

World as it is

Adaptations to breath-hold diving: from traditional divers to elite athletes

Jochen D Schipke¹, Ulrich Limper^{2,3}, Kay Tetzlaff⁴

¹ Research Group Experimental Surgery, University Hospital Düsseldorf, Düsseldorf, Germany

² German Aerospace Center, Institute of Aerospace Medicine, Cologne, Germany

³ Department of Anaesthesiology and Critical Care Medicine, Cologne-Merheim Medical Center, Hospital of Witten/Herdecke University, Cologne, Germany

⁴ Department of Sports Medicine, Medical Clinic, University Hospital Tuebingen, Germany

Corresponding author: Professor Jochen Schipke, Research Group Experimental Surgery, University Hospital Düsseldorf, Moorenstrasse 5, D-40545 Düsseldorf, Germany

ORCID: [0000-0002-1747-5657](https://orcid.org/0000-0002-1747-5657)

j.schipke@gmx.org

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Abstract

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Breath-hold diving exposes humans to repeated episodes of profound hypoxia and hypercapnia, eliciting physiological adaptations that enable prolonged underwater performance. This article summarises current knowledge on chronic adaptations in elite breath-hold athletes and traditional diving populations, including the Bajau sea nomads of Southeast Asia and the Korean Haenyeo divers. Evidence indicates that repeated apnoea induces adaptations across multiple physiological systems. Haematological changes include increased spleen size and enhanced splenic contraction, augmenting circulating haemoglobin and oxygen stores during apnoea. In elite divers, structured training can increase resting spleen volume, whereas the Bajau exhibit genetically associated splenic enlargement linked to variants near the PDE10A gene. Cardiopulmonary adaptations include modified pulmonary vascular responses to hypoxia, improved oxygen conservation, and metabolic shifts favoring efficient mitochondrial energy production. Molecular adaptations involve enhanced antioxidant defenses and activation of hypoxia-responsive pathways that may mitigate oxidative stress associated with repeated hypoxia-reoxygenation cycles. Emerging evidence also suggests neural plasticity and possible structural brain adaptations, although the long-term neurological consequences of chronic intermittent hypoxia exposure remain uncertain. Studies of traditional diving populations indicate that both phenotypic plasticity and genetic selection contribute to diving capacity, highlighting interactions between training and evolution. Despite these benefits, breath-hold diving also carries risks, including hypoxic blackout, decompression sickness, and potential neurological injury. Understanding the mechanisms underlying human tolerance to extreme hypoxia may have implications beyond diving physiology, including applications in cardiovascular medicine, hypoxic diseases, and rehabilitation. Further longitudinal, genomic, and mechanistic studies are needed to clarify the limits, benefits, and clinical relevance of these adaptations.

Introduction

Breath-hold diving has been practiced by humans for thousands of years, driven both by subsistence needs and, more recently, recreational and competitive sport. This practice subjects the body to repeated episodes of severe oxygen deprivation, creating selective pressure for physiological adaptation. Unlike gradual altitude hypoxia, apneic diving imposes acute arterial oxygen desaturation – often below 50% – while carbon dioxide accumulates.^{1,2} Elite competitive divers now achieve static apnoeas exceeding 8 min and descents beyond 100 m, performances that would rapidly incapacitate untrained individuals.³

Competitive diving represents the modern manifestation of a much older human relationship with underwater foraging. Traditional diving populations – including the Bajau people of the Coral Triangle, Moken sea nomads of the Andaman Sea, Japanese Amas and Korean Haenyeo divers – have practiced breath-hold diving for subsistence over multiple generations.^{4–6} These groups spend hours each day diving to depths of 20–70 m to harvest fish, shellfish, and sea cucumbers. Unlike athletes who train for performance peaks, traditional divers maintain diving practices throughout their lifespans, from childhood through old age, thereby creating sustained selective pressures that potentially favor genetic adaptations alongside phenotypic plasticity.⁷

The acute diving response – bradycardia, peripheral vasoconstriction, and splenic contraction – was already characterised in marine mammals by Scholander in 1940⁸ and later confirmed in humans.^{9,10} These reflexes serve to conserve limited oxygen stores for vital organs during submersion. However, chronic adaptations develop over months to years of regular diving, distinguishing experienced divers from novices.^{11,12} This article examines these chronic adaptations across multiple physiological systems, integrating findings from traditional populations and competitive athletes to illuminate both human plasticity and possible evolutionary adaptations to hypoxic stress.

