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Impact of protective clothing on thermal and cognitive responses

Thesis for the degree of Philosophiae Doctor

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Contents

Abstract

Current aircrew protective clothing is unable to the address the challenging situation that arises when the same clothing concept needs to provide sufficient thermal protection in water while also ensuring thermal comfort and optimal work performance during flights. Performance, safety and health all suffer when environmental thermal stress factors exceed the body's ability to compensate for disturbances in heat balance. Wearing protective clothing further increases the thermal stress, which increases the risk of human errors that can have fatal consequences.

This thesis addresses the fundamental mechanisms of how interactions among environmental temperature, clothing, work load, and physiological regulatory systems affect the working and emergency responses of helicopter pilots. The first part of this thesis investigated the impact of wearing protective clothing in a working situation on factors such as comfort, physiology and cognitive performance. The second part focuses on immersion in cold water, and in particular on the importance of improving heat balance during exposure to cold water.

This thesis has added to our knowledge of the ambient conditions required for thermal comfort and optimal performance in a working situation. In the emergency situation in cold water it also offers new knowledge about how to improve heat balance under extreme environmental conditions when wearing an immersion suit in cold waters.

The results of the studies described in this thesis have practical implications for the development of new types of protective clothing that will improve user safety without reducing comfort and work performance.

List of papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

Paper I

Færevik H, Markussen D, Øglænd GE, Reinertsen RE (2001). The thermoneutral zone when wearing aircrew protective clothing. Journal of Thermal Biology, 26, 419-425.

Paper II

Færevik, H, Reinertsen RE (2003). Effect of wearing aircrew protective clothing on physiological and cognitive responses under various ambient conditions. Ergonomics. Vol.46, no. 8, 780-799.

Paper III

Færevik H, Reinertsen RE. Initial heat stress on subsequent responses to cold water immersion while wearing protective clothing. Aviation Space and Environmental Medicine, under consideration, submitted May 2010, revised version sent August 2010.

Paper IV

Færevik H, Reinertsen RE, Giesbrecht GG. Leg exercise and core cooling in an insulated immersion suit under severe environmental conditions. Aviat Space Environ Med 2010; 81: 993-1001.

Introduction

Concern for how the thermal environment affects industrial workers has long been a public health and safety issue (134). In the South African gold-mining industry, for example, it was vital to acquire knowledge of how workers could acclimatize to the exceptional heat and humidity in deep mines (139). The frequently extreme requirements of the military and space industries have triggered further efforts to understand how thermal extremes affect human physiology and performance (34). The large number of ships and aircraft lost at sea during the Second World War attracted attention to survival at sea and the risks of hypothermia. Authorities of the countries at war were forced to develop methods of protecting crews against cold water immersion (66). Much research was done on designing protective equipment and on determining survival time as a function of water temperature.

More recently, the rise in maritime and intercontinental air traffic and the introduction of helicopter transport to offshore oil platforms have increased the risk of exposure to accidental immersion in cold water, while a sharper focus on occupational health and safety has brought this matter to more general attention. Offshore petroleum industry and fish-farm workers, fishermen and military personnel are all at risk of falling into the water. A wide range of protective clothing and equipment has therefore been designed to protect workers from the potential hazards of immersion in cold water. The requirement to wear protective clothing during work has offered new challenges to the working situation itself. By increasing external insulation and preventing evaporative heat loss, wearing protective clothing may cause thermal stress that can impair performance (47, 58).

Although the impact of temperature on performance and survival at sea have each been comprehensively reviewed, few studies have paid attention to the difficulty of reconciling thermal protection in water with requirements for thermal comfort at work. In order to ensure the best possible performance and protection of workers who are required to wear protective clothing, we need a better understanding of 1) the impact of thermal stress in a working situation and 2) the physiological responses to cold water in the event of immersion. To study this, this thesis focuses on Norwegian Sea King helicopter pilots who wear protective clothing, in order to determine the impact of temperature exposures and protective clothing on physiological and cognitive responses at work (in the air) and when exposed to cold water.

Aim of thesis

Norwegian Sea King helicopter pilots are required to wear immersion suits all year around, since they mostly operate over cold ocean regions. This influences the mechanisms of heat exchange between the body and the environment (47, 58). An immersion suit needs to protect the wearer during all phases of an emergency situation; escaping from a ditched helicopter, protecting against the initial cold-shock response and extending survival time in the event of cold-water immersion under severe environmental conditions (33). The protective clothing necessarily has a high insulation and evaporative resistance that reduces heat dissipation and may therefore cause heat stress (58). There is growing concern that the combination of high ambient temperature, solar radiation in the cockpit and protective clothing produce an unacceptable level of thermal strain, a lower level of comfort and deterioration of performance (29, 71, 90, 132). Aviator's protective clothing concepts therefore need to accommodate the potential conflict between thermal comfort and protection. Achieving thermal comfort and reduced heat strain requires an understanding of physiological heat balance and the heat exchange mechanisms between the person wearing protective clothing and the environment.

The thesis is divided in two main parts, which focus respectively on the normal working situation of helicopter pilots and the emergency situation in cold water after ditching. The overarching aims of this thesis are to improve our understanding of;

- how ambient temperature influence the thermal comfort and performance of pilots wearing aircrew protective clothing in a normal working situation.
- the impact of cold water immersion, particularly the importance of maintaining heat balance under severe environmental conditions when wearing aircrew protective clothing.

The study of these problems requires knowledge of 1) thermal responses to air and water 2) cognitive performance during thermal stress, and 3) the effect of protective clothing on heat-exchange mechanisms. The following section provides a brief review of the state of the art in these areas.

Background

Thermal responses to air and water

When human beings are exposed to heat or cold, thermoregulatory responses that protect them against extreme conditions are activated. The defense mechanisms against heat include rises in peripheral blood flow and evaporation of sweat, while in the cold, vasoconstriction and increased heat production by shivering or exercise are coupled in. The body strives to achieve thermal balance and homeostasis (5). Helicopter pilots face extreme temperature challenges that existing aircrew protective clothing solutions is unable to solve. In working conditions the heat gain is larger than heat loss; in an emergency situation in cold water the opposite situation occurs; heat loss is much larger than heat gain. The emergency situation in cold water is one of the greatest stressors to which the human body can be exposed and has been comprehensively studied (for reviews see 18, 25, 33, 67, 126). The many accidental drowning- and hypothermia-related accidents at sea (1, 109, 118), further emphasize the importance of understanding the factors that can influence survival in cold water.

To fully appreciate the extreme challenge for helicopter pilots and the influence on performance, safety and health, it is essential to understand the characteristics of the temperature-regulation system, the interaction between environmental temperature exposure and the body, cognitive performance during thermal stress, and clothing physiology.

Thermoregulation

The most powerful form of human thermoregulation is behavioral; through regulating clothing, changing posture, moving to a cooler area, seeking shelter, etc. In the case of helicopter pilots, the working situation and the protective clothing restrict the behavioral options and thermoregulation therefore depends to a great extent on the capacity of the body's own ability to thermoregulate, on cooling aids if available (12, 19, 78, 105) and on cockpit air-conditioning (10, 19).

One particular feature of the homeothermic human is that our internal body temperature rarely exceeds a range of ±2 °C, despite exposure to extreme variations in environmental conditions (65). Greater deviations in deep-body temperature affect cellular structures, enzyme systems and a wide range of temperature-dependent chemical reactions that occur in the body (4), and thus affect health, safety and performance. Thus, throughout our lifetime we maintain a large temperature differential between internal body temperature and the environment. Defending a deep-body temperature within such a narrow range necessarily requires a complex system of regulation. The temperature-regulation system consists of four main components; 1) thermoreceptors, 2) neural pathways mediating afferent information from thermoreceptors and the central nervous system (CNS), 3) control unit located in the hypothalamus and 4) effector system. Thermoreceptors are nerve endings located both in the skin surface and in deeper tissues (CNS, carotid artery, internal organs, skeletal muscles) which fire at different temperature ranges (55, 57). The morphology of cold thermoreceptors has been described in detail by Hensel (56). Afferent signals from peripheral and central thermoreceptors are transmitted by neurons to the preoptic area of the hypothalamus. The anterior hypothalamus controls heat loss, while the posterior hypothalamus participates in the regulation of vasoconstriction and shivering (77). Although numerous studies of the neurophysiological basis of the thermoregulatory system have been performed (6, 57, 77) it is still not fully understood. The link between sensory input and effector output is complex and how the signals are processed is still a matter of debate. A widely used model is the one proposed by Bligh (6), which suggests that homeothermia depends on a system of neuronal connections between sensors and effectors, modulation of the sensor/effectors relations by excitatory and inhibitory signals from elsewhere in the CNS, and crossing inhibitory influences between these pathways (6). Still under debate is the question of exactly which variable is regulated; change in heat content (136) or change in body temperature (9). Furthermore, it is still not certain whether temperature is regulated towards a “set point” (8, 36) or to an “interthreshold zone” (81, 84) between the activation of the appropriate effector mechanisms. Nevertheless, even small deviations from the preferred temperature range or set point may reduce physical and mental performance (42, 100). Effector mechanisms such as vasomotor activity, evaporative heat loss (sweating and respiratory) or shivering are activated to prevent fluctuations in internal temperature and maintain heat balance. Sweat glands, skin blood vessels and skeletal muscles serve as effector organs.

For a helicopter pilot, both the working situation in air and the emergency situation in cold water represent ambient conditions far beyond the range within which humans can regulate. The physiological responses (effector mechanisms) will only apply for a limited time before the system is no longer capable of compensating. Both the working conditions and emergency situation in cold water thus impose major stresses on the body and will affect human performance and survival.

The thermoneutral zone (TNZ)

The idea of a neutral zone of thermoregulation was proposed as long as 50 years ago in experimental work based on human calorimetry (45). The thermoneutral zone (TNZ) is defined as the range of ambient temperatures (T_a) within which the metabolic rate is constant and minimal, body core temperature (T_{re}) is held at steady state (81, 108) and thermal comfort is neutral (112). Under normal circumstances, the TNZ based on ambient temperature will necessarily be wide, since we regulate clothing and activity level to keep the microenvironment surrounding the skin within the neutral zone (112). For sitting, resting, nude subjects exposed to steady exposures to different ambient temperatures, the thermal comfort and neutral temperature sensations lie within the range of physiological thermal neutrality (28-30 °C T_a) where little physiological regulatory effort in required (30). With aircrew protective clothing, the TNZ will obviously be shifted downwards, but this ambient temperature range has never previously been defined. Within the TNZ, heat loss and heat production are balanced by regulating vasomotor tone as a response to environmental changes (112). Outside this range of T_a, the cold and warm thermoreceptors located in the skin will activate autonomic thermoregulatory responses for heat loss through sweating/respiration, or heat production through shivering or exercise (57). TNZ can also be affected by non-thermal factors (81), which may alter both the T_{re} values at which metabolic responses are activated and the magnitude of the metabolic response. Examples of non-thermal factors that impinge on the thermoregulatory system include exercise/post exercise (70), state of hydration (20), sleep (3), fever (7), motion sickness (85) and inert gas narcosis (83). Hence, non-thermal factors such as sleep deprivation or dehydration may well shift the thermal comfort zone of helicopter pilots during flight.

The TNZ has been widely studied and defined in animal studies (15). This is not only of theoretical interest, but has a practical purpose such as for defining housing conditions in which the zone of least thermoregulatory effort should be optimized (65). In human beings, the importance of TNZ has attracted less research attention, and most studies are of theoretical interest. Although there has been interest in defining the ambient conditions under which humans are thermally comfortable related to work performance, health and safety, this has not been directly related to defining the TNZ. In the example of helicopter flying, defining the ambient TNZ when wearing protective clothing is obviously of interest to define conditions where pilots experience minimal physiological strain and is of practical interest for the regulation of the cockpit environment.

Heat balance

To keep the body in heat balance, heat production must be equal to heat loss, according to the equation M - W- R - C - K - S – E = 0 (where M is metabolic heat production, W is mechanical work, R is radiation, C is heat loss by convection, K is heat loss by conduction, S is stored body heat and E is evaporative heat loss). Metabolic heat production is the rate of transformation of chemical energy into heat. During rest under thermoneutral conditions, this corresponds to a heat production rate of 80-100 Watt. Physical effort raises the metabolic rate and, depending on the mechanical efficiency of the exercise performed (between 0-25 %), most of the energy is converted to heat. During strenuous exercise, heat production may exceed 1000 Watt (32). Heat production can be increased in two ways; either involuntarily by shivering, or voluntarily by muscular exercise. Several pathways of heat loss are possible, although they are somewhat different in air and water. In air, heat is lost by convection as air blows over the skin, in water by replacement of the boundary layer surrounding the body. When there is a difference between the temperature of the body and the surroundings, heat is also lost by radiation in air, while radiation is insignificant in water. Evaporation of sweat is the main pathway of heat loss in air but insignificant in water. Evaporation of water from the respiratory tract is important both in water and air. Warming and moisturizing inspired cool dry air can contribute as much as 10 % of total body heat loss at rest, increasing with exercise and cooler air. Conduction plays a minor role in air, but becomes more important in water, which has a thermal conductivity 25 times greater than that of air at the same temperature (18, 88). A large contact surface between water and the body in the supine position further increases the conductive heat loss. The capacity of the body to retain or lose heat to the environment in air is dependent on the following external factors (47): temperature (air temperature, radiant temperature, and surface temperature), air movement and humidity (moisture concentration, not the relative humidity that might cause dripping sweat). Combined with metabolic heat production and clothing, these variables form the fundamental factors that define the human thermal environment (97).

