

Review articles

Predicting performance in competitive apnea diving. Part II: dynamic apnea

Erika Schagatay

Key words

Breath-hold diving, hypoxia, exercise, cardiovascular, respiratory, physiology, safety, review article

Abstract

(Schagatay E. Predicting performance in competitive apnea diving. Part II: dynamic apnea. *Diving and Hyperbaric Medicine*. 2010;40(1):11-22.)

Part I of this series of articles identified the main physiological factors defining the limits of static apnea, while this paper reviews the factors involved when physical work is added in the dynamic distance disciplines, performed in shallow water in a swimming pool. Little scientific work has been done concerning the prerequisites and limitations of swimming with or without fins whilst breath-holding to extreme limits. Apneic duration influences all competitive apnea disciplines, and can be prolonged by any means that increase gas storage or tolerance to asphyxia, or reduce metabolic rate, as reviewed in the first article. For horizontal underwater distance swimming, the main challenge is to restrict metabolism despite the work, and to direct blood flow only to areas where demand is greatest, to allow sustained function. Here, work economy, local tissue energy and oxygen stores and the anaerobic capacity of the muscles are key components. Improvements in swimming techniques and, especially in swimming with fins, equipment have already contributed to enhanced performance and may do so further. High lactate levels observed after dynamic competition dives suggest a high anaerobic component, and muscle hypoxia could ultimately limit muscle work and swimming distance. However, the frequency of syncope, especially in swimming without fins, suggests that cerebral oxygenation may often be compromised before this occurs. In these pool disciplines, safety is high and the dive can be interrupted by the competitor or safety diver within seconds. The safety routines in place during pool competitions are described.

Introduction

This series of articles deals exclusively with competitive apnea diving. This is fundamentally different from the repeated foraging and hunting diving activities undertaken by the Ama of Japan, or in spearfishing and team sports activities involving high levels of exertion during short dives, e.g., underwater hockey or rugby.¹⁻³ In competitive diving the aim is to perform one dive of maximal duration, distance or depth, whilst avoiding hypoxic syncope. The factors determining the limits of apneic duration at rest (static apnea, STA), a major prerequisite for performance in all competitive apnea disciplines, were summarised as:

- total body gas storage capacity in lungs, blood and tissues;
- tolerance to asphyxia;
- metabolic rate.⁴

Distance swimming, where physical work is added to the stressors, and diving to depth, where pressure effects are superimposed, each impose new, potentially limiting factors. The focus in this second article will be on the limiting factors of working apneas for maximal distance swimming in shallow water in dynamic apnea with (DYN) and without (DNF) fins. Few scientific studies directly concerning these disciplines have been done, and no previous review in this field exists. The main factors determining performance in the dynamic disciplines will be presented, but calculation of the relative influence of these factors is not possible given our

present knowledge. A model of the relationships between several of the factors involving calculations of gas exchange during deep working dives has been published,⁵ yet several conditions differ in horizontal diving.

In the past two decades, performance in competitive apnea diving has shown a surprising and escalating development: of 12 male and female world records in the six main competition disciplines in January 2009, only three remain unchanged one year later. A central issue is: can the safety measures taken during training and competition keep pace when records approach the human limits in duration, distance and depth? The thorough risk-management safety systems developed amongst elite divers and during competitions will be described here. The risks and pathological effects of apneic diving have been well reviewed recently.^{6,7} It is important to emphasize at the outset that record attempts and training for apnea sports should never be done without proper knowledge of the risks involved and how to prevent them. Without doubt, the beginner apneist is at higher risk than the elite free diver.

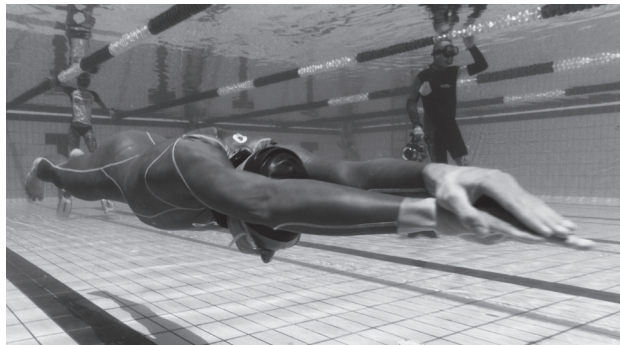
Working without breathing – dynamic apnea

Competitive dynamic apnea is performed in a pool, the aim being to cover the longest possible distance, without any time limitation. Distance swimming is initiated from a resting state and physical work starts simultaneously with

Figure 1
Record-holder Natalia Molchanova during DYN at the World Championships 2008



Figure 2
Record-holder William Trubridge during DNF at the World Championships 2008



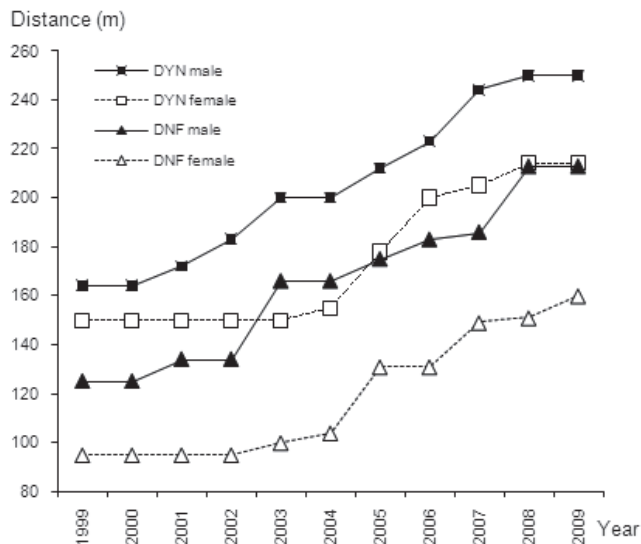
the dive. The two dynamic apnea disciplines, DYN and DNF differ in the presence of fins for propulsion (Figures 1 and 2). The physiological consequence is that in DYN, which is performed on the elite level almost exclusively with a monofin, the work is restricted to the legs, pelvis, lower abdomen and back, while in DNF the propulsion resembles breast stroke swimming, i.e., the whole body is at work, but with little dorsoventral flexion of the back compared to the dolphin-style kick used with a monofin. While there is one glide phase in DYN, there are two in DNF, one after each of the arm and leg strokes, which are performed separately. The record distances tell us something about the differences in energy requirements: the current world record in DYN is 250 m for men and 214 m for women, while in DNF the records are 213 m for males and 160 m for females (Figure 3). Thus, distances are 15–25% shorter in DNF than in DYN, whilst the dive times are similar, reflecting the greater energy cost when swimming without fins.

Anthropometrics may have a greater impact on results in DNF. Just as in swimming, there are benefits to having big hands and feet and a long arm reach.^{8,9} The smaller difference between DNF and DYN records among males could be because of their relatively larger hands and feet, and more powerful upper-body pull phase than females. Technical skill and work economy may also be more important in DNF, where energy wasted is greater due to thrust being smaller. As swimming propulsion is required over the entire horizontal distance attempted, except that obtained from the push-off from the pool sides involving explosive work, DNF is likely the energetically most demanding of all the apnea disciplines, with the ‘constant weight, no fins’ (CNF) depth discipline, involving passive sinking during the free-fall phase, second. The two major differences from deep diving are that in dynamic apnea work for propulsion is required during the entire dive, and no initial period of hyperoxia precedes the development of hypoxia. Apnea exceeding ten minutes at rest in STA may be impressive; yet swimming 250 m underwater on one breath indicates that the maximal human aerobic dive limit and anaerobic work capacity may exceed that formerly considered possible.