Haematological adaptations: the splenic reservoir

SPLenic CONTRACTION AND ENLARGEMENT IN ATHLETES

Splenic enlargement represents a well-characterised adaptation in breath-hold divers. The spleen serves as an erythrocyte reservoir; its contraction during apnoea elevates circulating haemoglobin, increasing oxygen-carrying capacity when oxygen is most limited. While splenic contraction occurs universally during apnoea, elite athletes demonstrate both larger resting splenic volumes and greater contraction magnitudes than untrained controls.¹³

Contraction can reduce splenic volume by 40 to 50% in elite divers, releasing up to 200 ml of blood and elevating haemoglobin concentration by 3 to 10% – potentially extending tolerable apnoea duration by 30 to 60 s.¹⁴ Longitudinal training studies demonstrate that resting splenic volume increases approximately 20% after eight weeks of structured apnoea training.¹⁵ This hypertrophy appears structural rather than transient, persisting weeks after training cessation. The mechanisms likely involve chronic sympathetic stimulation and smooth muscle proliferation within the splenic capsule, occurring independently of erythropoietin-mediated red cell production.¹⁶ Although splenic contraction consistently increases circulating haemoglobin during apnoea, its quantitative contribution to overall diving performance remains incompletely resolved, as improvements in apnoea duration likely reflect the integrated effects of multiple cardiovascular, metabolic, and neural adaptations rather than a single mechanism. This process may involve structural remodeling of the splenic capsule, although direct evidence in humans remains limited, and current knowledge is primarily based on functional and volumetric observations following apnoea training.^{14,15,17}

THE BAJAU: GENETIC ADAPTATION FOR LARGER SPLEENS

The Bajau people, sea nomads inhabiting the waters of Indonesia, Malaysia, and the Philippines, represent a case of possible genetic adaptation to diving. Bajau divers routinely descend to depths of 70 m while hunting fish with spear

guns, often spending up to five hours per day underwater throughout their lifetimes.¹⁷ Notably, a participant in one study reported a single dive duration of up to 13 min.¹⁸ Comparative studies reveal that Bajau individuals possess spleens approximately 50% larger than neighboring non-diving populations, even among Bajau who do not actively dive, suggesting genetic rather than purely training-induced enlargement.¹⁹ Genomic analyses identified positive selection signatures near the PDE10A gene, which regulates thyroid hormone levels and, consequently, spleen size. PDE10A variants associated with larger spleens occur at higher frequencies in Bajau than in agrarian Saluan neighbors, suggesting selection favoring enhanced oxygen storage capacity over multiple generations.¹⁹ This finding represents one example of recent human genetic adaptation to an environmental stressor. Whether Bajau individuals also exhibit enhanced splenic contractility during apnoea, or whether their constitutively larger spleens suffice to confer advantage, remains incompletely explored. However, the functional relevance of increased spleen size for actual diving performance in Bajau individuals remains to be directly demonstrated.

Haenyeo: lifespan diving practices

The Haenyeo ('sea women') of Jeju Island, South Korea, represent a culturally distinct but physiologically comparable group. Haenyeo, predominantly women, have harvested shellfish and seaweed through breath-hold diving for centuries. Recent comprehensive studies reveal these divers spend an average of 56% of their diving time underwater – up to five hours daily – the highest proportion documented in humans and exceeding some diving mammals.²⁰ They typically dive to 10–20 m, performing 15–31 dives per hour.²¹ Studies of aging Haenyeo reveal sustained diving capacity into their 60s and 70s, suggesting that accumulated adaptations resist age-related declines in respiratory function.²²

Recent genomic analyses demonstrate that Haenyeo possess both training-induced and genetic adaptations. Lee and colleagues (2017) identified gene variants associated with reduced diastolic blood pressure. An enhanced cold tolerance in Haenyeo compared to mainland Koreans has been described already earlier.²³ The blood pressure variants may represent selection for the protection of pregnancies, as Haenyeo historically dove throughout gestation. Physiological measurements revealed enhanced bradycardia during simulated dives – likely a training effect rather than genetic – with heart rates decreasing by 18.8 beats·min⁻¹ compared to 12.6 beats·min⁻¹ in non-diving controls.²⁴ These findings establish Haenyeo as the second documented population, after Bajau, exhibiting genetic adaptations for diving.

