTR) retrotransposons among teleosts. The expansion of these retrotransposons, which occurred around 15 million years ago, may have influenced gene expression and translocation, thereby contributing to the endothermic capabilities of opah. Furthermore, a total of 850 gene families have been identified as expanded in opah, along with 233 positively selected genes (PSGs). A significant number of the identified expanded gene families are involved in muscle fiber composition and the contractile machinery of muscles.

PSGs such as alg2, med12, and rmnd1 are key regulators of muscle formation and development, whereas robo4, utp14a, and utp15 regulate the genesis, regulation, and patterning of the vasculature. Consequently, these expanded gene families and PSGs identified in opah may be linked to the evolution of the counter-current retia mirabilia. The PSGs are also significantly involved in the metabolism of organic substances and nitrogen compounds. For example, agrp is responsible for regulating energy homeostasis; acsf4 and acot8 participate in lipid metabolism, and ndufa10, ndufs4, and cox15 encode fundamental proteins in the mitochondrial electron transport chain, which is essential for oxidative phosphorylation. Furthermore, gene families associated with carbohydrate metabolism (enolase, gapd), lipid metabolism (mcadd), and oxidative phosphorylation (atp1a1, cox7a2, cytc, and ndufv) have been identified as being expanded in the opah genome, suggesting improved physiological functions, such as enhanced aerobic performance, food digestion, and assimilation.

In addition to genomic analysis, Wang et al. (2021) examined the transcriptomic and proteomic features of the pectoral musculature in opah, identifying 100 genes that show the highest expression levels in the inner layer of this musculature. This group includes several expanded gene families, such as ATP synthase F0 subunit 6 (atp6), glyceraldehyde-3-phosphate dehydrogenase (gapdh), cytochrome c oxidase (cytc), and troponin (troponin), along with proteins like Atp6, Cytc, Gapdh, myosin, and troponin. These proteins are known to be involved in ATP biosynthesis, cytochrome-mediated heat production, glycolysis, and skeletal muscle contraction. The increased expression of these proteins likely indicates their involvement in endothermy, which is linked to thermogenesis and oxidative phosphorylation, thereby offering significant insights into the genetic basis of the evolutionary adaptation of 'whole-body endothermy' in opah.

A convergent amino acid change at the V198A location found in the conserved GRX domain of glutaredoxin3 (glrx3) has been noted. Since glrx3 plays a crucial role in Fe/S protein biogenesis and is

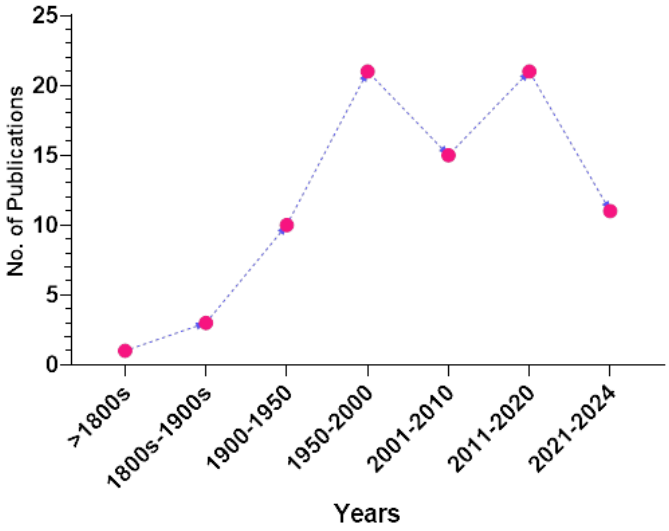

Figure 1. Year-wise publication trend on opah as a model species of investigation from the early 1800s to 2024.

indispensable for haemoglobin maturation, the substituted amino acid at the convergent site in opah could modify its ability to supply oxygen to the musculature, consequently affecting muscle strength and endurance; thus, supporting metabolic heat production by continuous movement of pectoral fins. In addition, 13 PSGs such as polr3, poc5, slbp, spata7, tubgcp6, scaper, tbc1d7, opa1, trim44, dnmbp, iars2, aim1, ncapg, along with one expanded gene family, crystalline, have been identified in opah, which is correlated with enhanced visual capabilities that are crucial for opah to capture active prey in the dark, frigid habitat at substantial depths (Wang et al., 2021).

Research trend on opah

A total of about 82 research papers and general articles have been published on opah to date. The year-wise publication trend indicates a gradual increase in research output from the 1800s to the 2000s. However, comparatively fewer studies were published during the early 2000s (2001-2010). A notable upward trend has been observed since 2011, highlighting the growing scientific interest and emerging significance of this species (Fig. 1).