Blood flow distribution: priority of regions versus overall shortage

Local hypoxia occurs in many sports and distribution of blood flow is the main problem, but in dynamic apnea, the challenge is to sustain propulsive work during progressive systemic hypoxia. During resting apneas, the diving response reduces heart rate and cardiac output, and directs the blood flow mainly towards the brain and heart, while the rest of the organism receives a more limited blood flow.^{4,10} The response is initiated at apnea onset and is thereby ‘hypoxia preventive’.¹¹ It is enhanced by facial chilling and has priority over other homeostatic responses, e.g., related to body chilling and immersion.^{12,13} The response develops and conserves oxygen even if the apnea is preceded by work,¹⁴⁻¹⁶ or starts simultaneously with work.¹⁷ It has been suggested that during swimming dives, working muscles will also receive part of the blood flow.¹⁸ In experiments simulating DYN, with apnea and work initiated at the same time, heart

Figure 3
Record development for DYN and DNF during the past decade



rate falls to a level intermediate between that of rest and of eupneic work, and apneic oxygen consumption ($\dot{V}O_2$) was reduced by 25% during exercise, and by 40% during resting apneas.¹⁹ The diving response will thus favor the central circulation and to some extent working muscle. However, when blood oxygen content is depleted, the main problem is the tolerance of the brain to hypoxia. While brain hypoxia will eventually lead to syncope, muscle asphyxia may lead to lost muscle force and loss of power in propulsion. The central question is which will occur first.

There are at least two mechanisms that prioritise brain oxygenation during immersed apnea: centralization of blood flow by peripheral vasoconstriction via the diving response, and CO_2 -induced cerebral vasodilation.^{10,20,21} During non-immersed, maximal resting apnea, skeletal muscle oxygenation decreased earlier than cerebral oxygenation.²² A study involving short resting and working apneas, showed that brain blood flow increased in both situations.²³ In the face of diminishing blood oxygen supply to working muscle, local muscle oxygen stores as well as hypoxia tolerance must be maximized in the dynamic apnea disciplines.

The efficiency of the diving response to conserve oxygen depends on both the rate of response development and the extent of reduction in cardiac output. It has been suggested that the onset of the response is affected by hypoxia and work, but not its final level of adjustment.²⁴ However, at least in trained divers, bradycardia is enhanced toward the end of the apnea.^{25,26} Some divers claim that by starting a dynamic apnea with a passive apneic phase, the diving response will be allowed to restrict peripheral blood flow more efficiently than if work starts immediately (personal communications from divers, 2008). This has not been validated yet and, although this is not a technique used in competition today, any such changes could enhance performance as long as peripheral muscle hypoxia is not the main limiting factor.

Myoglobin

Myoglobin is a heme protein involved in both oxygen transport and storage within the muscle cell. With enhanced local oxygen stores in the form of increased myoglobin, the environment in working muscles would be greatly improved in the diver, leaving elevated circulating oxygen levels for the brain and heart. High myoglobin concentration is regarded as an important adaptation to apneic diving in mammals, extending the time the diver can rely mainly on stored oxygen to sustain aerobic metabolism.^{27,28} In marine mammals, a difference in myoglobin concentration between swimming and other muscles develops in association with their start in diving activity, suggesting that this could be a result of training.²⁹ More myoglobin is present in the swimming muscles of species that perform long, deep, dives than those that make shorter, shallow dives.²⁸ Myoglobin has a much higher affinity for oxygen than haemoglobin, and for the stored oxygen in myoglobin to become available for aerobic metabolism, the partial pressure of oxygen has

to be low. If the diving response shuts off circulation at an early stage, the switch to myoglobin-derived oxygen would presumably occur earlier.³⁰ Swimming muscle mitochondrial density was found to be increased but capillary density much lower in seals compared to in dogs, suggesting that oxygen is mainly derived from within the muscle cells.³⁰

In humans, myoglobin may be mainly an oxygen diffusion facilitator.³¹ High-altitude dwellers have a higher muscle myoglobin concentration than lowlanders,³² but data on the effect of endurance training during hypoxia on myoglobin concentration are conflicting.^{33,34} Short-term altitude exposure (7–9 days at 4,500 m) leads to hypoxia-induced erythropoiesis but, at the same time, a down-regulation of myoglobin may occur in order to release iron for enhanced erythropoiesis.³⁵ This could be different during long-term exposure to altitude hypoxia, when iron availability is not limiting. Apnea training has been shown to elevate erythropoietin levels, which could possibly conflict in the short term with myoglobin elevation.³⁶ Thus, the situation in human divers remains unclear, as neither the presence of efficient vasoconstriction in working muscle during diving, nor their levels of myoglobin have been established. As will be seen in the next section, post-dive lactate levels are increased in DYN and DNF, indicating the contribution of anaerobic metabolism. Lactate accumulation will decrease the affinity of myoglobin for O_2 , thus facilitating diffusion of O_2 to mitochondria for sustained oxidative phosphorylation during apnea.³⁷ Thus, with lactate development in dynamic disciplines, increased oxygen supplies may be made available, leading to prolongation of aerobic metabolism in parallel with the anaerobic one.

Anaerobic metabolism and performance

Ama divers at Hegura, Japan, sustain repeated diving of limited depth and duration for several uninterrupted hours, with surface intervals of similar duration to the dives, spending nearly half of their working time underwater (Schagatay E and Lodin-Sundström A, unpublished observations, 2009). This suggests that these dives are within aerobic dive limits. In Korean Ama, pH was observed to decrease only slightly.³⁸ On the other hand, elite apnea divers may require both enhanced aerobic and anaerobic capacity to perform maximal competition dives. Aside from a small contribution from energy-rich phosphates, the production of lactate from muscle glycogen is the most important anaerobic process for energy production. Lactate increases after both resting apneas and apneas involving exercise, showing that a net production occurs during apnea.^{11,16,39,40} During eupneic work, part of the lactate produced in working muscles is catabolised by the less active muscles or used during recovery to resynthesize glycogen.⁴¹ However, during apneic diving, lactate removal from working muscles may be a significant problem due to selective vasoconstriction, and restricted blood flow may lead to considerable regional differences in lactate concentration.

To our knowledge there are no published studies on lactate levels after competition DNF and CNF dives. Preliminary data have been reported from experimental pool dives, showing in STA an elevation from 1.2 to 2.2 mmol·L⁻¹, and from 1.8 to 6.8 mmol·L⁻¹ in DYN, but information concerning the exact protocol, sampling site and times was lacking.⁴² We recently measured capillary lactate two to four minutes after competition dives during a world championship. In the same eight subjects, DYN and DNF resulted in similar levels of approximately 10 mmol·L⁻¹ (normal resting range: 1–2 mmol·L⁻¹; Schagatay E and Lodin-Sundström A, unpublished observations, 2009; Figure 4). The mean distances covered were 173 m in DYN and 135 m in DNF ($P < 0.001$), suggesting that the workload was significantly reduced by using fins. Capillary blood lactate levels were also elevated to over 5 mmol·L⁻¹ in two competition STA dives exceeding eight minutes. This demonstrates that the diving response effectively shuts down some areas from circulation, causing anaerobic metabolism even under resting conditions. These lactate levels are substantially higher than previously reported after both resting and working experimental apneas, and clearly show the importance of anaerobic pathways during maximal competition apneas. Interestingly the levels after dynamic apneas were in the same range as values seen after 200-yard, maximal-effort freestyle swims, despite only comparatively moderate levels of physical exertion in the apneic swims.⁴³

Hypoxia impairs endurance performance by causing premature muscle fatigue,⁴⁴ which could limit performance in dynamic apnea. The causes of muscle fatigue are complex, and only partially understood, and may be central or peripheral in origin.^{44–48} The traditional view, that acidification will be limiting to performance by disrupting the contractile processes,⁴⁹ has been challenged by more recent research, suggesting several possible mechanisms such as ATP depletion that results in intracellular accumulation of potassium, inorganic phosphate accumulation when creatine phosphate is hydrolysed, and negative effects on calcium availability and its binding to troponin.^{45,50} Acidosis-induced discomfort may, in itself, limit performance even before muscle functions are inhibited.⁴⁵ However, cerebral hypoxia may be the more acute problem in DNF, evidenced by the observation that one out of six of the DNF dives at a recent world championship resulted in syncope, while other disciplines had only a few cases (Schagatay E and Lodin-Sundström A, unpublished observations, 2009).