However, lifelong breath-hold diving imposes physiological costs. Haenyeo experience decompression sickness

(DCS) attributed to repetitive dives. A study of 527 active Haenyeo identified three symptom clusters: type 1 (musculoskeletal), type 2 (neurological and systemic), and mixed presentations.²¹ Type 2 symptoms, affecting the central nervous system, were more severe in older divers with longer diving careers, raising concerns about cumulative neurological effects. Additionally, repetitive diving has been associated with chronic headaches and analgesic overuse.²⁵ These findings underscore the need to balance adaptations against potential long-term health consequences. This likely reflects cumulative inert gas uptake during repetitive dives with short surface intervals.

Cardiopulmonary adaptations

PULMONARY VASCULAR CONTROL

Elite divers demonstrate refined pulmonary vascular control that optimises gas exchange under hypoxic conditions. During apnoea, pulmonary vascular resistance increases, reducing blood flow to under-aerated alveoli – a phenomenon termed hypoxic pulmonary vasoconstriction (HPV).²⁶ Another study showed a significantly smaller increase in total pulmonary resistance compared to controls after isocapnic hypoxia.

The authors suggest that this blunted response is a beneficial adaptation that allows for increased cardiac output with reduced right heart work, thus reducing cardiac oxygen utilisation in hypoxaemic conditions. Both vascular remodeling and altered endothelial function may contribute to this adaptation.²⁷ While acute apnoea induces hypoxic pulmonary vasoconstriction, trained divers may exhibit a blunted or more finely regulated response.

Whether traditional diving populations exhibit similar adaptations remains unexplored, though their sustained diving across lifespans suggests comparable or enhanced vascular plasticity.

CARDIAC METABOLIC ADAPTATIONS

Cardiac tissue must maintain function despite severe systemic hypoxia during prolonged apnoeas. Kjeld and colleagues (2018) analysed skeletal muscle biopsies from elite divers, revealing increased mitochondrial density and enhanced expression of genes involved in fatty acid oxidation – substrates that generate more ATP per oxygen molecule than glucose. These metabolic shifts likely extend to cardiac muscle, enabling sustained contractile function under oxygen-limited conditions.²⁸ Furthermore, divers exhibit reduced oxidative stress markers post-apnoea compared to controls, suggesting upregulated antioxidant defenses that mitigate hypoxia-reoxygenation injury.^{28,29} Such adaptations may confer cardioprotective effects analogous to ischaemic preconditioning observed in clinical settings.²⁹

Neural adaptations and cognitive considerations

The brain, despite representing only 2% of body mass, consumes approximately 20% of total oxygen.³⁰ Severe hypoxia threatens neuronal viability, yet elite divers tolerate arterial saturations that would induce unconsciousness in untrained individuals. Preliminary neuroimaging suggests structural changes in divers' brains. Increased hippocampal gray matter volume has been reported in some athletes, potentially reflecting neuroplasticity comparable to that observed with exercise-induced changes in non-divers.³¹ However, the functional significance and consistency of these findings remain debated. Some studies report subtle memory deficits among competitive divers, raising concerns about cumulative hypoxic exposure,³² though the causality and clinical relevance remain unclear. Traditional divers like the Haenyeo, who maintain cognitive function into advanced age despite decades of hypoxic exposure,³³ provide counterevidence against inevitable neurological harm, yet controlled neuropsychological assessments in these populations are lacking. However, direct evidence linking apnoea training to these structural changes remains limited.

Molecular mechanisms: hypoxia-inducible factors and oxidative defenses

At the cellular level, hypoxia-inducible factors (HIFs) orchestrate transcriptional responses to low oxygen. HIF-1 α and HIF-2 α are stabilised under hypoxia, activating genes that govern angiogenesis, erythropoiesis, and metabolic reprogramming.³⁴ Whether chronic intermittent apnoea in divers induces sustained HIF activation or altered HIF signaling thresholds remains incompletely characterised. Repeated hypoxia-reoxygenation also generates reactive oxygen species (ROS), which can cause oxidative damage. Yet divers exhibit elevated baseline antioxidant enzyme activities, superoxide dismutase, catalase, glutathione peroxidase, suggesting adaptive upregulation that mitigates oxidative stress.³⁵ This hormetic response, wherein moderate oxidative stress triggers protective adaptations, may underlie observed cardioprotective and neuroprotective effects.