When metabolic heat production (M) increases due to work, sweat evaporation is the main mechanism involved in maintaining body temperature within a narrow range. The environment is usually cooler than the skin temperature if no clothing is worn, and sweat will evaporate even at 100% relative humidity. However, clothing dramatically affects heat exchange mechanisms and this will be described more in detail later. In working situations at high work intensity and/or thermal stress due to ambient conditions and/or wearing protective clothing, the thermoregulatory system of the wearer will be unable to maintain thermal balance. As a consequence significant heat strain during work is experienced. Many occupations have work-places close to or over water, and in the event of an accident workers may fall into the water with a raised body temperature. Only a few studies exist on the effect of a raised body temperature when exposed to cold water (76, 113, 137), and this has never been investigated in subjects wearing protective clothing.

Maintenance of heat balance in cold water is much more demanding than in air, since heat loss from the body will rise dramatically because of the large heat-removing capacity of water. In the case of Norwegian military aircraft that operate over the North Sea and Barents Sea, this problem is further exacerbated by the fact that an immersion accident is most likely to occur in areas where extreme weather conditions are common (low air and water temperatures, wind and waves). It would therefore be of interest to identify methods for extending survival time by improving heat balance. Muscular exercise has great potential for increasing heat production (4, 32), but is generally not recommended, since high muscle blood perfusion during exercise increases heat loss to the water (95, 133). With adequate insulation, enough heat is retained to improve heat balance and attenuate core cooling (107), but this has yet to be demonstrated under the extreme environmental conditions faced by accidentally immersed aircrew.

Thermal comfort

Thermal comfort is defined as “that state of mind which expresses satisfaction with the thermal environment” (60, 97). The condition of thermal comfort is therefore sometimes defined as a state in which there is no driving impulse to correct the environment by behavioural activity (5). Thermal comfort and its determining factors have been reviewed by Parsons (97). Thermal comfort is dependent upon both environmental and individual factors and is influenced by the core and skin temperatures of the body (27, 31). The importance of thermal comfort (or discomfort) in working situations has been comprehensively investigated (77), since its relation to human health, performance and productivity is clear. A feeling of discomfort may lower morale and even lead to a refusal to work (97). Hence, there is an active interest in research on defining conditions of thermal comfort. *Thermal sensation* indicates how a person "feels" or senses the temperature. This sensation follows the neurological pathways of the cold and warm thermoreceptors described earlier. The actual sensation is formed in the brain in the somatosensory cortex. A sensation of cold is determined by skin temperature (T_{sk}), warmth initially on skin temperature, and then on deep body temperature (55). However, local cooling of the hands or feet may produce a whole-body sensation of cold that is not related to the T_{sk} (141). Furthermore, different skin regions have different thermosensitivity and different degrees of importance (14, 89). Warmth discomfort is closely related to skin wettedness (77). Rapid shifts in environmental temperatures change thermal comfort and sensation before skin and temperature are affected (31), indicating that thermal sensations are influenced by changes in heat loss from the body. Under transient conditions, thermal comfort may therefore be predicted more accurately from ambient conditions than from the skin and core temperature change (31). Fanger (27) published in 1970 *Thermal Comfort*, which describes the most widely used methods and principles for evaluating and analyzing thermal environments with respect to thermal comfort. Fanger (27) describes four essential conditions for a person to be in thermal comfort; 1) the body is in heat balance; 2) sweat rate is within comfort limits; 3) mean skin temperature is within comfort limits; 4) local discomfort is absent. It appears that the preferred ambient condition for thermal comfort is the same across geographic locations (warm/cold climates), age and gender (97). Outside this narrow comfort zone, the sensation of cold and warmth is affected by e.g. age, gender, and body composition and acclimation state.

Thermal discomfort represents a stimulus for behavioural activity (31). Helicopter pilots, however, cannot change to more comfortable areas or undress to alleviate heat strain. According to Hancock (44), a decrease in performance is more closely related to thermal discomfort than to physiological strain. Sea King helicopter pilots experience significant discomfort during flight (26), but how this affects their cognitive performance on certain important tasks required for flying has not yet been investigated.

Cognitive performance during thermal stress

Cognitive performance is defined as a set of mental processes such as information processing, learning, thinking, reasoning and remembering. Cognition thus plays a fundamental role in orientation, safety and decision-making, especially in avoiding critical situations. A large number of studies of accident frequency and productivity in the workplace have shown that human error increases in hot, moderate and cold environments (21, 39, 46, 77, 79, 102). This is highly relevant to helicopter flying, which represents a high-technology system that requires efficient and error-free performance.

Although it is well established that hot, moderate or cold environments influence cognitive performance, the underlying mechanisms involved are not fully understood (39, 99). It has been difficult to draw general conclusions about the relationship between performance and heat exposure, due to variations in experimental conditions, type of task, severity of exposure and duration (38, 39, 40, 99, 101). Some have reported little performance loss, while others have reported decrements in performance under identical ambient conditions (99).

Although an underlying causative model explaining the interaction between thermal environment and cognitive performance has not been established, the physiological responses to hot and cold environments have been well described. Work safety standards that provide threshold values for performance in hot and cold environments are therefore largely based upon physiological parameters. The basis of these theories is that the ambient temperature at which an individual can perform adequately is very close to the threshold temperature at which the body temperature can compensate physiologically for thermal strain (43). The most obvious effects of the thermal environment are those of distraction and manual dexterity in the cold (16, 97). Hancock and Vasmatzidis (37) challenge this basis upon which all occupational thermal stress exposures are founded. They claim that *task performance level* is the most sensitive reflection of human responses to thermal stress. Such responses are superior indices compared with the more traditional measurement of physiological parameters (38). More knowledge of interactions between physiological parameters and cognitive responses is necessary for a better understanding of the critical temperature limits for safe performance.

Pilcher et al (99) and Hancock et al (39) have performed the most comprehensive meta-analyses to date in order to quantify the effect of thermal stress on human performance. Pilcher (99) concluded from 22 studies that ambient temperatures above 32 °C and below 10 °C result in the greatest decrement in performance (when subjects are not wearing protective clothing). Both metaanalyses concluded that the type of task performed (complex vs simple), duration and intensity of exposure are key variables that influence how thermal conditions affect performance (39, 99). The metaanalysis of Hancock was consistent with the distraction theory that suggests that temperature stress forces the individual to allocate attention resources to appraise and cope with the threat, and reduces his capacity to process task-relevant information (39, 97). Other theories proposed include arousal theory (101), which suggests that performance depends on arousal level. A “boring” task such as vigilance will be de-arousing. A warm environment reduces arousal level and vigilance will be reduced (97). If the task is more demanding and arousing, a cool environment (0°) may be more arousing and may improve performance in a boring task (e.g. vigilance). There is a practical rationale to this; a driver who is tired will tend to fall asleep in a comfortable, excessively - warm environment (97). Furthermore, thermal sensation and comfort might also cause dissatisfaction that could affect performance and should be avoided. This is a factor of importance also for survival in cold water. It has been demonstrated that thermal sensation correlates with experienced thermal strain, which in turn affects cognitive performance (129).

Both human psychological and organizational factors affect flying performance and this topic has been comprehensively studied (87). Problems of flying performance due to environmental stressors have not been paid the same degree of attention (87). Stressors in the physical environment of pilots include vibration, noise, uncomfortable seats and temperature. Little research has aimed at determining how flying performance is affected by temperature. This is surprising since, in comparison with noise and vibration, temperature is much more severe and exposures to extreme values of both heat and cold exposures can be fatal.

Protective clothing

The most important function of personal protective clothing (PPE) is to protect the human body against harmful influences from the environment (e.g. physical, chemical, biological and thermal). For several decades, the development of protective clothing therefore aimed at improving the barrier effect of the garment which made it impermeable for water vapour (110). As it came to be realized that the discomfort of wearing PPE lowered the acceptability of PPE, awareness of improving thermal comfort when wearing PPE increased. The essential problem is that protective clothing directly affects heat exchange (heat and moisture transfer) between the skin and the environment (47, 48). This is mainly determined by the *thermal insulation* and the *evaporative resistance* of the clothing (58). Heat transfer through clothing takes place via dry and evaporative heat exchanges. Impaired heat exchange with the surroundings causes accumulation of heat and water vapour within the clothing microenvironment, and over time, skin temperatures and finally the core temperature will increase (116). Adequate protection is therefore obtained at the expense of disturbances in the heat balance. Wetting of the clothing by accumulation of sweat also gradually reduces the insulation effect and causes thermal discomfort (77). Impermeable clothing increases vapour pressure and condensation under the garment may occur (138,). This has further negative effects on the heat balance caused by dissipation of heat in the condensation process. *Evaporative resistance* is complex, but it can be directly measured on human subjects (69), by a sweating manikin (80) or by physical skin models (e.g. sweating hotplate) (72). A number of recent studies have developed more sophisticated methods for understanding heat and vapour transport in clothing (49, 138).

Clothing protects the body by reducing heat loss in cold environment (air or water), and in many cases, the insulation is the factor that can most readily be adjusted to reduce thermal stress . *Thermal insulation* can be determined by measurements made on a standing thermal manikin; values are given in Clo (1 Clo = 0.155 m^2K/W). A human being at rest feels comfortable at 21 °C T_a with a clothing insulation of 1 Clo (93, 135). In the case of Sea King helicopter aircrew, an immersion suit is required to protect a person for a minimum of six hours against hypothermia at sea temperatures as low as 2 °C (23). To achieve such level of protection, a minimum of 2.0-2.3 Clo insulation (measured in air) is required (19) at the cost of thermal comfort during flight (26). Clothing insulation is determined by clothing fit and ensemble thickness and is influenced by the body movements of the user and by air movement in the environment (48, 50, 51). Body movement causes a “pumping effect” that permits air exchange in the microenvironment of the clothing through openings (collars and cuffs etc.), reducing the thickness of the insulating air layer within the clothing. Clothing insulation is further affected by compression by wind and water (50, 51).

The impact of protective clothing on physiological responses has been comprehensively reviewed by several authors (47, 58, 96), all of whom emphasize the impact of clothing on the heat exchange mechanisms between the body and the environment and how this affects thermal comfort and heat balance. Much effort has been put into developing standards and methods for the assessment of human response to thermal environments and defining requirements for protective clothing (97). These can generally be divided into standards for moderate (60), hot (61, 62) or cold environments (63), or deal with protective clothing for immersion in cold water (59). Their principal aim is to provide guidelines for acceptable exposure to environmental conditions (98). Although standards are useful and offer a major contribution to describing methods to assess human responses to thermal environment, assessment of transient thermal environments is still at an early stage and no standard method yet exists (97). In the case of Sea King helicopter personnel a realistic accident scenario would involve moving from a warm working cabin environment (up to 40 °C air temperature) to sudden immersion in cold water (0-2 °C water temperature). Furthermore, the test conditions for cold water immersion are often not very realistic (59). A general recommendation is that standards should be used as guidelines for assessment of thermal strain on the human, and that for each type of work, metabolic rate, environmental conditions and the thermal properties of clothing must be individually quantified (97).

Several studies have emphasised the significant contribution made by clothing ensembles to the development of heat stress in pilots under hot ambient conditions (10, 28, 92, 103, 119, 121). Helicopter pilots will have little benefit of ventilation cooling through garment openings (cuffs and collars) because of their static sitting position in the seat and because openings around the wrists, ankles and neck are sealed to protect against water ingress in the event of cold water immersion. Vallerand et al. (132) reported that cockpit temperatures can be very high, and environmental cooling systems do not always have sufficient capacity to handle the heat stress associated with solar radiation, high ambient temperature and the reduced heat dissipation ability of protective clothing ensembles. There is growing concern that the interaction of heat stress and protective clothing may produce an unacceptable level of thermal strain and reduced comfort, resulting in deterioration of performance. Little is known about how ambient temperature affects physiological and psychological responses in helicopter pilots wearing protective clothing in northern climatic zones.