The high lactate levels recorded after competition dives in elite apneists in our studies seem to contrast with the findings of a fall in post-apneic lactate after long-term apnea training in triathletes.⁵¹ The authors suggested that this reduction, which could be a result of either reduced cellular production or increased catabolism, or both, is an adaptive response to hypoxic work. The increase in lactate in that study was low compared to our observations,⁵¹ suggesting that apneas were far from maximal. The lowered lactate levels seen in such voluntary non-competition dives after training may indicate

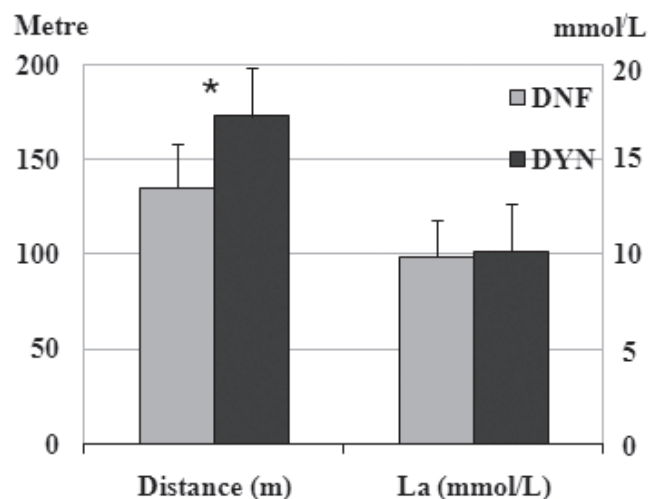
that maximal dives could be significantly extended before performance-limiting hypoxia develops.

During competitive dives, accumulation of factors leading to fatigue cannot be allowed to reach levels intolerable to the working muscles, or the dive will be terminated due to loss of propulsion. Directly after an in-competition dynamic apnea, the athlete is occasionally unable to walk and may feel the effects of the dive in the legs for some time, being unable to perform another productive competition dive in the same discipline for hours or even days. During the first minutes after a maximal competitive dive, there is also an oxygen debt that must be paid back, and blood and tissue CO₂ accumulation, which has to be released.⁵² However, normal arterial oxygen saturation was recorded within two minutes even after dynamic competition dives leading to syncope (Schagatay E, unpublished observations, 2009). Apneic swimming may be a good model for the study of the mechanisms behind hypoxic limitation of work in the presence of hypercapnia as compared to hypocapnic or eupneic hypoxia.

Preparations before diving

Preparations for sports competition are often as important to the outcome as events taking place during the actual competitive performance. This section deals with some preparatory methods explored by divers to enhance performance. Different strategies may be used and there is little consensus among divers as to what works best. While the general rule a few years ago was to perform a warm-up protocol including dives, as well as long periods of various breathing techniques, more recently no-warm-up and no-warm-up/no-breathe-up approaches have been adopted by some top divers; the physiological background to these approaches is largely unknown.

Figure 4
Mean (SD) distance covered (m) and blood lactate concentration (mmol·L⁻¹) after DNF and DYN competition dives in 8 divers; * $P < 0.001$



BREATHE UP, OR NOT?

Just as in STA, specialized breathing techniques are often used before dynamic disciplines to enhance performance.⁴ The effect of 'yoga breathing' is to lower the large, 'slow' tissue stores of CO₂ and maximize O₂ storage, allowing longer apneas before asphyxia develops.^{52,53} Yoga breathing is also used to improve relaxation and mental focus. Some divers also perform 'classical' hyperventilation just before diving, mainly to lower lung and blood CO₂ levels and delay the onset of involuntary breathing movements.^{4,54} Finally, as in STA, lung packing is used to increase the O₂ stores at the start of the dive.^{4,55,56} In dynamic apnea, however, lung packing has to be balanced against other performance requirements. Air volume for achieving neutral buoyancy at the optimal swimming depth is pre-set by the placement of neck and hip weights, and a horizontal position across the entire arm- and leg-stroke cycle is essential for reduced drag. Lung packing must also allow for efficient swimming and for turning at each pool end, but hydrostatic pressure effects may allow more packing than in STA. Dry STA and immersed DNF performance were both increased by approximately 12% after packing in trained divers, despite more packing in DNF.⁵⁷ An important aspect is to avoid 'packing blackout', caused by brain hypoxia, which may occur when the diver does not submerge quickly or deep enough after packing and the high intrathoracic pressure, by impeding venous return, causes a dramatic fall in blood pressure.⁵⁶ Excessive lung packing may even cause temporary asystole, leading to syncope, and air embolism.^{58,59}

While nearly all divers use lung packing to some extent, an increasing number of divers use a 'no-breath-up' approach without yoga breathing or hyperventilation, as they believe that the consequent rapid CO₂ accumulation and massive contractions of the diaphragm will lead to improved performance once they can overcome the associated discomfort. The rising pCO₂ does not appear to positively affect the diving response, but other explanations may be that the hypercapnia-induced cerebral vasodilatation enhances brain oxygenation,^{20,21} and possibly that the mechanical effects of the involuntary breathing movements enhance brain oxygenation by restoring cardiac output.⁶⁰ However, the relative proportion of the 'struggle phase' does not seem to affect the total apneic time achieved, implying that a longer struggle phase does not by necessity lead to prolonged apnea.⁶⁰ Differences in individual predisposition may affect the outcome of different strategies, and it appears that the preferred method in one diver may even limit performance in another. Such a lack of a common physiologically logical approach is demonstrated in other sports as well, but the effects in apnea may be greater as the sport is rapidly developing and no general consensus concerning productive methods has yet been reached, and few studies exist.

WARM UP, OR NOT?

Repeated apnea, sometimes called short-term training, leads

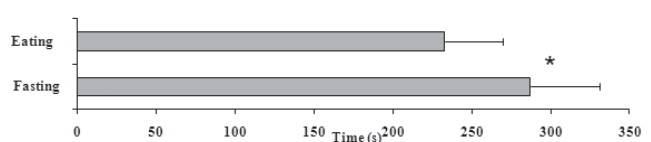
to prolongation of apnea times.⁶⁰⁻⁶² This increase in apneic duration has, at least in non-divers, both psychological and physiological components.⁶¹ The prolongation occurs without changes in pre-apneic pCO₂, lung volume, or the diving response, most likely from the release of erythrocytes from the spleen, which enhances blood O₂ storage capacity.^{62,63} These erythrocytes remain in circulation for several minutes after a warm-up apnea and would be fully saturated and contribute to oxygenation at the onset of the competition dive.⁶⁴ They may also enhance CO₂ transport out of tissues before the start of apnea and buffering capacity during the apnea. Another plausible contributor to the increased apneic duration across serial apneas could be reduced CO₂ sensitivity. A long-term reduction of the hypercapnic ventilatory response with apnea training has been noted;⁶⁵ however, there was no reduction in CO₂ sensitivity with repeated apneas at short intervals, ruling out this effect.⁶⁶

Despite the apparent physiological logic behind warm-up dives, many top divers claim they perform better without and both approaches have their advocates, across all disciplines. The no-warm-up approach suggests the possibility that a shock response is part of the most powerful protective responses against hypoxia, quite similar to the massive diving response observed during involuntary experimental dives in seals wherein the human experimenter controls the duration.⁶⁷ However, the voluntary nature of human competitive apnea would speak against such an influence. Since apnea duration is inversely proportional to the metabolic rate,^{54,68} any physical activity elevating oxygen consumption just before a dive would be counterproductive. The build up of hypoxia-related factors with incomplete recovery between warm-up dives could also limit performance in the dynamic disciplines, and the cooling effect of water on the face, maximizing the diving response, may be lost with time spent in the water.⁶⁹

EATING OR FASTING?