Individual variability and genetic factors

Variability exists in adaptive responses to apnoea training. Some individuals demonstrate substantial splenic hypertrophy, while others show minimal changes despite identical training.¹³ Genetic polymorphisms in genes regulating hypoxic sensing (e.g., EPAS1, EGLN1) or vascular function (e.g., NOS3, ACE) may modulate individual adaptive capacity. The Bajau case demonstrates that population-level genetic selection can enhance diving-related traits, but within-population variability likely reflects polygenic architecture, in which numerous variants collectively influence the phenotype. Age, sex, and prior training history also contribute. Women generally exhibit

smaller baseline splenic volumes but comparable relative contraction percentages.¹⁷ Whether sex differences in diving performance reflect physiological constraints or sociocultural factors remains debated, though Haenyeo divers demonstrate that women can sustain elite diving performance across lifespans.

Potential risks and maladaptive consequences

While adaptations generally enhance hypoxic tolerance, potential maladaptive consequences warrant consideration. As humans lack the ability of cognitive perception of hypoxia, severe hypoxic episodes can trigger loss of motor control ('blackout'), particularly during ascent when ambient pressure decreases, and arterial oxygen precipitously drops.³⁶ Competitive divers occasionally experience blackouts, requiring rescue to prevent drowning.³⁷ Whether repeated blackouts cause cumulative neural injury remains unknown. Additionally, concerns exist regarding the risk of arterial gas embolism (AGE);³⁸ rapid ascents from depth may generate intrapulmonary pressure gradients that force gas into the pulmonary veins.³⁹ Traditional divers, whose gradual ascents and conservative depth limits contrast with competitive extremes, appear to avoid such pathology, suggesting that dose-response thresholds distinguish beneficial adaptation from harmful exposure.

Clinical and evolutionary implications

Understanding diving adaptations holds clinical relevance beyond performance optimisation. Chronic obstructive pulmonary disease, obstructive sleep apnoea, and high-altitude illnesses involve chronic or intermittent hypoxia. Mechanisms enabling divers to tolerate severe hypoxia, enhanced antioxidant defenses, metabolic flexibility, cerebrovascular autoregulation, may inform therapeutic strategies for these conditions. Intermittent hypoxic training protocols, inspired by diving and altitude physiology, are being explored for cardiovascular rehabilitation.⁴⁰ Additionally, perioperative risk stratification might benefit from understanding individual hypoxic tolerance, potentially identifying patients at elevated risk for complications during anaesthesia.

From an evolutionary perspective, the Bajau provide a case study of recent human adaptation. Their genetic signatures demonstrate that within the last few thousand years, selection can reshape human physiology in response to environmental pressures. This challenges the notion that human evolution is solely ancient history, revealing ongoing adaptive processes in contemporary populations.⁷ Whether other diving populations harbor similar genetic adaptations, or whether phenotypic plasticity alone suffices to explain their capabilities, remains an open question with implications for understanding the interplay between genes and environment in shaping human diversity.

Future directions and knowledge gaps

Gaps still persist in our understanding of diving adaptations. Some areas that could benefit from further investigation include:

- » Longitudinal studies tracking adaptations from novice to elite status remain relatively uncommon, which would help strengthen causal inference regarding training effects.
- » Molecular profiling of HIF pathway dynamics, mitochondrial function, and epigenetic modifications across training timescales could help elucidate underlying mechanisms.
- » Comparative genomic studies of Moken, Haenyeo, and other traditional diving populations could help determine whether genetic adaptations analogous to those of the Bajau exist elsewhere, or whether the Bajau represent a unique evolutionary outcome.
- » Neuroimaging studies combining structural MRI, functional MRI, and neuropsychological testing could help clarify whether cognitive changes in divers reflect detrimental hypoxic injury or benign plasticity.
- » Safety thresholds distinguishing adaptive from maladaptive hypoxic exposure remain to be fully defined; establishing evidence-based guidelines for training intensity and recovery could help reduce injury risk while optimising performance.
- » Translational research exploring whether diving-derived adaptations can be pharmacologically or behaviorally induced in non-divers could potentially yield novel therapeutic interventions for hypoxic diseases.

Conclusions

Breath-hold diving appears to elicit physiological adaptations spanning hematological, cardiopulmonary, metabolic, and neural systems. Elite athletes can develop these adaptations through intensive training, while traditional populations such as the Bajau and Haenyeo have sustained diving practices across generations, potentially embedding these adaptations into their genomes. The interplay between phenotypic plasticity and genetic selection in shaping human diving capacity may offer insights into principles of adaptive physiology and evolutionary medicine. Continued research integrating exercise physiology, genomics, and clinical medicine has the potential to reveal therapeutic applications of these adaptive mechanisms while enriching our understanding of human biological diversity and resilience to environmental challenges. This should be interpreted cautiously, as such findings rather suggest potential heritable genetic adaptations rather than fully established genomic embedding.

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