Problem assignment

Protective clothing for helicopter aircrew must satisfy the end users' requirements for comfort and mobility in a working situation and at the same time provide the best possible safety in an emergency situation (25). A questionnaire addressed to 90 Norwegian Sea King helicopter aircrew members demonstrated that survival in cold water is their highest priority (23). Nearly all the aircrew (92%) stated that an immersion suit must ensure survival for 12 hours under all weather conditions (23). In a worst-case scenario, victims may be unable to enter a dinghy, and an immersion suit must protect from hypothermia under severe conditions, including low ambient and water temperature and waves that continuously flush over them. Hence, visibility (85%), prevention of water ingress (78%) and mobility in an emergency situation (68%) also take high priority among the users. At the same time, they emphasize thermal comfort at high and low cockpit temperatures (49%), moisture transport outwards (39%) and mobility in a working situation (68%) as important requirements. This questionnaire makes it clear that making protective clothing for over-water flights must involve a series of compromises among conflicting requirements. The most difficult part is to reconcile requirements for thermal comfort during flight and thermal protection in water.

When the end-user requirements had been identified and their importance prioritized, the basis for further investigation of some of the thermal problems experienced by helicopter pilots was given. The literature review further revealed some gaps in our knowledge that remained to be filled;

First, two problem areas for the working situation for helicopter pilots were addressed. Although heat stress during flight is a known problem, little is known about the ambient conditions under which aircrew wearing immersion suits start to experience thermal discomfort and heat stress (Paper I). Then, what is the impact of different ambient temperatures on flight performance when protective clothing is being worn (Paper II)? Flying is a task that requires sustained concentration and attention, and performance errors may well have fatal consequences (71). Although an association between heat stress and pilot error has been demonstrated from studies in hot climates (29), little is known about the situation for helicopter pilots in cooler northern climate zones where pilots are required to wear well-insulated immersion suits. Furthermore, while the physiological effects of heat stress are well known, the mechanism underlying the relationship between physiological heat stress and impaired performance in raised ambient temperatures is still not fully understood.

Thereafter, the emergency situation was analyzed and two problems addressed: Although much research has been done on the effects of cold water immersion and survival at sea (25, 66, 122, 126, 128), little attention has been paid to the fact that in many emergency situations a person may face a heat-stress problem before being exposed to cold water. Passive or active pre-immersion warming has been shown to accelerate the onset of hypothermia in naked subjects immersed in cold water (76, 113), but this has never been studied in subjects wearing protective clothing (Paper III). Improving heat balance might extend survival time in cold water. Hypothermia is the greatest long-term threat to immersed victims, and environmental factors are significant in determining heat loss from the body (17). Voluntary leg exercise has great potential for improving heat balance when wearing a well-insulated immersion suit (107), but this has never been investigated under realistically severe environmental conditions (Paper IV).

This thesis is divided in two main parts: the first part considers the impact of the thermal environment and protective clothing on factors such as comfort, physiology and cognitive performance. The second focuses on immersion in cold water, and in particular on the importance of maintaining heat balance during exposure to cold water.

Hypotheses

The principal hypothesis of this thesis is that "reconciling requirements for thermal protection in water with requirements for thermal comfort and cognitive performance during helicopter flights is impossible with existing aircrew protective clothing". I further hypothesise that wearing protective clothing produces a downward shift in the ambient temperature required for thermoneutrality that is far beyond typical cockpit temperatures. The subsequent heat stress will have detrimental effects on the cognitive performance of pilots. I hypothesise that in an emergency situation, heat stress experienced during flight will affect subsequent responses to cold-water immersion. Furthermore, under severe environmental conditions, additional heat production is required to improve the maintenance of heat balance and attenuate core cooling when wearing a well-insulated immersion suit.

The hypotheses were tested by pursuing the following questions:

Paper I: What is the thermoneutral zone when aircrew protective clothing is being worn?

Paper II : What impact do different ambient temperatures have on cognitive performance when protective clothing is worn?

Paper III : How does heat stress due to wearing protective clothing during work affect responses to subsequent immersion in cold water?

Paper IV: Can intermittent periods of leg exercise improve heat balance and attenuate core cooling under severe environmental conditions when wearing a well-insulated immersion suit?

Summary of individual papers

Paper I

Norwegian helicopter pilots are required to wear a dry immersion suit all year round in order to protect themselves in the event of accidental immersion in cold water. Heat stress and thermal discomfort can be significant problems for pilots wearing protective clothing, due to its insulation properties and prevention of evaporative heat loss (26). Both the heat load in the cockpit and wearing an immersion suit influence the thermal stress experienced by the user. Regulation of ambient cockpit temperature downwards might alleviate the thermal stress experienced.

The aim of this study was to define the ambient temperature range of thermoneutrality (TNZ) where no discomfort or heat stress is experienced when wearing protective clothing, as this has not earlier been defined. In naked resting subjects TNZ has been determined to lie between 28-30 °C (30). We hypothesised that wearing protective clothing will displace the TNZ to a lower range of ambient temperatures which is far beyond typical cockpit temperatures. Eight male volunteers participated in 12 experiments on separate days. In series A (control), subjects wore only shorts and sat quietly on a chair in a climatic chamber for one hour during exposure to seven different environmental temperatures (15, 20, 25, 28, 31, 35 and 40 °C). In series B, the subjects wore typical protective clothing as used by helicopter pilots in the Royal Norwegian Airforce (2.2 Clo for the whole clothing concept) including helmet, and were exposed to five different ambient temperatures (0, 10, 14, 18 and 25 °C). Measures included skin (T_{sk}) and rectal temperature (T_{re}), heart rate (f_c) oxygen consumption (VO_2), sweating and assessment of thermal sensation and comfort ratings. The criteria for thermoneutrality were defined as T_{sk} between 33-35 °C, no change in T_{re}, the lowest stable metabolic rate and the subjective sensation of temperature and thermal comfort is neutral.

This study demonstrated that the criteria for thermoneutrality were met at 28-31 °C T_a in subjects wearing shorts, and wearing a dry immersion suit caused a downward shift of the TNZ to 10-14 °C T_a. This temperature range is far below typical cockpit temperatures in the Sea-King helicopter (26). Subjects wearing protective clothing started to sweat and experienced thermal discomfort even at an ambient temperature of 18 °C. The practical implication of these findings is that efforts should be made to reduce thermal stress by regulating cockpit temperature downwards if possible, or to consider use of personal cooling aids at cockpit temperatures of 18 °C when aircrew are wearing protective clothing (2.2 Clo).

Paper II

Flying requires pilots to be concentrated and alert all the time, and it has been shown that thermal stress may impair pilot performance (90, 92), which may contribute to a higher risk of pilot error and reduced flight safety. Wearing protective clothing increases the thermal load by increasing insulation and preventing evaporative cooling (47). Although physiological heat stress and discomfort are experienced at typical ambient cockpit temperatures (26), little is known of how ambient thermal conditions affect the cognitive performance of the pilots wearing aircrew protective clothing.

The aim of this study was to investigate the effect of wearing aircrew protective clothing on physiological and cognitive responses under low, moderate and high ambient temperatures. A further aim was to correlate any observed performance changes with physiological parameters. We hypothesized that typical cockpit temperatures cause heat stress, which will have detrimental effects on the cognitive performance of aircrew wearing protective clothing. Low (0 °C), moderate (23 °C) and high (40 °C) ambient temperatures were investigated. Exposure to low ambient temperature (0 °C) was the control condition, and was not expected to induce any thermoregulatory or cognitive performance changes. Eight male volunteers (six medical students and three pilots in the Royal Norwegian Airforce) were exposed for three hours to the three different ambient conditions on separate days. They wore typical aircrew protective clothing (2.2 Clo for the whole clothing concept) and helmet. Physiological variables (T_{re}, T_{sk}, heart rate, oxygen consumption, sweating), microclimate in the clothing, subjective evaluations of thermal sensation and comfort and cognitive performance (vigilance and multiple choice reactions) were measured during the test. Performance was measured as correct, incorrect, missed reactions and reaction time.

The study demonstrated that there was significantly higher heat stress in the 40 °C series than at 23 °C or 0 °C, as shown by a rise in T_{re}, T_{sk}, heart rate, increased body water loss and subjective discomfort. Multiple choice reactions were unaffected by ambient temperature, but a significant deterioration in vigilance performance was observed under 40 °C ambient conditions compared to 0 and 23 °C. This performance deterioration correlated with an increase in T_{re} of 1.2 °C. Although subjects started to sweat and experienced thermal discomfort at 23 °C T_a, no negative effect on cognitive performance was observed. We concluded from this study that cognitive performance is virtually unaffected unless the ambient temperature is high enough to produce an increase in body core temperature. The practical implication of this study is that moderate cockpit ambient temperature (23 °C) is tolerable with respect to certain cognitive performance tasks required for helicopter flying, while high cockpit temperatures (40 °C) may over time lead to deterioration of flight performance. However, the results of laboratory studies of cognitive tasks must not be transferred to "real life" situations without careful consideration.

Paper III

In cold-water emergency situations, helicopter aircrew will probably enter the water with a raised body temperature due to the requirement to wear protective clothing during operations. This study explored the potential effects of an initial raised body temperature on survival in cold water. In the long term, maintaining body temperature during cold-water immersion is of critical importance for avoiding the lethal effects of hypothermia. Warming by pre-immersion exercise or passive pre-warming has been demonstrated to accelerate core cooling during subsequent cold water immersion (CWI) (76, 113). However, wearing protective clothing significantly alters the thermoregulatory responses to CWI by offering protection against the effects of cold water.

The aim of this study was therefore to investigate the effect of prior warming by exercise on the subsequent physiological response to CWI when wearing an immersion suit. We hypothesized that wearing a dry immersion suit would eliminate long-term differences in core cooling during CWI between normothermic and pre-warmed subjects. Two different groups of physically similar male subjects (age; 24.7±4.2 years, ht; 183.1±6.5 cm, wt; 86.7±15.0 kg, body fat; 16.8±3.3 %) were used to gather data under two conditions, baseline (Base-CWI) and pre-warming by exercise (Warm-CWI) when wearing a dry immersion suit (2.97 Clo). In Warm-CWI seven subjects rested (20 min), and then cycled on an ergometer cycle (20 min) before immersed in water at 5° C (T_w) (140 min). In Base-CWI, six subjects were directly immersed in 5° C T_w after resting. Physiological variables measured during the test; T_{re} , T_{sk}, heart rate, oxygen consumption, ventilation and respiratory frequency. T_{re} and T_{sk} was significantly higher after Warm-CWI start of CWI, resulting in faster core cooling rate, drop in T_{re} and T_{sk} during the first 10 min. No differences in cardiovascular or respiratory responses were observed in the same initial period, indicating that the immersion suit protected well against the cold-shock response in both series. In the long term (0-140 min), the overall core cooling rate did not differ between Warm-CWI (0.34±0.11 °C • h-1) and Base-CWI (0.31±0.05 °C • h-1). Heat production was similar between conditions.

In conclusion, when entering cold water with a raised T_{re} and T_{sk}, different thermal responses during the first 10 min is observed, but the protection in the immersion suit eliminates long-term differences in core cooling rate between between normothermic and pre-warmed subjects.

Paper IV

This study explored the worst-case emergency scenario in cold water, where aircrew are exposed to severe conditions, including low ambient and water temperature, wind and waves. Under such conditions the immersion suit must ensure survival and protect from hypothermia for up to 12 hours (23). Additional heat production through leg exercise has great potential to offset at least some of the heat loss to the cold water when a well-insulated immersion suit is worn. Although exercise has been shown to increase heat loss due to increased blood perfusion in the exercising limbs in subjects wearing swimsuits (95, 133), intermittent periods of leg exercise reduced core cooling in subjects wearing a well-insulated immersion suit under calm conditions (107). This has not earlier been studied under severe conditions.

The aim of this study was to evaluate the effect of intermittent periods of leg exercise on heat balance and core cooling under severe environmental conditions when wearing a well-insulated immersion suit. We hypothesized that compared to passive conditions, intermittent periods of leg exercise (15 minutes per hour) will result in; 1) a greater rate of heat production that will offset the elevated rate of heat loss and hence 2) decrease the subsequent core cooling rate and 3) improve thermal sensation and comfort. On two separate days, seven male subjects were immersed in 2 °C water with an air temperature of -2 C, wind 5 m · sec^{-1} and waves of 30-40 cm high. Subjects wore woollen underwear, a flight suit and a 3 mm neoprene immersion suit (2.97 Clo for the whole clothing concept). The subjects were immersed for 180 minutes while either passive (NonEx) or performing moderate leg exercise for the final five minutes of each 20-minute period (LegEx). Heart rate, metabolism, T_{re}, T_{sk} , and skin heat flux were measured. A subjective evaluation of thermal sensation and comfort was obtained every 20 minutes (NonEx) or immediately before and after each exercise period (LegEx).