The benefits of fasting before maximal-duration performance in STA may be obvious as metabolism is restricted when energy intake is low.⁴ Elite apneists fasting overnight showed an increase of 23% in apneic duration compared to apneas 1.5 h after a meal (Schagatay E and Lodin-Sundström A, unpublished observations, 2009; Figure 5), twice the prolongation previously reported in inexperienced subjects.⁷⁰ Fasting before active swimming disciplines

Figure 5
Mean (SD) apneic duration after eating and after 12 h fasting in 10 divers; * $P < 0.001$



with higher energy requirements for muscle work may be more questionable, as lowering of blood glucose and liver glycogen might limit performance. While most divers practise overnight fasting before STA, many take some form of energy supplementation, but avoid large meals, before dynamic events. This discipline-specific difference in strategy was supported by the findings of lower blood glucose values before STA events (range 4.3–5.0 mmol·L⁻¹), compared to before dynamic and depth disciplines (range 4.5–6.5 mmol·L⁻¹; Schagatay E, unpublished observations, 2008). It has been suggested that breath-holding may be safer after carbohydrate ingestion as the more rapid build up of CO₂ will force the diver to interrupt the dive earlier,⁷⁰ but this is questionable in elite divers where hypoxia may be the main limiting factor.

Work economy

When pre-dive O₂ stores and CO₂ buffering capacity have been maximized, and baseline starting conditions have been optimized, the next task is to limit energy expenditure during swimming. Work economy is important in most sports but it is a crucial factor in apnea, as the limited oxygen stores set the outer limits for performance. A balance between restricted use of the stored oxygen reserves and the metabolic cost of swimming is essential. Several factors affect work economy during swimming.⁷¹ The metabolic power used to create thrust for propulsion through the water should be applied with utmost efficiency, and here the position in the water, buoyancy and anthropometrics determining biomechanical efficiency are all important factors. Correct weighting is essential for performance in the dynamic disciplines. Without proper weighting, energy is expended for maintaining the appropriate depth, such that both over- and under-weighting may cause problems. The position in the water also depends on individual lung volume and pre-dive lung packing, though final adjustments can be achieved by altering swimming depth; final weighting is often done in test runs just before competition. A challenge in DNF is to be correctly weighted and remain horizontal during the two glide phases despite the shift in the centre of buoyancy.

Swimming speed must not be too slow, as basic body functions will continue to consume oxygen at a steady rate, while the rate of oxygen consumption used for swimming should be kept within limits that allow sustained muscle function without developing performance-limiting hypoxia. Water resistance rises exponentially with increasing speed, thus increasing the work of swimming. Trained swimmers use less oxygen than untrained swimmers at a given swim speed and swim faster at a given $\dot{V}O_2$.⁷¹ A relatively high proportion of former competitive swimmers is found among the top athletes in the dynamic disciplines compared to other apneic disciplines, confirming that swimming technique and work economy are likely essential factors for performance in these disciplines. The greater distances reached in DYN, despite similar lactate accumulation and durations, show that the main difference lies in the faster speed and greater

efficiency with fins. In a study comparing crawl kick with kick using small bi-fins at the same metabolic power, speed was increased by 0.2 ms⁻¹. At similar speeds, the energy cost of fin swimming was about 40% lower than without fins because of a 40% lower kick frequency; mechanical efficiency improved by about 10%.⁷² The work economy using a monofin is likely further improved compared to small bi-fins.

Efficient turning is essential in both dynamic disciplines, and in DNF, which is usually performed in a 25 m long pool, it accounts for a considerable proportion of the propulsive force for each length of the pool. In DYN, which is mostly done in a 50 m pool, it is more likely a hindrance, as the sinusoidal stroke and relatively higher propulsive speed have to be interrupted at each turn.

Physical fitness and apnea performance

While technical skill is of great advantage in the swimming apnea disciplines, it is less obvious how general physical fitness relates to performance in all apnea disciplines. A high haemoglobin (Hb), for example, will lead to both enhanced $\dot{V}O_2$ max and increased oxygen storage, but high $\dot{V}O_2$ max is not in itself related to performance, as the diver needs to minimize $\dot{V}O_2$ during apnea. It is the oxygen storage aspect of high Hb which is important. Although breath-hold duration has been reported to be correlated to $\dot{V}O_2$ max,^{73,74} two months of physical training leading to enhanced $\dot{V}O_2$ max did not increase the physiologically determined easy-going phase, showing that the two are not causally connected.⁷⁴

Earlier studies on the effects of physical fitness on the diving response have been conflicting with a positive effect, no effect, or a negative effect reported.^{75–77} We found no enhancement of the cardiovascular diving response after long-term physical training,⁷⁴ nor a correlation between competition results and hours of general physical training during two months preceding a major apnea competition (Schagatay E, unpublished observations, 2006). While swimming-muscle strength is necessary for performance, excessive muscle is costly in terms of oxygen consumption even when inactive. On the other hand, increased blood volume associated with high lean body mass may contribute to apneic duration, so the net effect is difficult to assess.⁴ The morphological characteristics of competitive apneists have not been studied, but the impression is of greater variation in body composition compared to athletes in other sports.

While the benefits of general physical fitness for apnea performance may be uncertain, apnea-specific training has clear positive effects.^{4,74} Some of the performance-related effects reported are:

- increased total lung volume;
- enhanced erythropoiesis;
- enhanced conscious tolerance of hypoxia;
- decreased sensitivity to hypercapnia;
- later occurrence of diaphragm contractions;

- greater psychological tolerance of diaphragm contractions;
- more pronounced diving response;
- decreased arterial desaturation rate reflecting decreased apneic metabolic rate;
- slower depletion of pulmonary oxygen and
- longer apnea times.⁴

Thus, a specific ‘apnea fitness’ may be reached only by apnea-related training. Additional effects are suggested by inter-group comparisons, e.g., larger spleens and higher Hb, but these differences could also reflect pre-selection and such factors need to be studied further.

Equipment

Although apneic diving is far less technology-dependent than other diving, and limiting energy expenditure is more important than maximising speed, part of the improvement in performance in the swimming disciplines has been the result of technological development. The thrust caused by human hands and feet for propulsion in water is poor compared to that by flippers of marine mammals. Only a few years ago, in both DYN and CWT, bi-fins were the main means of propulsion, whilst now, at elite levels, monofins predominate. Blade size and flexibility modifications (allowing customization), increasing the angle between foot and blade for biomechanically more efficient kicking, and drag reduction are essential in this ongoing development. While most fins used are still made of fiberglass, new materials with better mechanical properties, e.g., carbon fibre, are being introduced; but the experience of the swimmer is also essential to fin-swimming efficiency.⁷⁸

As any failure to be correctly weighted will cause unnecessary energy expenditure to remain horizontal and at the right depth, the diver uses hip, neck and sometimes leg weights for basic buoyancy adjustments and better density distribution, depending on regional density differences due to body composition, lung volume and suit used. Divers are better weighted than previously, with well-designed weights, adjusted carefully for the predicted lung volume.

The use of low-drag suits developed for swimmers has improved hydrodynamics further, with gains in distance per stroke by 5% compared to swimming trunks.⁷⁹ Whether the recent ban on such suits in swimming competitions will be extended to AIDA* competitions remains to be seen. However, the drag of naked human skin is low with values comparable to those of slender fish such as eels.⁸⁰ To further reduce drag, masks are often replaced by goggles and a nose clip in distance disciplines. Divers may also shave head and

Footnote: AIDA – The International Association for the Development of Freediving was established in 1992. It is the official sports body for the administration of international freediving competitions and the recognition of world records, and sets the standards for freediving education. The AIDA Assembly is made up of representatives of the increasing number of affiliated national freediving associations, <www.aida-international.org>.