Among the total publications, the majority focus on distribution (36 studies; 43.90%), followed by biology (10 studies; 12.19%) and endothermy (6 studies; 7.31%). Additional research areas include general information (6.10%), storage quality (4.88%), taxonomy (4.88%), isolation of biomolecules (3.66%), sensory system (3.66%), species description (2.44%), parasite infestation (2.44%), catch statistics (2.44%), anatomy (2.44%), physiology (1.22%), morphology (1.22%), habitat (1.22%), nutritional quality (1.22%), and developmental biology (1.22%), each represented by relatively few studies (Fig. 2).

Further analysis of year-wise trends across research themes reveals a consistent and increasing focus on endothermy. Particularly after 2005, studies investigating opah endothermy gained substantial scientific attention and continue to show a progressive trajectory (Fig. 3).

These findings underscore the timeliness of the present review, particularly in synthesizing knowledge on the endothermic capability of opah and identifying directions for future research. In addition to endothermy, research on distribution, storage quality, biomolecule isolation, and catch statistics also demonstrates an upward trend. Considering the overall research trajectory of this unique species, the analysis suggests the importance of integrating distributional studies with investigations of endothermic regulation. Such a combined approach may enhance understanding of the expanding ecological occupancy and biogeographic patterns of opah across different eco-regions, as indicated by Bo et al. (2022).

Concluding remarks

The case of whole-body endothermy in the opah fundamentally redefines the long-standing “cold-blooded” paradigm traditionally ascribed to teleost fishes. By sustaining elevated body temperatures throughout the body, opah transcends the limitations of regional endothermy and demonstrates that full systemic thermal regulation is both physiologically attainable and ecologically advantageous in a pelagic fish lineage. This capability is underpinned by a highly integrated suite of adaptations, including continuous pectoral fin-driven metabolic heat production and an elaborate counter-current heat-exchange system within the gill arches that minimizes thermal dissipation at the critical interface with the environment.

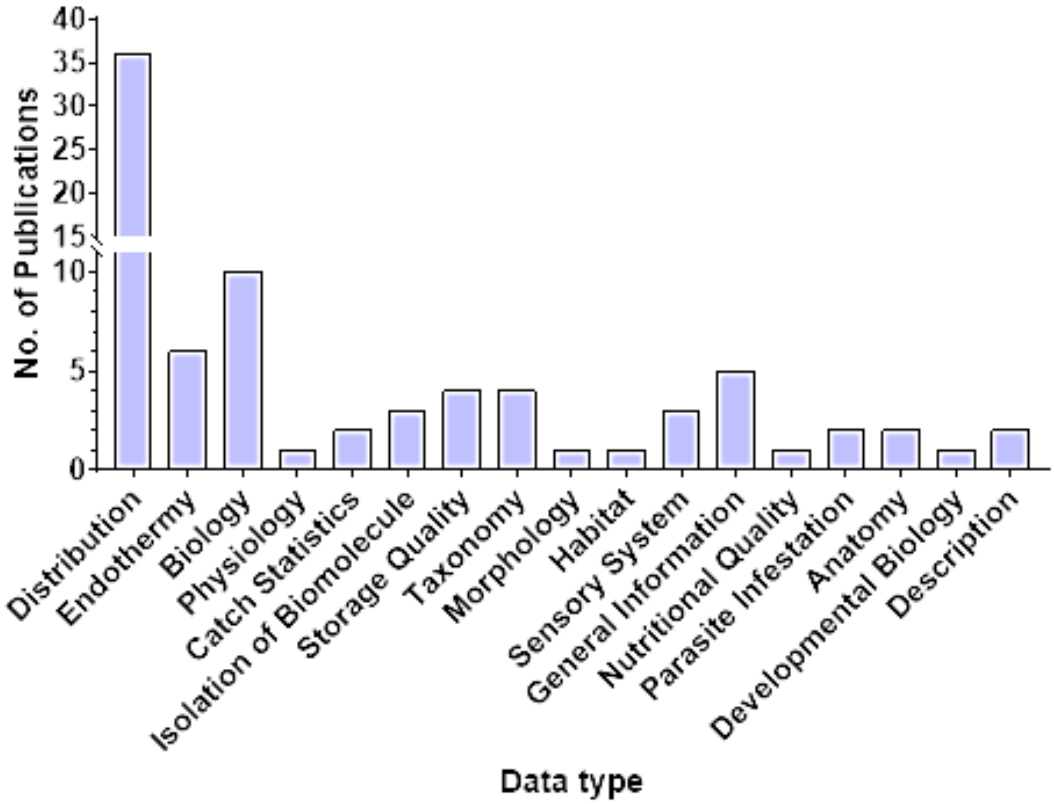

Figure 2. Bar graph showing the number of publications across different subject categories related to opah worldwide from the 1800s to 2024.