As predicted, intermittent periods of leg exercise resulted in a greater rate of heat production that offset the elevated rate of heat loss resulting in a net positive heat gain (10%) compared to lying still in the water. As a result a decreased core cooling rate and better thermal sensation and comfort was observed in the LegEx conditions compared to NonEx. The results suggest that when an insulated immersion suit is worn in cold water under extreme environmental conditions, five minutes of leg exercise every twenty minute might potentially provide a survival advantage at sea.

Discussion

The following discussion of the papers is divided into two main parts; thermal comfort and performance in air when wearing aircrew protective clothing (papers I and II) and the emergency situation in cold water (papers III and IV).

Thermal comfort and performance in air (papers I and II)

Ambient conditions required for thermoneutrality when wearing aircrew protective clothing

Paper I demonstrated that the existing solution for aircrew protective clothing did not fulfil requirements for thermal comfort at typical cockpit temperatures in Sea King helicopters operating in cool northern climatic zones. 18 °C T_a represented the threshold for when pilots start to experience sweating and discomfort when wearing protective clothing (2.2 Clo). The study confirmed that for sitting resting nude subjects the criteria for thermoneutrality (for definition see paper I) lie in the range of 28-30 °C T_a (30), and that wearing aircrew protective clothing affected heat exchange between the body and the surroundings and produced a downward displacement of the TNZ to 10-14 °C. These findings correlate well with data from our field study of Sea King rescue helicopter pilots (26), in whom increased skin temperatures and sweating caused significant discomfort during flights when wearing protective clothing (2.2 Clo) at an ambient cockpit temperature of 18.6±1.3 °C. A more recent study of 26 flights of Canadian Search and Rescue helicopters over a period of eight months (winter, spring and summer season), confirmed that an cockpit temperature of 18 °C represents the cockpit temperature at which aircrew wearing immersion suits (2.2 Clo) start to experience thermal discomfort, and 25 °C T_a represented a condition of thermal discomfort and perceived heat stress (19).

Paper I further demonstrated that the criteria for thermoneutrality (as defined in Paper I) are not met at one single ambient temperature, but rather at a range of temperatures. This is supported by several studies suggesting that there is a range of ambient temperatures within which heat loss and heat production are regulated by adjusting blood flow (81, 112). Small oscillations in finger and foot temperature were observed at T_a of 10-14 °C when protective clothing was worn, indicating regulation of heat balance through vasomotor control to keep the body within the thermal neutral zone (112, paper I). Metabolic and thermal responses stabilised within this range, but outside these T_a metabolic and thermal responses changed.

Once the capacity of the vasomotor control response is exceeded, the autonomic responses of sweating (above the upper critical limit of the TNZ) or shivering (below the lower critical limit of the TNZ) are coupled in. Paper I further demonstrated that the insulation in the clothing was not sufficient to prevent shivering at a T_a of 0 °C (T_{lc}).

Thermal comfort and work rate

Thermal comfort is important for the acceptance of wearing PPE by the users, and this is closely related to achieving body heat balance (27). However, the body may well be in heat balance but still uncomfortable because of sweating at high temperatures or vasoconstriction at low T_a (97). The main factors contributing to disturbances in heat balance during flights are *metabolic heat production* due to work, *ambient temperature* in the cockpit and *protective clothing*. For comfort, both sweat rate and mean skin temperature should be within a certain range determined by the work rate; outside this range complaints about thermal discomfort will be made (96). Metabolic rate during flying varies, depending on different phases of flight and type of aircraft (120). Oxygen consumption within the TNZ (10-14 °C) when wearing aircrew protective clothing was $0.3\ l \cdot min^{-1}$ (Paper I) as compared to $0.5\ l \cdot min^{-1}$ during helicopter flights (26) . This corresponds to a metabolic heat production of $88\ W \cdot m^{-2}$ during flight, and for Sea-King helicopter pilots, the metabolic rate is relatively stable over time. A higher work rate during flight will significantly affect the sweat rate and shift the comfort zone to a lower ambient temperature (96). Ducharme (19) simulated aircrew backender activities that involve a workrate above resting level. Interestingly, the level of physiological strain (increased T_{sk}, T_{re} and dehydration) and saturation of the microenvironment in the clothing after 60 minutes of work in 25 °C (19), was equivalent to ours when subjects were exposed to an environmental temperature of 40 °C at rest wearing the same clothing (Paper II). This emphasises that the combined effect of wearing protective clothing at sufficiently high T_a has a significant impact on the level of heat stress even at a low metabolic rate (Paper II). A relatively low metabolic rate, a stable heart rate and no increase in T_{re} during flight, demonstrates that Sea King Helicopter pilots are in heat balance at ambient cockpit temperature of at 18 °C, but are still uncomfortable due to raised skin temperature and sweat rate (26, Paper I).

Thermal comfort and sweating

Warmth discomfort is highly related to skin wettedness due to sweating (77). In papers I and II, the onset of sweating was determined by the increase in humidity in the microclimate of the clothing and the subjective sensation of sweating. Impaired heat exchange with the surroundings due to wearing protective clothing (47) caused a downward shift of the threshold for sweating compared to nude subjects (paper I). Both papers I and II demonstrated accumulation of water vapour due to sweating inside the immersion suit at T_a above 18 °C. At an ambient temperature 40 °C, relative humidity inside the clothing continuously rose until 100% saturation was reached (paper II). Ducharme's more recent study of Canadian helicopter search and rescue aircrew demonstrated similar findings (19). At 40 °C T_a, the accumulation of heat and water vapour within the clothing microenvironment over time caused cardiac output, skin temperatures and finally T_{re} to increase, demonstrating a non-compensable physiological strain (paper II). This thesis supports the conclusions of previous studies, that wearing immersion suits prevents evaporative cooling, resulting in increased heat storage in the body (116). With the restrictions on the body heat exchange, physical work in personal protective clothing becomes even more stressful (58).

Insulation and evaporative resistance of protective clothing

The evaporative resistance of protective clothing is influenced by the fabric construction and design of the immersion suit (110). The suit worn in papers I and II was the British Mark 10 survival suit (2.2 Clo for whole clothing concept), consisting of a double layer of cotton ventyle that permits transmission of water vapour in air, while in water the fibres expand, so that the interfibre spaces no longer transfuse liquid. The same immersion suit was used in a study by Sullivan and Mekjavic (116), who investigated the effect of the clothing microenvironment of four different types of protective clothing worn by helicopter personnel operating in Canadian coastal waters (Gore-tex, cotton ventyle, Nomex insulate and Nomex neoprene). This study demonstrated that for all concepts the increase in environmental heat load (when T_a was gradually increasing from 20-40 °C), was accompanied by increases in temperature in the clothing microenvironment. The vapour pressure within the clothing microenvironment increased in spite of little increase in ambient vapour pressure, and was dependent on differences in the evaporative resistance in the fabric of the suit. The dry suits with a water-permeable fabric (made of cotton ventyle and Goretex) resulted in less of an increase in T_{re} (0.2-0.3 °C) than the neoprene suit (1.2 °C). In comparison, our study (Paper II) demonstrated an increase in T_{re} of 1.2 °C in the cotton ventyle suit when exposed to a T_a of 40 °C. This difference can be explained by differences between the test protocols (test duration and gradually increasing T_a) and higher insulation values in the clothing concept in our study. We used two layers of woollen underwear (as normally used during Sea King helicopter flights in Norwegian coastal waters), while Sullivan and Mekjavic only used one layer of cotton underwear. The higher total insulation value due to more layers of underwear in the clothing concept has been shown to eliminate the benefit of higher evaporative efficiency in the fabric of the outer garment, resulting in similar thermal strain during helicopter flights (24). This underlines the importance of taking the whole clothing concept and the heat exchange mechanisms through the clothing system into account in the design of protective clothing. The choice of fabrics in the outer layer must allow for evaporative cooling during flights, while careful selection of the type, thickness and number of layers of underwear is necessary to alleviate thermal stress during flights. Recent studies in our laboratory (105) have demonstrated that phase-change materials (PCM) integrated in clothing can be used to reduce thermal stress and improve thermal comfort at low work rates when protective clothing is worn. However, this is only possible if such adaptive materials are carefully positioned and evaluated as a part of the total heat exchange mechanism through the clothing system, together with the capacity of the body to maintain thermal neutrality and comfort (105). The challenge is to achieve thermal comfort during flights without decrements in the protection in the event of immersion in cold water. One way to achieve this is by improving insulation in those areas of the body that are particularly exposed to heat loss in cold water (106), while allowing for evaporative cooling in zones of the body with a high potential for heat exchange through sweating (13, 117).

Aircrew protective clothing and performance in warm climatic zones

Paper II hypothesized that typical cockpit temperatures cause heat stress, which will have detrimental effects on cognitive performance when wearing protective clothing. The finding in Paper II that a 1.2 °C increase in T_{re} in 40 °C causes decrements in performance is most relevant to flights in warmer climatic zones. Although ambient cockpit temperatures in the Sea King helicopter occasionally rise to 40 °C in flight, cockpit temperatures seldom remain so high for very long. In warm climatic zones, heat stress is a concern for aviators regardless of whether or not they are wearing protective clothing (29, 90). Protective clothing further increases the heat stress and has been shown to cause severe decrements in operational tolerance limits and performance in pilots (10, 92, 104, 121). Ambient temperatures up to 40 °C are commonly reported when flying in hot, humid conditions (10), and the situation inside the cabin is even worse due to solar radiation. As a result, the temperature inside the cockpit is often reported to be 2-4 °C higher than the exterior ambient temperature (119). Such ambient conditions are far above the TNZ defined in Paper I, and as reported in Paper II, a T_a of 40 °C causes T_{re} to increase to 38.4 °C, which resulted in impaired performance. In agreement with the findings in Paper II, Caldwell (10) reported that US army helicopter pilots could not fly safely when wearing chemical biological protective clothing (CPC) in 40 °C without some kind of cockpit cooling equipment (10). Reardon et al (104) reported increases in heart rate, body core temperature, dehydration, poorer performance and other symptoms such as nausea, dizziness, headache and thirst, during simulated 2*2 hours helicopter flights at 38 °C when protective clothing was being worn. This is particularly noteworthy considering that many US military conflicts take place in part of the world where high ambient temperatures are common and the threat of chemical warfare is high (10). Norwegian military pilots too are currently engaged in military operations in geographical areas where ambient heat stress is a risk. Personal air or liquid water cooling systems has been shown to alleviate heat stress during flights under hot conditions (12, 86). However, not all helicopters have access to personal cooling systems or are able to regulate cockpit thermal conditions. Liquid and other cooling garments have also been tried out by Norwegian Sea King helicopter pilots; however, these were not widely accepted by the users.

Aircrew protective clothing and performance in cooler climatic zones

The results of Paper I suggest that heat stress caused by wearing protective clothing might be a problem even under winter conditions in northern countries, by shifting the TNZ to a much lower range of ambient temperatures. In northerly climatic areas, 23 °C represents a more realistic cockpit temperature (19). Although wearing protective clothing during flights causes thermal discomfort and increased skin temperatures at an ambient temperature of 18 °C (19, Paper I), Paper II found no decrements in performance in 23 °C and explained this by the lack of an increase in deep-body temperature. As far as cognitive performance is concerned, therefore, 23 °C is a tolerable ambient temperature in spite of the fact that cockpit temperature lies outside the thermoneutral zone when PPE is worn. Grether (35) and Hancock (42) similarly concluded that higher ambient temperatures result in more severe decrements in performance than moderate temperatures.

Possible mechanisms explaining degradations in performance under thermal stress

Uncompensable physiological strain

The mechanisms explaining the results are thoroughly discussed in Paper II, but some further discussion is provided in the following paragraphs. Paper II correlated the physiological findings with performance parameters, and the results support the theory that decrements in performance are related to the actual physiological thermal state of the body. We did not observe any decrements in performance before T_{re} passively rose to above 38 °C. This finding supports earlier studies that demonstrated that changes in performance are linked to dynamic changes in deep body temperature (2, 21, 38, 40, 44). When the total thermal load causes the deep body temperature to increase out of the comfort level, heat storage in the body will accumulate over time and performance breakdown will soon be observed (40). Hancock and Warm (43) suggest that performance is relatively stable over a wide range of ambient temperatures until a specific threshold limit is reached, at which point compensatory mechanisms begin to fail. When an individual can use physiological mechanisms (such as evaporation of sweat) to partially neutralize the impact of the increased ambient thermal load, this does not represent an uncompensable change (2). In our case, the combination of the evaporative resistance in the immersion suit combined with sufficiently high ambient temperature caused a situation in which compensatory effector mechanisms were not sufficient to keep the body in heat balance, with the result that T_{re} increased and performance was affected (Paper II).