Figure 6
Weine Gustavsson being coached during his preparation prior to a DYN competition dive



body, or use swim caps to reduce drag. In swimmers, body shaving increased distance per stroke by 5–10% thereby reducing the physiological cost of swimming.^{81,82}

Psychological requirements

Once gas-storage, anaerobic capacity and work economy have been maximized, remaining paths to increased performance are to improve the diver’s tolerance to asphyxia and the mental performance during hypoxia. While the biological tolerance of brain cells to hypoxia may be improved by training,⁸³ psychological effects of training may also help to improve tolerance to the discomfort of the urge to breathe and the capacity to focus and perform during hypoxic conditions. The capacity to cope with aching muscles and respiratory distress, and the alertness to end the dive in time are essential. Apneists use a variety of relaxation techniques in their mental preparation, both in training and in the immediate lead-up to a competition dive, but these have been little studied to date.⁴ A coach may have an important role in this process during competition before dives and in the critical phase following a dive, when instructions to breathe and focus are often given (Figure 6). While in deep diving there is no way to interrupt a dive once at depth – it is an all-or-nothing event, as there is no return once commenced except back to a surface that may be far away – in static and dynamic apnea, mental stamina will have a strong influence on apnea duration and results.

Recovery from an apnea dive

After the performance of a competitive dynamic dive there is unlimited time to rest, thus accumulation of hypoxia-related factors leading to fatigue are acceptable consequences, but the hypoxic threat to consciousness is a main obstacle. There is a delay in the nadir of arterial oxygen saturation after apnea

Figure 7
Safety diver accompanying Martin Stepanek during a DYN swim, World Championships 2006

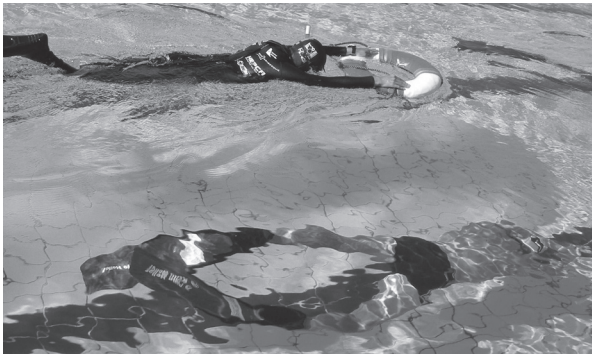


Figure 8
Per Westin surfacing from a DYN competition dive; note the safety diver immediately available to assist



Figure 9
The surface safety protocol: the diver removes his goggles, signals OK after which he says he is OK



termination, because of the circulation time from the lung to the brain, especially with vasoconstriction.¹⁷ Therefore, the recovery and safety procedures are particularly focused on this period.

To avoid syncope after surfacing, most divers use 'hook breathing', in which the breathing cycle is interrupted on inspiration and ends with a Valsalva-like manoeuvre, the subsequent expiration being done against some resistance. This technique, which awaits scientific evaluation, resembles the post-dive breathing pattern used by Ama divers who exhale against resistance, making a characteristic whistling or moaning sound (Schagatay E, unpublished observations, 2009). Ama divers state that the technique speeds up their recovery. This may be especially important after deep diving, where it would probably also aid in reversing the blood shift into the thorax, but it is used in all apnea disciplines.

There is, at present, no evidence that repeated syncopes cause any long-term effects on cognitive functions.⁸⁴ Elevation of S100B, a marker of brain damage, occurs after long, experimental apneas, but only to levels not normally associated with brain damage.⁸⁵

Safety procedures during AIDA competitions

While distance swimming in a pool is an occasional cause of death in recreational breath-hold divers, pool competitions under AIDA rules have been comparatively safe because of the rigorous safety systems put in place. Well-trained safety divers follow the competitor at arm's length throughout the swim to provide immediate assistance in the water at the first signs of hypoxia (Figures 7 and 8). In all apnea disciplines, whether in a swimming pool or open water, a surface protocol must be performed by the diver within 15 s of surfacing. This involves removing the facial equipment, showing an 'OK' hand-signal, and stating verbally "*I am OK*", in that order (Figure 9). Any failure to perform this procedure, in the correct order and without overlap between the three manoeuvres will lead to disqualification. The diver is not allowed any physical help within 30 s after a dive if it is to be registered as successful, but may receive instructions from the coach. Other causes for disqualification are dipping of the airways underwater during this period, or so-called 'post-blackout mechanical movements' involving involuntary repeated nodding of the head suggesting 'micro syncopes', or hypoxic loss of motor control (known amongst the divers as "sambas") compromising the surface protocol.

Should syncope occur, the safety diver will first do a 'blow, tap, talk' procedure (similar to the shake and call at the start of basic life support – BLS), with which, in over 90% of cases, the diver resumes breathing within seconds. If further support is needed, rescue breathing is initiated and, in extreme cases, full BLS. Trained medical personnel and equipment for oxygen treatment are immediately available on site. To date, there have been no fatalities during AIDA-

organized competitive apnea events. Competition regulations require competitors to have an annual medical assessment, and medical personnel at the competition site can remove an athlete from competition should a medical problem arise.

The safety measures adopted during competitions make these events much safer than the training done by many apnea athletes, or diving by spear fishermen and recreational freedivers without proper safety education and training. Freediving on any level should only be done with a dive buddy with enough knowledge to assist in an adverse event. Hyperventilation should not be practised by recreational free divers and diving time, depth and resting intervals should be kept to sensible limits based on individual ability. It cannot be overemphasized how important it is to contact diving schools that provide proper apnea diving education, whether one wishes to start freediving for pleasure, food gathering or competition. Any activity involving maximal apnea attempts will always carry a great risk of syncope, and should only be practised in the presence of trained safety divers. The goal with serious dive training should not be to get closer to one's existing limits, but rather to move these forward by proper training, in order to maintain the same safety margins. This is possible as many factors essential for performance can be improved by training. The safety

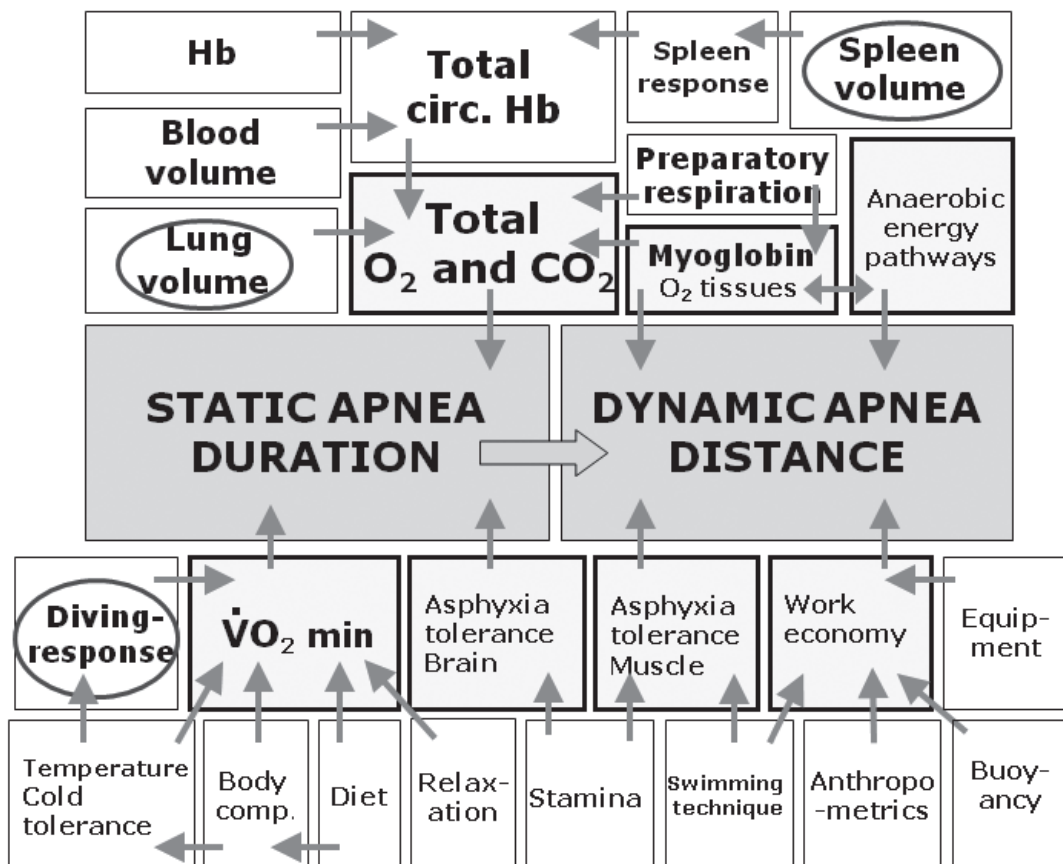
systems developed by competition divers will likely keep pace with increased results at least in the pool disciplines. These measures could be imported to other diving activities, a process which is currently taking place in Sweden, where recreational freediving education within the Swedish Sports Diving Federation is developing similar safety routines.