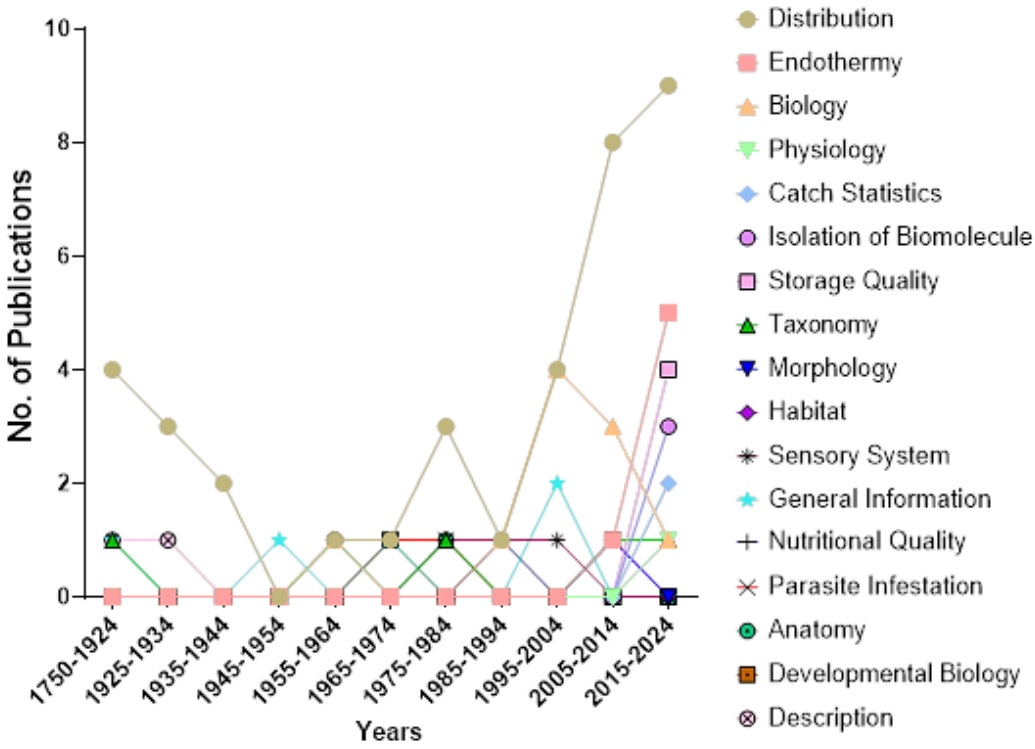

Figure 3. Line graph illustrating the subject-specific, year-wise research trends on opah, highlighting the marked increase in studies on endothermy after 2005.

At the systems level, whole-body endothermy in opah confers expanded vertical habitat utilization, enhanced sensory processing (particularly retinal and neural function under low-temperature regimes), and

sustained cardiac output at depth. These traits likely translate into improved prey detection and capture efficiency in mesopelagic environments, reinforcing the ecological significance of endothermy as a driver of niche expansion. Importantly, the opah condition challenges the canonical dichotomy between ectothermy and endothermy in fishes, instead supporting a continuum of thermoregulatory strategies shaped by ecological demand and biomechanical constraints. From an evolutionary perspective, opah endothermy challenges traditional views of thermoregulation in ectothermic vertebrates and highlights convergent evolution of heat-retention mechanisms in response to ecological pressures. It underscores how selective advantages in foraging, predator avoidance, and habitat utilization can drive the emergence of energetically costly physiological traits.

Despite these advances, several aspects of opah biology remain insufficiently explored. Future research should focus on the ontogeny of thermal regulation, particularly the timing of rete development and metabolic upregulation, as well as the energetic trade-offs associated with maintaining elevated body temperatures. Integrative approaches combining biologging, respirometry, and ecological modeling are needed to resolve energy budgets under variable thermal and oxygen regimes. Such data will be pivotal for predicting species responses to ongoing oceanographic changes, including warming, deoxygenation, and altered prey fields. Given that metabolic demand in endothermic fishes scales nonlinearly with temperature and activity, opah may exhibit heightened sensitivity or, conversely, adaptive buffering to climate-driven environmental variability.

In conclusion, the opah exemplifies a remarkable evolutionary breakthrough that not only “breaks” the cold-blooded rule but also expands the conceptual boundaries of vertebrate thermoregulation. Continued interdisciplinary research integrating physiology, genomics, ecology, and oceanography will be critical to fully elucidate the mechanisms and ecological consequences of this unique adaptation, offering broader insights into the resilience and adaptability of marine organisms in a rapidly changing ocean.

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