Thermal sensation and comfort

The results of Paper II further demonstrated that performance decrements are not so closely linked to thermal sensation and comfort. If the latter correlation was found, we would expect a deterioration of performance at an ambient temperature of 23 °C T_a. This is in contrast to the theory of Hancock and Vastmatzidis (37), which claims that work performance begins to fail before current physiological heat stress limits are reached. The threshold at which comfort fails is much lower in terms of stress level than physiological threshold values (43). The results of Paper II suggest that subjects compensate for the thermal discomfort, possibly through increased arousal or motivation. However, we should not overlook the importance of the subjective reports of the pilots during flight (26), and further investigations are needed to determine whether experienced thermal discomfort in itself might result in performance deficit.

Acclimatization and duration of exposure

Other factors influencing performance include level of acclimatization, personal arousal and level of training (39). Exposure to heat has been demonstrated to be made somewhat more tolerable by increased duration, possibly due to heat acclimatization (39). Pilcher (99) suggested that experimental sessions of less than two hours in hot conditions had a stronger negative impact on performance than longer durations. This suggests that working in environments with high ambient temperatures would be expected to produce an initial deterioration in performance, which could be explained by the notion that people do adapt to some extent to extreme ambient conditions. The results of Paper II do not support this theory; on the contrary, better performance was found at the beginning of the test in some of the more complex tasks, which might be explained by a higher level of arousal. This is in accordance with Hancock and Vastmatzidis (37) who explain the arousal theory as follows: *"when environmental temperature (or body core temperature) rises, the arousal level of the performer increases, which in turn causes performance to improve. At some critical point of ambient (or core) temperature, no further improvement is possible and performance decreases with increasing heat (and arousal)".*

Nature of the tasks

Although it has been demonstrated that heat stress can eventually lead to impaired pilot performance and operational endurance (10, 90, 91, 119), this is still a controversial issue in practice, since the nature of the task and skill in performing it can be important variables in performance degradation during thermal stress (44). To define threshold limits for performance, therefore, the *nature of the activity* must be described (38, 39, 97). Attention, vigilance and fast decision-making are important cognitive tasks for a pilot, and paper II simulated these tasks under different thermal ambient conditions in a controlled laboratory setting. Like earlier studies, Paper II demonstrated that Vigilance was particularly vulnerable to heat stress (Paper II, 39, 99).

Furthermore, temperature stress is not always a bad thing, e.g. cognitive responses have been shown to actually benefit from mild cold exposure but are negatively affected by heat (39). Thermal ambient conditions seem to have various influences on different performance tasks.

For example, cold exposure has a negative effect on performance tasks such as reasoning, learning and memory (below 18 °C WBGT or below), while hot exposure (26 °C WBGT or above) results in small improvement in these tasks (39). In contrast, attention and perceptual tasks are more negatively affected by hot exposure than by cold (99). Paper II thus demonstrated that attention tasks (vigilance) were more affected by heat stress than more complex cognitive tasks. This thesis supports current theories that heat stress affects cognitive performance differentially, depending on the type of cognitive task, and that it appears that a relationship can be established between the effects of heat stress and deep body temperature (38).

The magnitude of the stress level experienced by a pilot will necessarily involve the interaction of several stressors, and in that context, occupational stress exposure limits should be based on evaluation of degradation of the task itself under realistic exposures (39). Although it is difficult to distinguish between different stressors (e.g., noise, vibration, temperature, etc.), our results emphasize the necessity of always including the thermal environment in occupational stress analysis when considering performance degradation.

In summary, having analyzed the thermal working environment for helicopter pilots wearing immersion suits, this thesis concludes that pilots experience thermal discomfort at ambient cockpit temperatures above 18 °C (Paper I). However, cognitive performance is virtually unaffected unless the combination of wearing an immersion suit and sufficiently high ambient temperature results in an uncompensable physiological strain that produces a dynamic increase in T_{re} (Paper II).

Immersion in cold water (papers III and IV)

While the above discussions concentrated on the work situation and the potential hazards of wearing protective clothing in flight, the next two papers focused on the emergency situation in cold water (Papers III and IV).

Short-term response to cold water

Exposure to cold water causes a rapid fall in T_{sk} that induces a cold-shock response that include an inspiratory gasp reflex, hyperventilation, reduction in breath hold time and cardiovascular responses (52, 82, 127). This response is extremely critical if the immersion occurs in choppy water or includes submersion from a ditched helicopter, and increases the chances of aspirating water and drowning. As discussed in paper III, the immersion suit attenuated the cold shock response by reducing the area of skin directly exposed to cold water, in both prewarmed and normothermic subjects. This is in agreement with previous studies, which have demonstrated that wearing protective clothing significantly alters the thermoregulatory response to cold water immersion by offering protection against the immediate cold shock response (53, 68, 73, 124, 125). Although convective heat loss results in different thermal responses during the first ten minutes after entering cold water with a raised body temperature, the insulation and air layer within the immersion suit allows for a higher T_{sk}, reducing the temperature gradient from the skin to the water (Paper III). As a result, T_{sk} were kept above the maximal firing rate of cold receptors (17-20 °C; 5, 123). This was also demonstrated in paper IV. This is very important, because it reduces the powerful drive to increase respiration and hence the risk of aspirating water and drowning (127). A much larger heat loss and rapid fall in T_{sk} has been demonstrated in studies where subjects were only wearing swimsuits (76, 113, 137) than in the studies in this thesis (Papers III and IV). This due to a much steeper body to water temperature gradient and a much larger surface area of skin exposed to cold water. In the studies of subjects wearing swimsuits, they were exposed in a sitting position with water up to their neck exposing a large area of the body to cold water (76, 113, 137). In Papers III and IV, subjects were kept in a supine floating position in the immersion suit, which meant that the upper parts of the body were exposed to air, which has much lower heat conductivity than water. The skin surface area exposed to cold water is therefore much less when an immersion suit is worn.

Long-term responses to cold water

In cold water, the innate protection mechanism against heat loss is shivering, but this is not sufficient to balance the heat loss in the long term, and deep body temperature will eventually drop. An unprotected individual exposed to cold water loses heat rapidly, and shortly after exposure to cold water will reach a critical core temperature below 35 °C, which is defined as hypothermia. The time taken to reach critical lower body temperatures depends on the rates of heat loss and heat production. This will depend on a range of individual factors; insulation in body fat and muscles, clothing, fitness level, nutritional status, gender, age and health status (11, 18, 74, 75). Jacob et al (64) suggest that aerobic fitness level can significantly influence heat balance and the core cooling rate during water immersion. Furthermore, insulation and the surface area-mass ratio is of particular importance in water (25, 54, 66). Hence, children are more vulnerable to heat loss than adults (114). Active or passive warming before immersion in cold water has been shown to increase heat loss from the body and accelerate the onset of hypothermia in subjects wearing swimsuits (76, 113,137). Paper III demonstrated that the immersion suit eliminates these long-term differences in core cooling between *pre* exercised and resting individuals. Paper IV further showed that increased heat production through leg exercise *during* CWI reduces core cooling, improves thermal comfort and reduces the sensation of cold.

Toner et al (129) showed that a more intense shivering response is associated with perceived thermal stress. Paper IV demonstrated that subjects felt uncomfortable due to increased shivering response when not performing leg-exercise. Five minutes of intermittent leg exercise every 20 minute was sufficient to reduce the discomfort associated with the more vigorous shivering (Paper IV). Thus, activity improves both physiological and psychological factors that favor survival in cold water.

Exercise in cold water has great potential for increasing heat production and thus improving heat balance. Physical activity increase metabolic heat production tenfold or more, while shivering has less capacity (4, 22, 32, 33, Paper IV). However, the benefit of exercising in water is controversial, since several studies have demonstrated increased convective heat loss due to high muscle perfusion (52, 68, 95, 133). Exercise produces a tenfold increase in muscle blood flow which has significant consequences for total body insulation (95, 133). The amount of heat delivered to the exercising limbs increases and overall tissue conductance increase largely through removal of the 70-90% of total body insulation which has been thought to be provided by poorly perfused muscle in resting individuals (133). As a result, a higher rate of heat loss from the skin is observed in subjects wearing only swimsuits (76, 113, 137). In contrast, Papers III and IV demonstrated that with adequate insulation provided by an immersion suit, enough of the body heat content from exercise before or during immersion is retained, in spite of the increased muscle blood flow. Paper IV further demonstrated that wearing an insulated dry immersion suit attenuated the convective heat loss observed when physically active. Although heat loss increased due to exercise (especially in the legs), there was a net heat gain due to the much greater heat production from exercise compared to shivering. Furthermore, leg movements alone disturb both the water and the boundary layer on the outside of the body and the potential air layer that is inside the suit (115). This contributes to a change in the thermal resistance of the suit system and explains the increase in convective heat loss during periods of exercise periods. During exercise, both increased vasodilatation and decreased fixed insulation in the suit due to water splashing over the front of the suit (which was normally exposed to air), may have contributed to the increased heat loss during the periods of exercise (Paper IV).

Severe environmental conditions affect heat balance during CWI

Paper IV is the first study to demonstrate reduced core cooling when wearing a well-insulated immersion suit in severe environmental conditions. The impacts of environmental factors (wind, waves, low sea and air temperatures), are significant in determining the rate of heat loss from the body during cold water immersion and are associated with significantly shorter survival times (17, 115). According to Steinman's field observations, increased activity levels is required to maintain stable body posture and airway freeboard, thus increasing peripheral circulation and decreasing effective tissue insulation in rough environmental conditions (115). However, the results of this thesis imply that when insulation in clothing is sufficiently high, activity in rough water has a significant positive effect by decreasing core cooling rate (Paper IV). This is in agreement with earlier studies that emphasised the importance of the thickness of insulation in the dry suit for the core cooling rate (107, 135). This is of great importance for Norwegian Sea King helicopter aircrew operating in the North and Barents Sea regions where severe environmental conditions are normal. If the aircraft suffers engine failure when flying over sea, they must perform a controlled emergency landing and will then be exposed to cold water (~2 °C), low air temperatures, waves and wind. According to Sea King rescue crew, search and rescue operations in these remote areas may well last for up to 12 hours (23). Under these severe conditions the immersed victim will continuously lose heat even when wearing a well-insulated immersion suit. Paper IV showed that a 5-15 minutes work –rest schedule of leg-exercise at a moderate intensity results in a net positive heat gain (10 %) compared to lying still. This procedure probably provides a practically significant survival advantage at sea for victims awaiting rescue, by extending the time to severe hypothermia (Paper IV).

The importance of wearing a well insulated dry suit

The importance of wearing a dry immersion suit in preventing heat loss from the body when lying still in the water has been demonstrated by Hayward (53), who found a 60-fold greater core cooling rate when wearing light clothing (52) than an insulated dry immersion suit (53). Other studies of subjects wearing wet suits have also demonstrated higher rates of heat loss and core cooling, and reduced tissue insulation when exercising than when at rest (94, 140). These studies indicate that, even in a wet suit-protected individual, exercise increases heat loss as much as heat production in cold water, emphasizing the importance of the degree of insulation in a immersion suit (94, 140). A dry immersion suit prevents direct contact between the water and the skin, thus keeping skin temperatures higher than in a wet suit, for example. Reinertsen et al (107) studied the importance of insulation value of dry immersion suits when performing leg exercises in cold water. This study demonstrated that intermittent periods of leg exercise did not alter the core cooling rate when wearing uninsulated dry immersion suits, while such behavior delayed core cooling in subjects wearing well-insulated dry suits. Without any confirming measurement of heat loss, they assumed that the overall heat loss is not enhanced by periods of leg exercise when wearing a well insulated immersion suit (107). In paper IV we introduced eight heat flux sensors to provide measurements of heat loss under more severe environmental conditions that included wind, waves, cold ambient temperature and near-freezing water. Although heat loss is enhanced during the leg exercise periods, it is counteracted by the high heat production, resulting in a more positive thermal situation (decreased core cooling) for the subjects compared to lying still. This thesis extends previous work by demonstrating the importance of insulation in the dry immersion suit in improving heat balance under more severe conditions.

To summarize, heat loss in cold water is highly dependent on the severity of the conditions and whether or not one is wearing an immersion suit. A well-insulated immersion suit provides excellent protection against critical short-term responses when exposed to CWI, in both prewarmed and normothermic subjects (Paper III). The immersion suit eliminates long-term differences in core cooling between pre-warmed and resting individuals (Paper III). Increasing heat production by intermittent periods of leg exercise is likely beneficial for better maintenance of heat balance under severe environmental conditions when wearing a well insulated immersion suit (Paper IV).

Methodological considerations

The methods used for evaluation of thermo physiology, heat exchange and thermal comfort in this thesis are widely used in research laboratories worldwide. They are based on years of experience in the Work Physiology Laboratory, and have already been described in a number of journal papers and textbooks.