Competitive apnea is here to stay, no matter what view is adopted by the medical community. As in politics, dialogue is the key to maximising safety, rather than a wall of silence or demands to ban the sport.⁸⁶ Clearly we best serve the cause of safety by providing sound advice to athletes on how to avoid injury, based on knowledge of the competition conditions associated with the specific apnea disciplines and data from physiological laboratory and field studies.

Predicting performance

By adding new factors to the figure used for static apnea in the first article,⁴ we obtain an overview of the major physiological, psychological and physical factors predicting performance in the dynamic disciplines (Figure 10). The main factors have arrows directly into the discipline boxes, and these in turn are determined by a number of factors placed further out (arrows indicating interactions between

Figure 10
Factors predicting performance in the competitive apnea pool disciplines
 (arrows indicating interactions between non-adjacent boxes have been omitted for clarity)



non-adjacent boxes have been omitted for clarity). All factors determining static apneic duration also affect the dynamic disciplines, as indicated by the horizontal arrow between the two, but a new set of factors related to work is added by DYN and DNF. Most biological factors show both a component of inherent individual variation and a component of variation induced by training. Ideally, when the detailed interdependencies among these factors have been determined, and these can be reliably measured, the model could be used to predict individual performance at a given state of training, but such predictions are premature due to the limited data available from dynamic apnea disciplines. Individual differences in predisposition for apneic diving are remarkable, and increased recruitment of athletes to the sport and improved training methods may forward these limits beyond those considered realistic today. In a survey of 17 world-championship participants in 2008, the divers predicted a future limit for DYN to be around 325 m. This could physiologically be within reach with improvements in work economy, gas storage capacity, anaerobic capacity and further technological developments, and in these pool disciplines safety can be kept high as the dive can be interrupted by the competitor or safety diver within seconds. Further improvements in the current world records in DYN and DNF ultimately depend on the balance between total gas storage, anaerobic capacity and the metabolic requirements at the optimal swim speed, individual stamina and brain tolerance to asphyxia, without resulting in syncope.

Conclusions

A successful diver in the dynamic apnea disciplines is likely to possess superior swimming skill and excellent work economy, balancing speed and restricted energy expenditure to achieve maximum distance within the limits set by maximized gas storage capacity and the tolerance of the brain to asphyxia. Anthropometrically for DNF, a strong upper body, long arm reach and big hands and feet may be beneficial. For DYN, the diver should, instead, have a good fin-swimming technique, flexible back and pelvic region, and a powerful diving response, shutting off the circulation to non-working areas. High lactate values after competition dives indicate that the anaerobic capacity of muscle is important to maximal performance. Enhanced myoglobin concentration in swimming muscles could contribute to prolonging the aerobic dive limit, and high local tolerance to hypoxia is important for successful performance. These factors all affect the metabolic part of the model but, as in other apnea disciplines, the highest possible gas storage and minimum oxygen saturation requirements for alert consciousness at apnea termination set the outer limits for dynamic performance. Just as in static apnea, the diver can spontaneously terminate the dive at any time and breathe, and psychological 'stamina' (self discipline) as well as good judgement is essential for performance. Future physiological research should be directed towards determining myoglobin levels as well as local anaerobic capacity in these highly specialized athletes. Studies of blood flow redistribution by

the diving response in laboratory models of dynamic apnea will determine which areas are 'sacrificed' and which are prioritized, an aspect central to defining performance.

Acknowledgements

I wish to thank the elite divers who participated in our studies and gave permission for their photos to be used, my co-workers in the Environmental Physiology Group and other laboratories for their scientific contributions, Dr Matt Richardson and Mr Christian Ernest for reviewing the manuscript and Mr Kimmo Lahtinen for Figures 1 and 2.

References

- 1 Rahn H, Yokoyama T, editors. *Physiology of breath-hold diving and the Ama of Japan*. Washington: Natl Acad Sci, Natl Res Council Publ; 1965. p. 227-36.
- 2 Frisch J, Baker R, Hobbs J-PA, Nankervis L. A quantitative comparison of recreational spearfishing and linefishing on the Great Barrier Reef: implications for management of multi-sector coral reef fisheries. *Coral Reefs*. 2008;27:85-95.
- 3 Davis FM, Graves M, Guy H, Prisk GK, Tanner TE. Carbon dioxide responses and breath-hold times in underwater hockey players. *Undersea Biomed Research*. 1987;14(6):527-34.
- 4 Schagatay E. Predicting performance in competitive apnea diving. Part I: static apnea. *Diving and Hyperbaric Medicine*. 2009;39(2):88-99.
- 5 Ferretti G. Extreme human breath-hold diving. *Eur J Appl Physiol*. 2001;84:254-71.
- 6 Pollock NV. Breath-hold diving: performance and safety. *Diving and Hyperbaric Medicine*. 2008;38(2):79-86.
- 7 Lindholm P, Lundgren CEG. The physiology and pathophysiology of human breath-hold diving. *J Appl Physiol*. 2009;106(1):284-92.
- 8 Toussaint HM, Jansen T, Kluft M. Effect of propelling surface size on the mechanics and energetics of front crawl swimming. *J Biomechanics*. 1991;24(3,4):205-11.
- 9 Geladas ND, Nassis GP, Pavlicevic S. Somatic and physical traits affecting sprint swimming performance in young swimmers. *Int J Sports Med*. 2005;26:139-44.
- 10 Elsner R, Gooden B. *Diving and asphyxia: a comparative study of animals and man*. Physiological Society Monograph 40. Cambridge: Cambridge University Press; 1983. p. 1-175.
- 11 Schagatay E, Andersson J, Nielsen B. Hematological response and diving response during apnea and apnea with face immersion. *Eur J Appl Physiol*. 2007;101:125-32.
- 12 Andersson J, Schagatay E, Gislén A, Holm B. Cardiovascular responses to cold water immersions of the forearm and face, and their relationship to apnea. *Eur J Appl Physiol*. 2000;83:566-72.
- 13 de Bruijn R, Richardson M, Schagatay E. Oxygen-conserving effect of the diving response in the immersed human. *Diving and Hyperbaric Medicine*. 2009;39(4):193-9.
- 14 Lindholm P, Sundblad P, Linnarsson D. Oxygen-conserving effects of apnea in exercising men. *J Appl Physiol*. 1999;87:2122-7.
- 15 Andersson JPA, Linér MH, Rünow E, Schagatay EKA. Diving response and arterial oxygen saturation during apnea and exercise in breath-hold divers. *J Appl Physiol*. 2002;93:882-6.
- 16 Andersson JPA, Linér MH, Fredsted A, Schagatay E. Cardiovascular and respiratory responses to apneas with and

- without face immersion in exercising humans. *J Appl Physiol*. 2004;96(3):1005-10.
- 17 Andersson JPA, Evaggelidis L. Arterial oxygen saturation and diving response during dynamic apneas in breath-hold divers. *Scand J Med Sci Sports*. 2009;19:87-91.
 - 18 Butler PJ, Woakes AJ. Heart rate in humans during underwater swimming with and without breath-hold. *Respiration Physiol*. 1987;69:387-99.
 - 19 Wein J, Andersson JP, Erdeus J. Cardiac and ventilatory responses to apneic exercise. *Eur J Appl Physiol*. 2007;100:637-44.
 - 20 Grubb RL, Raichle ME, Eichling JO, Ter-Pogossian MM. The effects of changes in PaCO₂ cerebral blood volume, blood flow, and vascular mean transit time. *Stroke*. 1974;5:630-9.
 - 21 Rasmussen P, Stie H, Nielsen B, Nybo L. Enhanced cerebral CO₂ reactivity during strenuous exercise in man. *Eur J Appl Physiol*. 2006;96:299-304.
 - 22 Palada I, Obad A, Bakovic D, Valic Z, Ivancev V, Dujic Z. Cerebral and peripheral hemodynamics and oxygenation during maximal dry breath-holds. *Respir Physiol Neurobiol*. 2007;157:374-81.
 - 23 Kjeld T Pott FC, Secher NH. Facial immersion in cold water enhances cerebral blood velocity during breath-hold exercise in humans. *J Appl Physiol*. 2009;106:1243-8.
 - 24 Smeland EB, Owe JO, Andersen HT. Modification of the 'diving bradycardia' by hypoxia or exercise. *Resp Physiol*. 1984;56(2):245-51.
 - 25 Schagatay E *The human diving response - effects of temperature and training*. Thesis, Department of Animal Physiology, Lund University, Lund; 1996.
 - 26 Lemaitre F, Buchheit M, Joulia F, Fontanari P, Tourny-Chollet C. Static apnea effect on heart rate and its variability in elite breath-hold divers. *Aviat Space Environ Med*. 2008;79:99-104.
 - 27 Kooyman GL, Ponganis PJ. The physiological basis of diving to depth: birds and mammals. *Ann Rev Physiol*. 1998;60:19-32.
 - 28 Polasek LK, Davis RW. Heterogeneity of myoglobin distribution in the locomotory muscles of five cetacean species. *J Exp Biol*. 2001;204:209-15.
 - 29 Noren SR, Williams TM, Pabst DA, McLellan WA, Dearolf JL. The development of diving in marine endotherms: preparing the skeletal muscles of dolphins, penguins, and seals for activity during submergence. *J Comp Physiol*. 2000;B(171):127-34.
 - 30 Davis RW, Polasek L, Watson R, Fuson A, Williams TM, Kanatous SB. The diving paradox: new insights into the role of the dive response in air-breathing vertebrates. *Comp Biochem Physiol*. 2004;A(138):263-8.
 - 31 Wittenberg BA, Wittenberg JB. Transport of oxygen in muscle. *Annu Rev Physiol*. 2000;51:857-78.
 - 32 Reynafarje B. Myoglobin content and enzymatic activity of muscle and altitude adaptation. *J Appl Physiol*. 2000;17:301-5.
 - 33 Terrados N, Jansson E, Sylvén C, Kaijser L. Is hypoxia a stimulus for synthesis of oxidative enzymes and myoglobin? *J Appl Physiol*. 1990;68:2369-72.
 - 34 Masuda K, Okazaki K, Kuno S, Asano K, Shimojo H, Katsuta S. Endurance training under 2500-m hypoxia does not increase myoglobin content in human skeletal muscle. *Eur J Appl Physiol*. 2001;85:486-90.
 - 35 Robach P, Cairo G, Gelfi C, Bernuzzi F, Pilegaard H, Viganò A, et al. Strong iron demand during hypoxia-induced erythropoiesis is associated with down-regulation of iron-related proteins and myoglobin in human skeletal muscle. *Blood*. 2007;109:4724-31.
 - 36 de Bruijn R, Richardson M, Schagatay E. Increased erythropoietin concentration after repeated apneas in humans. *Eur J Appl Physiol*. 2008;102(5):609-13.
 - 37 Giardina B, Ascenzi P, Clementi ME, de Sanctis GD, Rizzi M. Functional modulation by lactate of myoglobin. *J Biol Chem*. 1996;271(29):16999-7001.
 - 38 Qvist J, Hurford WE, Park YS, Radermacher P, Falke KJ, Ahn DWA, et al. Arterial blood gas tensions during breath-hold diving in the Korean ama. *J Appl Physiol*. 1993;75:285-93.
 - 39 Olsen CR, Fanestil DD, Scholander PF. Some effects of apneic underwater diving on blood gases, lactate and pressure in man. *J Appl Physiol*. 1962;17: 938-42.
 - 40 Ferrigno M, Ferretti G, Ellis A, Warkander D, Costa M, Cerretelli P, et al. Cardiovascular changes during deep breath-hold dives in a pressure chamber. *J Appl Physiol*. 1997;83(4):1282-90.
 - 41 Melbø JI, Jebens E, Noddeland H, Hanem S, Toska K. Lactate elimination and glycogen resynthesis after intense bicycling. *Scand J Clin Lab Invest*. 2006;66:211-26.
 - 42 Tagliabue P, Susa D, Sponsiello N, La Torre A, Ferretti G. Blood lactate accumulation in static and dynamic apneas in humans [abstract]. *Human Behaviour and Limits in Underwater Environment*, Special Conference on Breath-hold Diving. Pisa: CNR Inst Clin Physiol; 2005. p. 113.
 - 43 Greenwood JD, Moses GE, Bernardino FM, Gaesser GA, Weltman A. Intensity of exercise recovery, blood lactate disappearance, and subsequent swimming performance. *J Sports Sci*. 2008;26(1):29-34.
 - 44 Taylor AD, Bronks R, Smith P, Humphries B. Myoelectric evidence of peripheral muscle fatigue during exercise in severe hypoxia: some reference to m. vastus lateralis myosin heavy chain composition. *Eur J Appl Physiol*. 1997;75:151-9.
 - 45 Westerblad H, Allen DG, Lännergren J. Muscle fatigue: lactic acid or inorganic phosphate the major cause? *News Physiol Sci*. 2002;17:17-21.
 - 46 Fitts RH. Highlighted topic: Fatigue mechanisms determining exercise performance. The cross-bridge cycle and skeletal muscle fatigue. *J Appl Physiol*. 2008;104:551-8.
 - 47 Secher NH, Seifert T, Van Lieshout JJ. Fatigue mechanisms determining exercise performance. Cerebral blood flow and metabolism during exercise: implications for fatigue. *J Appl Physiol*. 2008;104:306-14.
 - 48 Amann M, Calbert JAL. Highlighted topic: Fatigue mechanisms determining exercise performance. Convective oxygen transport and fatigue. *J Appl Physiol*. 2008;104:861-70.
 - 49 Metzger JM, Moss RL. Greater hydrogen ion-induced depression of tension and velocity in skinned single fibres of rat fast than slow muscles. *J Physiol*. 1987;393:727-42.
 - 50 Bangsbo J, Madsen K, Kiens B, Richter EA. Effect of muscle acidity on muscle metabolism and fatigue during intense exercise in man. *J Physiol*. 1996;495(2):587-96.
 - 51 Joulia F, Steinberg JG, Faucher M, Jamin T, Ulmer C, Kipson N, et al. Breath-hold training of humans reduces oxidative stress and blood acidosis after static and dynamic apnea. *Resp Physiol Neurobiol*. 2003;137:19-27.
 - 52 Linér MH, Linnarsson D. Tissue oxygen and carbon dioxide stores and breath-hold diving in humans. *J Appl Physiol*. 1994;77(2):542-7.
 - 53 Andersson J, Larsson J, Schagatay E. Yoga-breathing, apnea and alveolar gas exchange. *26th Annual Scientific Meeting, European Underwater Baromedical Society*. June 18-22,