Ambient condition

One weakness of the study described in Paper I is that we lack information about temperatures between the selected temperatures in the study. We do not know what would have happened at 9 °C or 15 °C, for example, and can therefore not exclude a broader zone of thermoneutrality. Nor did we include radiation in our laboratory setting in Papers I and II. This was included in a more recent study by Ducharme (19), and our results are still comparable to this study, which concluded that ambient temperatures of 23-25 °C do not cause any significant detrimental change in the physiology of aircrew when workload is low, as it is for helicopter pilots.

Protective clothing

The immersion suit worn in Papers I and II was the Mark 10 (Beaufort, UK) consisting of cotton ventyle (2.2 Clo for the whole clothing concept). In Papers III and IV we used a 3 mm neoprene suit (Helly Hansen, Norway) with higher insulation (2.97 Clo for the whole clothing concept). The neoprene suit is also frequently used during Sea King helicopter flights in Norway. A study comparing these two suits using the same test protocol as in paper III recorded higher heat stress and discomfort ratings during work, but better protection in cold water when the neoprene suit was worn (24). For this reason the neoprene suit was selected in the cold water immersion studies.

Choice of subjects

In Paper III, we were unable to use the same subjects in the two groups, so that a pair-wise statistical analysis could not be carried out. In order to reduce the effect of individual variance we matched the anthropometric data of the subjects, but the results should be interpreted with some caution. In paper IV the test subjects were a mixture of pilots and medical student’s i.e. a selected cohort of highly motivated subjects who were more capable of withstanding the detrimental effects of heat stress. A different population with lower motivation might not have the same ability to withstand the heat stress, and decrements in performance might occur earlier. In paper IV we selected young fit subjects with little variation in body fat. However, we did not measure the subjects' VO_{2max}, and can therefore not exclude the possibility that differences in aerobic fitness level influenced the cooling rate and the ability to sustain a certain level of leg-exercise intensity over time. However, they were their own controls, so comparison between series still persists.

Work intensity in cold water

In Paper IV we deliberately did not control work intensity precisely because we wanted to simulate a very realistic test in which the subject lies in a supine position as he would in a real accident. For the same reason we did not introduce ergometer cycles or similar equipment to control intensity as in previous studies (131, 133). Earlier studies have demonstrated that the intensity and duration of exercise and whether it involved legs, arms or both (131) are factors influencing its effects on core cooling. Leg exercise has been demonstrated to be many more times thermally efficient than arm or a combination of arm and leg exercise, because the higher surface-to-volume ratio of the arms results in greater heat loss than from the legs (131). Most studies on exercise in cold water involved continuous exercise. A work intensity of 4-5 MET is required to maintain thermal equilibrium for one hour below the thermoneutral water temperature (defined to be 34 °C at rest) (111). In practice such a high intensity cannot be continued consistently for a long period of time in water (111), so an interval-based regime of leg exercise is more adequate. In the present study work periods of five minutes every 20 minutes were based on the experience gained in previous experiments, where this work/rest schedule could be maintained for a long period of time (up to six hours) (107, 135). The study demonstrates that the length of the bouts of exercise (5 minutes) and the self-controlled exercise intensity (between 600-900 W) in this study was sufficiently high to slow the core cooling rate compared to lying still. It is important to note that even within this anthropometric group there were differences between subjects in the leg exercise intensity chosen. One subject chose an exercise intensity that was so high that he was able to increase his core temperature during three hours of immersion.

Conclusions

The following principal conclusions can be drawn from the findings of this thesis:

Existing aircrew protective clothing is unable to reconcile the requirements for thermal protection in water with those for thermal comfort during helicopter flights. Wearing aircrew protective clothing (2.2 Clo) causes a downward shift of the ambient temperature range required for thermoneutrality to 10-14 °C. These ambient conditions are below typical Sea King Helicopter cockpit temperatures operating in Northern cool climatic zones. Thermal discomfort is experienced at cockpit temperatures of 18-23 °C when wearing protective clothing, but this is tolerable as far as cognitive performance is concerned.

The thesis has further demonstrated that at an ambient condition of 40 °C, the evaporative resistance of the protective clothing causes accumulation of heat and water vapor within the clothing microenvironment. The resulting increase in sweat rate, cardiac output, skin temperatures and finally T_{re} is evidence of an uncompensable physiological strain. This thesis thus concludes that cognitive performance is virtually unaffected unless wearing an immersion suit combined with sufficiently high ambient temperature results in an uncompensable physiological strain resulting in increase core temperature (Paper II).

Heat stress due to working in aircrew protective clothing will not affect long-term core cooling rate during subsequent cold water immersion (Paper III). Aircrew protective clothing protects well against the initial effects of CWI, described as the “cold shock response” (Papers III, IV). The thesis has also shown that under severe environmental conditions five minutes of leg exercise every twenty minutes might improve heat balance resulting in a net positive heat gain (10%) compared to lying still in the water (Paper IV). This procedure reduces the core cooling rate and has a positive effect on subjective perception of thermal comfort and reduced cold sensation (Paper IV).

Practical applications

Paper I

The practical implications of the findings of this paper are that efforts should be made to increase thermal comfort by regulating cockpit temperature downwards (if possible) or considering the introduction of personal cooling aids at cockpit temperatures of as low as 18 °C when aircrew protective clothing (2.2 Clo) is worn.

Paper II

The practical implications of this study are that moderate cockpit ambient temperatures (23 °C) are quite tolerable as far as certain cognitive performance tasks required for helicopter flying are concerned, while high cockpit temperatures (40 °C) may over time lead to deterioration of flight performance when aircrew protective clothing is worn.

Paper III

The results of Paper III are relevant to occupations in which people are required to wear protective clothing due to the risk of being exposed to cold water when their body temperature is elevated. The practical implication of this study is that heat stress after working in protective clothing will not increase the risk incurred by falling in cold water, because 1) of aspirating water and drowning, since the protective clothing attenuates the cold shock response and 2) the immersion suit protects well against the long-term core cooling.

Paper IV

Five minutes of leg exercise every twenty minutes might improve heat balance when a well-insulated immersion suit is worn under severe environmental conditions. This procedure potentially provides a significant survival advantage at sea for victims awaiting rescue by extending the time to severe hypothermia. This is of significant importance for Norwegian Sea King helicopter aircrew operating in the North and Barents Sea regions where severe environmental conditions are common.

Future perspectives

This thesis addresses the difficulties of reconciling requirements for thermal protection and thermal comfort for helicopter pilots when wearing aircrew protective clothing. However, protective clothing for many sectors of the workforce has the same problem of resolving trade-offs between protection and comfort (firefighters' clothing, cold-weather clothing, chemical-biological clothing, etc.). Even people working in extreme cold may face the problem of heat stress at work when wearing protective clothing if the intensity of their work is high. In situations with rapid changes in work intensity and/or variations in ambient conditions, the limitations of the thermoregulatory system of the wearer will not be able to handle this alone to maintain thermal balance; for example, the rise in petroleum activity in the high north, willl face workers with conditions of extreme cold (http://www.sintef.no/ColdWear). Thermal protection and thermal comfort are both related to heat and moisture transfer in clothing. This has traditionally been regarded as two separate processes; however this issue needs to be addressed as a set of related phenomena (138). More recently, we have started to look at the influence of liquid sweat, which is often a problem for impermeable clothing evaporation and condensation. Complex models have been developed to understand these mechanisms (49, 138).

Recent years have seen a sharpening of focus on developing “smart textiles” that might help to solve the difficulties of reconciling contradictory requirements of personal protective clothing. An example is the development of the Helly Hansen SeaAir helicopter transportation suit (http://www.sintef.no/Presserom/Pressemeldinger/Prisbelont-for-intelligent-rednings--og-helikopterdrakt/). Today, developments in materials have led to a revolutionary way of thinking of protection. Performance and comfort can be improved by new textiles that can adapt their thermal and moisture-transmission properties to changing environment conditions and exercise levels. The safety and efficiency of operations can be improved by incorporating instrumentation in clothing for monitoring vital physiological parameters of the wearer. To do this, future research will need to develop a fundamental understanding of how comfort and performance can be improved by the use of stimulus-responsive textiles that adapt their properties to environmental changes. Research should be done to develop advanced materials that will provide a significant increase in performance because they are utilized in accordance with the body’s own regulatory mechanisms to provide optimal function. The main goal for the development of new materials for protective clothing must be to improve ergonomics and thermal comfort while maintaining an adequate level of protection. Clearly, making clothing that supports the thermoregulation of the human body is the most effective way of improving thermal comfort. By improving the mechanisms that affect thermal and moisture transport through several layers of fabric, thermal comfort can be improved. Material experts, product designers and clothing physiologist therefore need to collaborate in the development of more sophisticated protective clothing.

Many of the processes that occur in textiles are still not completely understood, and we can expect that intensive research will be done on this topic in the future (110). There is a trend towards realistic test methods that more closely resemble “real-life conditions”. Test conditions should be set according to a thorough assessment of how and under what conditions protective clothing will be used. Future research will need to pay more attention to understanding the situation of the worker and how specific tasks are performed. Development in the field of protective clothing must be take place on the basis of user needs; only then will appropriate solutions to some very complex problems be found.

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Paper I

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The thermoneutral zone when wearing aircrew protective clothing

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Abstract

The aim of this study was to determine the thermoneutral zone (TNZ) in subjects wearing aircrew protective clothing. TNZ were first defined in naked subjects to a temperature range of 28–31°C. Wearing aircrew protective clothing caused a displacement of the TNZ to 10–14°C ambient temperature (T_a). Discomfort increased at ambient temperatures above this range, as a result of increases in metabolic rate, mean skin temperature (MST) and sweating. The practical implication of this study is that cockpit temperature in Sea King helicopters should be regulated to lie between 10°C and 14°C (T_a) in order to prevent heat stress in pilots when wearing aircrew protective clothing. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Temperature regulation; Basal metabolism; Protective clothing; Mental performance; Mean skin temperature; Thermal comfort; Heat stress; Helicopter pilot

1. Introduction

Humans are not very well adapted to cold and can tolerate only small falls in body temperature. In the cold, man uses behavioural adaptation (clothing, shelter, moving to a warmer environment) or physiological mechanisms (vasoconstriction) to decrease heat loss, or increases heat production through exercise or shivering. Humans cope better with heat and are capable of increasing heat loss either behaviourally (by moving to a colder environment) or physiologically (by increased peripheral blood flow or evaporation of sweat). The range of ambient temperature (T_a) within which basal metabolic rate is minimal and constant is called the thermoneutral zone (TNZ) (Risbourg et al., 1991). Despite the obvious importance of the TNZ, this zone of thermoregulation has attracted little research in humans since experiments revealed its existence more than 50 years ago.

Within the range of TNZ, the control of thermal balance is accomplished by the regulation of skin blood flow (Hardy, 1961). Metabolic rate rises at a T_a below the lower critical temperature (T_{lc}) and above the upper critical temperature (T_{uc}) of TNZ (Withers, 1992). The relationship between metabolic rate and T_a below T_{lc} generally conforms to a physical model for endothermic heat balance, where $M = C(T_b - T_a)$ (M is metabolic rate, T_b is body temperature, T_a is ambient temperature and C is the thermal conductance). This is not a physical constant, but can be varied by behavioural and physiological thermoregulation. The conductance varies in naked subjects, and is dependent on the thickness of, and bloodflow to, subcutaneous tissues. A large bloodflow to the skin increases heat loss and conductance is high. When T_a decreases below T_{lc} vasoconstriction occurs and the insulation value of the superficial shell of the body is higher while conductance is lower.

Under normal circumstances evaporation of sweat is sufficient to keep the body in heat balance. However, some working situations require protective clothing capable of limiting heat exchange with the surroundings by increasing insulation and preventing evaporative heat loss, but which may cause significant heat stress for the

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user. This is known to be a severe problem for military pilots, who are required to wear protective clothing during flights, possibly resulting in fatigue and impaired pilot performance (Nunneley, 1989; Hancock, 1981). Field studies of Sea King helicopter pilots, for example, have demonstrated that they experience significant heat stress during flight (Færevik and Reinertsen, 1998). Sea King pilots and crew members in Norway are required to wear a survival suit all year around when operating in the North Sea and Barents Sea region with low sea temperatures. The heat stress is caused by a combination of the survival suit, the large cockpit canopy that increases radiation, and limited possibilities to regulate ambient temperature inside the cockpit. Nor do pilots have the possibility to behaviourally move to a cooler environment. It is therefore interesting to define the ambient conditions within which pilots are thermally comfortable and do not experience any physiological heat stress.