- Stockholm, Sweden; 2000, p 80-83.
- 54 Lin YC, Lally DA, Moore TO, Hong SK. Physiological and conventional breath-hold breaking points. *J Appl Physiol.* 1974;37:291-6.
- 55 Örnhammar H, Schagatay E, Andersson J, Bergsten E, Gustafsson P, Sandström S. Mechanisms of "buccal pumping" ("lung packing") and its pulmonary effects. In: Gennser M, editor. *24th Annual Scientific Meeting, European Underwater Baromedical Society 1998.* Stockholm, Sweden; 1998. p. 80-3.
- 56 Andersson J, Schagatay E, Gustafsson P, Örnhammar H. Cardiovascular effects of "buccal pumping" in breath-hold divers. In: Gennser M, editor. *24th Annual Scientific Meeting, European Underwater Baromedical Society 1998.* Stockholm, Sweden; 1998. p. 103-6.
- 57 Overgaard K, Friis S, Pedersen RB, Lykkeboe G. Influence of lung volume, glossopharyngeal inhalation and PET O₂ and PET CO₂ on apnea performance in trained breath-hold divers. *Eur J Appl Physiol.* 2006;97:158-64.
- 58 Andersson JPA, Linér MH, Jönsson H. Asystole and increased serum myoglobin levels associated with "packing blackout" in a competitive breath-hold diver. *Clin Physiol Funct Imaging.* 2009;29(6):458-61.
- 59 Linér MH, Andersson JPA. Suspected arterial gas embolism after glossopharyngeal insufflation in a breath-hold diver. *Aviat Space Environ Med.* 2010;81:1-3.
- 60 Dujic Z, Uglesic L, Breskovic T, Valic Z, Heusser K, Marinovic J, et al. Involuntary breathing movements improve cerebral oxygenation during apnea struggle phase in elite divers. *J Appl Physiol.* 2009;107:1840-6.
- 61 Hentsch U, Ulmer HV. Trainability of underwater breath-holding time. *Int J Sport Med.* 1984;5:343-7.
- 62 Schagatay E, van Kampen M, Andersson J. Effects of repeated apneas on apneic time and diving response in non-divers. *Undersea Hyperb Med.* 1999;26:143-9.
- 63 Schagatay E, Andersson J, Hallén M, Pålsson B. Physiological and genomic consequences of intermittent hypoxia. Selected contribution: role of spleen emptying in prolonging apneas in humans. *J Appl Physiol.* 2001;90:1623-9.
- 64 Schagatay E, Haughey H, Reimers J. Speed of spleen volume changes evoked by serial apneas. *Eur J Appl Physiol.* 2005;93:447-52.
- 65 Schaefer KE, Hastings BJ, Carey CR, Nichols JR. Respiratory acclimatization to carbon dioxide. *J Appl Physiol.* 1963;18:1071-8.
- 66 Andersson J, Schagatay E. Repeated apneas do not affect the hypercapnic ventilatory response in the short term. *Eur J Appl Physiol.* 2009;105: 569-74.
- 67 Elsner RE. Heart rate response in forced versus trained experimental dives in pinnipeds. *Hvalrådets Skr.* 1965;48:24-9.
- 68 Åstrand PO. Breath holding during and after muscular exercise. *J Appl Physiol.* 1960;15:220-4.
- 69 Schagatay E, Holm B. Effects of water and ambient air temperatures on human diving bradycardia. *Eur J Appl Physiol.* 1996;73:1-6.
- 70 Lindholm P, Conniff M, Gennser M, Pendergast D, Lundgren C. Effects of fasting and carbohydrate consumption on voluntary resting apnea duration. *Eur J Appl Physiol.* 2007;100(4): 417-25.
- 71 Holmér I. Oxygen uptake in swimming man. *J Appl Physiol.* 1972;33(4):502-9.
- 72 Zamparo P, Pendergast DR, Termin B, Minetti AE. How fins affect the economy and efficiency of human swimming. *J Exp Biol.* 2002;205:2665-76.
- 73 Israel S. Der erweiterte atemanhaltenversuch als funktionsprüfung für das atmungs-herz-kreislauf-system. *Theorie und Praxis der Körperkultur.* 1958;7:650-4. German.
- 74 Schagatay E, van Kampen M, Emanuelsson S, Holm B. Effects of physical- and apnea training on apneic time and diving response in humans. *Eur J Appl Physiol.* 2000;82:161-9.
- 75 Strömme SB, Kerem D, Elsner R. Diving bradycardia during rest and exercise and its relation to physical fitness. *J Appl Physiol.* 1970;28:614-21.
- 76 Arnold RW. Extremes in human breath hold, facial immersion bradycardia. *Undersea Biomed Res.* 1985;12:183-90.
- 77 Mazzei B, Lauro A, Feraco E, Corsonello F, Mollace V, Biffi A. Il "Diving reflex": influenza dell'età e del training. *Med Sport.* 1988;41:353-8. Italian.
- 78 Minak G. Evaluation of the performances of free-diving fins. *Sports Engineering.* 2004;7:153-8.
- 79 Starling RD, Costill DL, Trappe TA, Jozsi AC, Trappe SW, Goodpaster BH. Effect of swimming suit design on the energy demands of swimming. *Med Sci Sports Exercise.* 1995;27(7):1086-9.
- 80 Alexander, RMcN. 1977. Swimming. In: Alexander RMcN, Goldspink G, editors. *Mechanics and energetics of animal locomotion.* London: Chapman and Hall; 1977. p. 222-48.
- 81 Sharp RL, Costill DL. Influence of body hair removal on physiological responses during breaststroke swimming. *Med Sci Sports Exerc.* 1989;21(5):576-80.
- 82 Johns R, Houmar AJA, Kobe RW, Hortobagyi T, Bruno NJ, Wells JM, et al. Effects of taper on swim power, stroke distance, and performance. *Med Sci Sports Exerc.* 1992;10(24):1141-6.
- 83 Sharp FR, Ran R, Lu AN, Tang Y, Strauss KI, Glass T, et al. Hypoxic preconditioning protects against ischemic brain injury. *Neuro Rx.* 2004;1:26-35.
- 84 Ridgway L, McFarland K. Apnea diving: long term neurocognitive sequelae of repeated hypoxemia. *Clin Neuropsych.* 2006;20:160-76.
- 85 Andersson JPA, Linér MH, Jönsson H. Increased serum levels of the brain damage marker S100B after apnea in trained breath-hold divers: a study including respiratory and cardiovascular observations. *J Appl Physiol.* 2009;107:809-15.
- 86 Walker D. Deaths from breath-hold diving [letter]. *Diving and Hyperbaric Medicine.* 2009;39(3):178.

Submitted: 13 January 2010

Accepted: 22 January 2010

Erika Schagatay, PhD, is Professor in the Environmental Physiology Group, Department of Engineering and Sustainable Development, and at the Swedish Winter Sports Research Centre, Mid Sweden University, Östersund, Sweden.

Address for correspondence:

Environmental Physiology Group

Department of Engineering and Sustainable Development

Akademigatan 1, Mid Sweden University

83125 Östersund, Sweden

Phone: +46-(0)63-165512

Fax: +46-(0)63-165700

E-mail: <Erika.Schagatay@miun.se>