The aim of this study was to determine the thermoneutral zone (TNZ) in subjects wearing aircrew protective clothing, as this has not earlier been defined. The study also aimed to define how thermal conductance under ambient conditions below T_{lc} changes in naked subjects and subjects wearing aircrew protective clothing. In naked, resting subjects the TNZ has been defined as lying between 28 and 30°C ambient temperature (Gagge et al., 1967), and we hypothesised that wearing protective clothing will cause displacement of the TNZ to a lower range of ambient temperatures.

2. Material and methods

The following criteria were used to define the TNZ; (1) The range of ambient temperature within which the basal metabolic rate is minimal and constant (Risbourg et al., 1991), predicting that the metabolic rate will increase below T_{lc} and above T_{uc}. (2) Mean skin temperature (MST) between 33–35°C (Savage and Brengelmann, 1996), predicting that the MST will decrease below T_{lc} and increase above T_{uc}. (3) The subjective sensation temperature and thermal comfort is neutral, predicting that subjects will be thermally uncomfortable below T_{lc} and above T_{uc} (Åstrand and Rodahl, 1986).

Eight male volunteers participated in the study. The mean ($\pm$SD) age, weight, height and percent body fat of the subjects was 23.6 ± 1.3 years, 83.7 ± 11.0 kg, 184.1 ± 5.3 cm, $12.5 \pm 1.7\%$. The subjects were asked to retire to bed at their usual time on the night before each exposure. They abstained from exercise and taking caffeine, alcohol or snuff for 24 h before exposure. Subjects were not permitted to eat 3 h before the test in order to avoid a rise in metabolic rate after feeding. None of the subjects were smokers. All subjects were in good health and had undergone an electrocardiogram test. The Ethical Review Committee of the Faculty of Medicine at the Norwegian University of Science and Technology approved the experimental procedure. The subjects were free to withdraw from the chamber environment at any time.

2.1. Experimental protocol

Subjects reported to the preparation room at least 1 h before the test. Registration of weight, height and body fat were made. Percentage body fat was calculated using the Durnin and Wommersley 4-site skinfold thickness measure (Durnin and Womersley, 1974). Body surface in square metres (A_{Du}) was calculated using the following formula (DuBois, 1919): $A_{\mathrm{Du}} = 0.202 \cdot W_{\mathrm{b}}^{0.425} \cdot H_{\mathrm{b}}^{0.725}$, where W_{b} is the body weight in kg, and H_{b} is the body height in meters. The subjects were then fitted with thermistors and heart rate recorder. To provide baseline measurements of oxygen consumption ($\mathrm{VO_2}$), skin and rectal temperature and subjective evaluations, the subjects sat quietly outside the climatic chamber for 20 min. The subjects were then moved to the climatic chamber where they sat at rest for a further 60 min.

Each subject was first exposed to a range of ambient temperatures wearing only shorts (series A). They were then exposed to a lower range of temperatures, wearing aircrew protective clothing (series B) in order to determine the displacement of TNZ. In series B they dressed as pilots normally do for helicopter flights, with long legged/long sleeved underwear (200 g Ullfrotte), a woollen whole-body overall, leather gloves, helmet and uninsulated survival suit (Mark 10, Beaufort, England). The insulation value of the whole clothing ensemble was 2.20 Clo, measured on a thermal manikin. In series A they were exposed to seven different ambient conditions; 15°C, 20°C, 25°C, 28°C, 31°C, 35°C, and 40°C, respectively. In series B they were exposed to five different conditions; 0°C, 10°C, 14°C, 18°C, and 25°C, respectively. The subjects were exposed randomly to the different environmental condition to avoid any order effects. The tests were carried out at the same time of the day on separate days with at least a one-day interval between the tests. Subjects were not permitted to drink or eat during the experiment.

During the experiments, rectal temperature (T_{re}) was measured with a thermistor probe (YSI-700, Yellow Springs Instrument, USA, accuracy $\pm$0.15°C) inserted 10 cm beyond the anal sphincter. Skin temperatures were measured using thermistors (YSI-400 Yellow Springs Instrument, USA, accuracy $\pm$0.15°C) at 13 locations (forehead, chest, lower arm, abdomen, underarm, middle finger, neck, scapula, front of thigh, back of thigh, shin, calf and surface of foot). The weighted average formula of Teichner (1958) was used to define mean skin temperatures (MST). Heart rate (f_c) was recorded using a Polar Sports Tester (Polar Electro, Finland). All logged data were transferred to a computer for graphically and numerically displaying the results every minute and processed using TempLog 3.1. Oxygen consumption (VO_2) was logged for a period of 10 min after 40 and 60 min in the climatic chamber using a Cortex MetaMax Portable Metabolic Testsystem (Cortex Biophysic GmbH, Germany). To ensure stabilised measures of VO_2 the mean of the last 2 min (of the 10 min measure period) were used for statistical analysis. A questionnaire developed by Nielsen et al. (1989) was used to obtain information about local and overall thermal sensation, shivering/sweating and thermal comfort. Thermal sensation of the body, feet and hands was evaluated according to the following rating: 1 very cold, 2 cold, 3 cool, 4 slightly cool, 5 neutral, 6 slightly warm, 7 warm, 8 hot, 9 very hot. Thermal comfort was evaluated according to the following rating: 1 comfortable, 2 slightly uncomfortable, 3 uncomfortable, 4 very uncomfortable. Shivering/sweating was also evaluated on a graded rating; 1 heavily shivering, 2 moderately shivering, 3 slight shivering, 4 not at all shivering/sweating, 5 slightly sweating, 6 moderately sweating, 7 heavily sweating. Environmental conditions (air temperature, radiation and relative humidity) were measured continuously with an Indoor Climate Analyser T1213 (Brüel & Kjær A/S, Denmark). Thermal conductivity (C) was calculated from the following formula (Withers, 1992): $M = C(T_b - T_a)$, $C = M/(T_b - T_a)$, where M is metabolic rate, T_b is body temperature and T_a is ambient temperature.

2.2. Statistical analysis

Time-dependent changes in rectal temperature, mean skin temperatures and heart rate were assessed by two-way analysis of variance for repeated measures (ANOVA). A within-group study design was used. All data were tested for effects of time, ambient conditions and interactions between the two measures. When ANOVA revealed a significant main effect, a contrast test was used as a post hoc test to identify significant differences between temperatures. Kawashima (1993) has shown that it takes 30 min for rectal and skin temperature, heart rate and metabolism to stabilise at a higher ambient temperature, so the mean values of the last 30 min were analysed further using Student's *t*-test for paired samples. Differences in oxygen consumption and the various ratings on thermal comfort, thermal sensation, degree of shivering or sweating were also assessed by Student's *t*-test for paired samples. The measures after 60 min were used in the statistical analysis in order to be sure that the readings had stabilised. The Shapiro Wilks test was used to test for normal distribution. Results are presented as means ±SD for eight subjects. All differences reported are significant at the $p \leqslant 0.05$ level. SPSS 10.0 (SPSS inc. Chicago, USA) was the software used for processing the statistical material.

3. Results

3.1. Oxygen consumption

In series A (naked) VO_2 was lowest at 28°C ($3.9 \pm 0.7\,ml \cdot kg^{-1} \cdot min^{-1}$) and highest at 15°C ($5.1 \pm 1.1\,ml \cdot kg^{-1} \cdot min^{-1}$). VO_2 at 28°C was significantly lower than at 15°C, 35°C and 40°C (T_a) (Fig. 1). In series B (wearing aircrew protective clothing), VO_2 was lowest at an ambient condition of 10°C ($4.1 \pm 0.7\,ml \cdot kg^{-1} \cdot min^{-1}$) and 14°C ($3.9 \pm 0.4\,ml \cdot kg^{-1} \cdot min^{-1}$) (Fig. 1). VO_2 at both 10°C and 14°C was significantly lower than at 0°C, 18°C, and 25°C. There were no significant differences between 10°C and 14°C.

3.2. Rectal temperature

For both series A and B, statistical analysis by ANOVA demonstrated that the time-dependent change in rectal temperature (T_{re}) was highest during the first 30 min under all ambient conditions, and that the T_{re} then stabilised during the last 30 min. One exception was the 40°C (series A) where T_{re} continued to increase throughout the experiment. When the means for the last 30 min for all subjects in series A were compared, it was

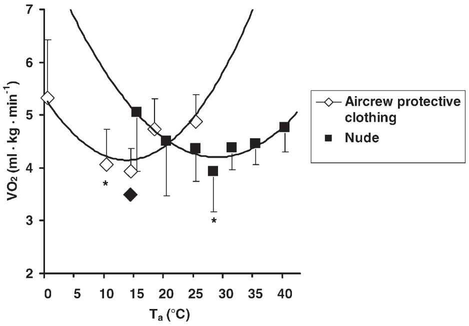

Fig. 1. Changes in metabolic rate (VO_2) in subjects wearing only shorts (series A) after 60 min exposure to seven different ambient temperatures (T_a), or wearing aircrew protective clothing (series B) at five different ambient temperatures ($n = 8$). In series A (nude), (*) indicates significantly lower VO_2 at 28°C (T_a) as compared to 15°C, 35°C and 40°C. In series B (wearing aircrew protective clothing), (*) indicates significantly lower VO_2 at 10°C as compared to 0°C, 18°C and 25°C, and (◆) indicates significantly lower VO_2 at 14°C as compared to 0°C, 18°C and 25°C.

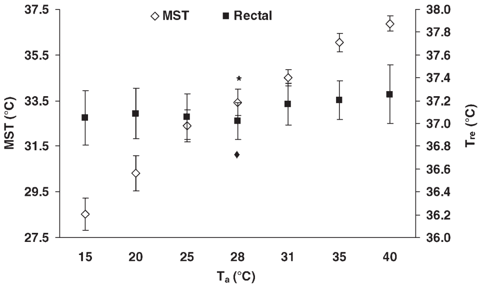

Fig. 2. Mean ± SD of mean skin (MST) and rectal temperature (T_{re}) during the last 30 of 60 min exposure to seven different ambient temperatures (T_a) in subjects only wearing shorts (series A) ($n = 8$). (◆) indicates significantly lower T_{re} at 28°C (T_a) as compared to 31°C, 35°C and 40°C. (*) indicates significantly differences in MST between all T_a in relation to 28°C.

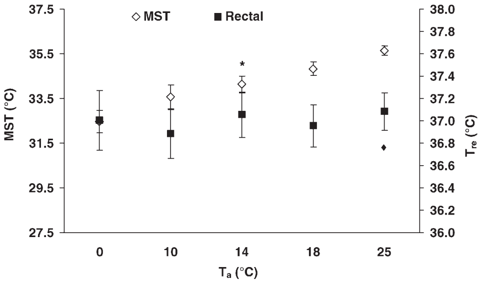

Fig. 3. Mean ± SD of mean skin (MST) and rectal temperature (T_{re}) during the last 30 of 60 min exposure to seven different ambient temperatures (T_a) in subjects wearing aircrew protective clothing (series B) ($n = 8$). (◆) indicates significantly higher T_{re} at 25°C (T_a) as compared to 10°C. (*) indicates significantly differences in MST between all T_a in relation to 14°C.

found that T_{re} was unchanged at temperatures below 28°C, but was significantly higher at ambient condition 31°C, 35°C and 40°C compared to 28°C (Fig. 2). In series B, T_{re} was significantly lower at 10°C (36.9 ± 0.2°C) compared to 25°C (37.1 ± 0.2°C) (Fig. 3). No other differences in T_{re} between ambient conditions were observed.

3.3. Mean skin temperature

Most skin temperatures stabilised after 30 min at the different ambient temperatures in series A. However, at the two lowest ambient conditions (15°C and 20°C) MST continued to fall throughout the experiment. MST was very responsive to changes in T_a. When MSTs during the last 30 min in series A were compared, significant differences were found between all ambient temperatures (Fig. 2). Mean skin temperature rose at T_a higher than 28°C and fell at T_a below 28°C. The criteria for thermoneutrality (MST of 33–35°C) were fulfiled at both T_a of 28°C (33.4 ± 0.6°C) and 31°C (34.5 ± 0.4°C). In series B, MST stabilised after 30 min at all ambient temperatures, except at 0°C, where it continued to fall throughout the experiment. At 10°C and 14°C (T_a) there were no significant time-dependent changes in MST throughout the whole experiment. When MSTs during the last 30 min in series B were compared, they were found to rise with increasing ambient temperatures and fall at lower ambient temperatures (Fig. 3). MST differed significantly between all ambient conditions. An T_a of 10°C (33.6 ± 0.6°C), 14°C (34.2 ± 0.4°C) and 18°C (34.8 ± 0.3°C) fulfiled the criteria for thermoneutrality (MST of 33–35°C). Finger and foot temperatures stabilised and demonstrated the least variations at 25°C, 28°C and 31°C in series A. Finger and foot temperature showed a slight increase and thereafter stabilised when T_a was 35°C or 40°C. At T_a of 15°C and 20°C finger and foot temperatures did not stabilise and continued to fall throughout the experiment. In series B, finger and foot temperatures stabilised at 10°C, 14°C, 18°C and 25°C, but at 0°C (T_a) continued to fall throughout the experiment.

3.4. Subjective evaluations

Taking all subjective evaluations together, the feeling of thermal neutrality was not limited to a single temperature, but was closest to the ambient temperatures of 25°C, 28°C or 31°C in series A. All subjects stated that they felt most comfortable at 25°C (T_a). At lower ambient temperatures (15°C and 20°C) and higher ambient temperatures (35°C and 40°C) subjects were significantly more uncomfortable. Similarly, the overall thermal sensation of the body, hands and feets was closest to neutral at ambient temperatures of 25°C, 28°C and 31°C. Subjects stated that they were slightly warmer at T_a of 31°C than 25°C, but there were no significant differences between 25°C and 28°C. At ambient temperatures of 35°C and 40°C, all subjects stated they were sweating significantly more than at 31°C. At lower temperatures, subjects started shivering at 20°C, and shivered significantly more compared to temperatures at and above 25°C.

In series B, there were no significant differences in subjective sensations of thermal comfort between ambient temperatures of 10°C, 14°C and 18°C. The subjects were significantly more uncomfortable at 0°C and 25°C than at either 10°C or 14°C. Most subjects stated that they were not shivering/sweating at all at ambient temperatures of 0°C and 10°C. Some subjects voted that they started sweating slightly at 14°C and 18°C. At 25°C all subjects were sweating significantly. The thermal sensation of the body was closest to neutral at 10°C (4.9 ± 0.6, 5 = neutral) and 14°C (5.4 ± 0.5). Thermal sensation of hands and feet's were closest to neutral at 10°C (5.0 ± 0.5 and 4.8 ± 0.7, respectively). The subjects were significantly cooler at 0°C and significantly warmer at 18°C and 25°C compared to 10°C and 14°C.

3.5. Heart rate

In series A, the heart rate (f_c) fell at low temperatures (15°C and 20°C) and increased at higher temperatures (35°C and 40°C). There were wide inter-subject variations in heart rate. When the results for the last 30 min were compared, there were no differences in heart rate between 25°C (61 ± 10 beats $\cdot$ min^{-1}), 28°C (64 ± 4 beats $\cdot$ min^{-1}) and 31°C (63 ± 7 beats $\cdot$ min^{-1}). Heart rate was lowest at T_a of 15°C (56 ± 7 beats $\cdot$ min^{-1}), and highest at 40°C (70 ± 8 beats $\cdot$ min^{-1}). The only T_a at which f_c stabilised were 28°C and 31°C. Heart rate at 28°C and 31°C (T_a) was significantly higher than f_c at 15°C and 20°C and significantly lower than f_c at 35°C and 40°C. In series B, f_c increased significantly with time when T_a was 25°C, and the mean of the last 30 min at this temperature was also highest (68 ± 7 beats $\cdot$ min^{-1}). The heart rate at 25°C was significantly higher than f_c at 0°C (58 ± 9 beats $\cdot$ min^{-1}) 10°C (56 ± 5 beats $\cdot$ min^{-1}) and 14°C (58 ± 7 beats $\cdot$ min^{-1}) (T_a).

4. Discussion

The maintenance of a constant body temperature is important for pilots, since raised body temperature is correlated with impaired pilot performance (Nunneley, 1989). The main purpose of this study was to determine the thermoneutral zone (TNZ) in subjects wearing aircrew protective clothing. The hypothesis that wearing protective clothing will affect heat exchange with the surroundings and cause displacement of TNZ was clearly supported.

In naked resting subjects, VO_2 was lowest at 28°C (0.33 ± 0.08 l $\cdot$ min^{-1}) and this is close to the value that Nielsen et al. (1989) demonstrated under thermoneutral condition (VO_2 at 0.32 l $\cdot$ min^{-1}). Weight-specific VO_2 was used when comparing the different exposures in order to compensate for weight differences. TNZ has earlier been defined as lying between 28 (T_{lc}) and 30°C (T_{uc}) ambient temperatures (Gagge et al., 1967). Resting subjects will strive to combat the rise in body temperature by sweating above T_{uc} and to prevent a fall in body temperature by shivering below T_{lc}. This energy demanding thermoregulatory processes will cause an increase in metabolism below T_{lc} and above T_{uc} in order to keep the body in heat balance (Davson and Sagal, 1975). Even though some subjects reported that they started shivering at an ambient temperature of 20°C, we did not observe any significant increase in metabolic rate at 20°C or 25°C. Most subjects did not report shivering until T_a was as low as 15°C, this was also demonstrated by an increase in VO_2. The results of the VO_2 measurements suggest that T_{lc} in naked resting subjects is lower than the earlier suggested 28°C. This suggestion is in accordance with Kawashima (1993), who demonstrated a rise in metabolic rate at 22°C but no significant increase at 25°C (T_a). A significant increase in metabolic rate was found at higher ambient temperatures (35°C and 40°C). This suggests that T_{uc} is close to 31°C in naked, resting subjects. This suggestion is supported by the observation that subjects also started sweating at 35°C (T_a). Protective clothing (2.20 Clo) clearly affected metabolism in these sitting, resting subjects. The observation of the lowest values of metabolic rate shifted from 28°C (T_a) to 10°C (0.33 ± 0.06 l $\cdot$ min^{-1}) and 14°C (0.32 ± 0.03 l $\cdot$ min^{-1}) (T_a) when with protective clothing. At both lower (0°C) and higher T_a (18°C and 25°C) the metabolic rate increased significantly. The insulation of the clothing was not sufficient to prevent shivering at 0°C, as was demonstrated by an increase in VO_2. Shivering caused subjects to feel more uncomfortable and they also stated that they felt slightly cooler at 0°C compared to higher T_a. At ambient temperatures closer to T_{uc} vasoactivity is no longer sufficient to regulate heat balance and active sweating occurs. To prevent an increase in body temperature, the produced sweat must evaporate. Even though the survival suit used in the present study has some evaporative properties, it was not sufficient to ensure evaporative cooling at 18°C (T_a). As a result, there was a significant increase in metabolism at 18°C (T_a). Subjects stated that they were sweating and that their clothing felt damp and they were warm and significantly uncomfortable at ambient temperatures above 18°C.

The significant differences in MST between all different ambient temperatures in naked subjects demonstrates that skin temperatures are very sensitive to changes in ambient conditions, due to the rapid implementation of vasoconstrictive responses. Calorimetric studies of naked male subjects have shown that MST values of 33°C–35°C cover the TNZ (Hardy and BuBois, 1937; Savage and Brengelman, 1996). Ambient temperatures of 28°C–31°C fulfilled the criteria for thermoneutratility in naked subjects. MST did not stabilise after 30 min when naked subjects were exposed to the lowest temperatures (15°C and 20°C), and both the low mean values (28.5 ± 0.7°C, 30.3 ± 0.8) and the continuous fall in MST suggests that 15°C and 20°C (T_a) is below T_{lc}. This is in agreement with the findings of Kawashima (1993), who demonstrated that MST does not stabilise at lower temperatures. At higher temperatures (35°C and 40°C) skin temperatures stabilised close to T_{re} temperature and were outside the TNZ. The high values of MST (36.0°C and 36.9°C) at 35°C and 40°C indicate that vasodilatation is at its maximum while T_{re} is also increasing, and this helps to maintain the core-skin gradient and thereby ensure dissipation of heat. T_{re} was significantly higher at 31°C, 35°C and 40°C than at 28°C. Rectal temperature is not very sensitive to small changes in T_a, and is therefore not a very good indicator of the TNZ. The observed increase in metabolic rate below T_{lc} at 15°C prevented T_{re} from falling. Wearing aircrew protective clothing clearly affected MST and caused a displacement of thermoneutral temperatures from 28°C and 31°C to a lower range of 10°C, 14°C and 18°C (T_a). The increased metabolism at 25°C caused a significant rise in MST. Within the TNZ, control of thermal balance is achieved by regulation of the skin blood flow (Hardy, 1961). This is accomplished by vasomotoractivity in the extremities (hands and feet), characterised by small oscillations within the TNZ. This was observed at T_a of 10°C and 14°C, indicating that these temperatures produce the TNZ. This is supported by the finding that subjective thermal sensation of hands and feet was close to neutral at these T_a. At the lowest ambient temperature (0°C) the skin temperatures in fingers and feet were falling throughout the experiment, indicating that vasoconstriction of peripheral vessels was occurring. Finger and foot temperatures were not oscillating and continuously increasing at 18°C and 25°C (T_a), indicating that the vessels were dilated in order to increase heat loss. The result from the skin temperatures of the extremities suggests that TNZ while wearing protective clothing lie within the range of 14°C to 18°C.

Heart rate rose at the highest T_a, and fell at lower T_a. The increase in heart rate and vasodilatation causes an increase in peripheral bloodflow and thus heat dissipation at higher T_a (Hardy and BuBois, 1937). Heart rate decreases in colder environments due to vasoconstriction. Although wide individual variations made it difficult to determine the TNZ, heart rate was significantly higher at 35°C and 40°C in naked subjects, and lower at 15°C and 20°C. This indicates that the TNZ is between 25°C and 31°C. When subjects were wearing protective clothing, the only significant difference in heart rate was observed in an increased heart rate at 25°C compared with 0°C, 10°C and 14°C, while the TNZ shifted downwards. It may be concluded that heart rate was not a good indicator of thermoneutrality.

Fanger (1970) suggested that heat balance was necessary for a subjective sensation of thermal comfort. Discomfort increased when MST was outside the TNZ. This is in agreement with Gagge et al. (1967), who demonstrated that the subjective sensation of discomfort correlates well with changes in MST. The subjective evaluations of thermal sensation and comfort in this study indicate that TNZ is in the range of 25°C and 31°C in naked subjects, and shifted to a lower T_a range of 10°C to 18°C when subjects were wearing aircrew protective clothing. The subjective evaluations indicated a wider TNZ than suggested by the physiological measurements, and it is possible that the scale for subjective evaluation is not sensitive enough to locate significant changes with small variations in T_a.

The results from this study suggests that TNZ wearing protective clothing is between 10°C and 14°C. During helicopter flights VO_2 has been measured to $0.53 \pm 0.02\,\mathrm{l\,min^{-1}}$ ($n = 6$) using the same clothing as in the current experiment (Færevik and Reinertsen, 1998). The ambient condition in cockpit during these 2 h flights were 18.6 ± 1.3°C. This T_a is somewhat higher than the suggested thermoneutral condition determined when subjects were sitting still in the laboratory. Even this cool cockpit condition (18°C) caused MST above 35°C, subjective sensation of thermal discomfort and increased sweat production, indicating that the subjects was outside TNZ.

Thermal conductance at 28°C was calculated to be $0.04\ \mathrm{W\,m^{-2}\,{}^{\circ}C^{-1}}$ in naked subjects and $0.01\ \mathrm{W\,m^{-2}\,{}^{\circ}C^{-1}}$ at 10°C (T_a) in those wearing protective clothing. The fall in heat conductance with protective clothing reflects a reduction in heat flow to the surroundings from the body when wearing protective clothing. In naked subjects the insulation is low and conductance is correspondingly high. Protective clothing is a barrier to heat dissipation, and heat has to be transported to all the clothing layers, resulting in a fall in thermal conductance. The results of this study are summarised in Fig. 4. This figure illustrates the change in thermal conductance calculated from the T_{lc} values in both series A and B.

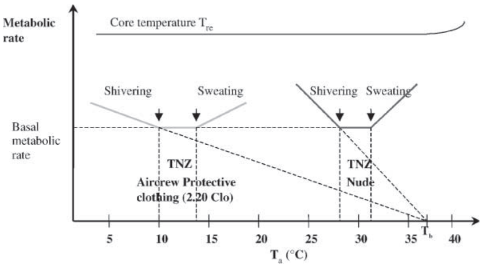

Fig. 4. The displacement of the thermoneutral zone (TNZ) when wearing aircrew protective clothing. The figure illustrates the thermal conductance based on the estimated lower critical temperature (T_{lc}) for both series. In series A (nude) thermal conductance was calculated at T_{lc} of 28°C to $0.04\ \mathrm{W\,m^{-2}\,{}^{\circ}C^{-1}}$ and in series B (wearing aircrew protective clothing) it was calculated at T_{lc} of 10°C to $0.01\ \mathrm{W\,m^{-2}\,{}^{\circ}C^{-1}}$. T_b is body temperature.

5. Summary

This study has shown that the criteria for thermoneutrality were met at 28°C and 31°C (T_a) in naked subjects, and shifted downward to 10°C and 14°C (T_a) when subject wore aircrew protective clothing. It also suggests that 10°C mark the T_{lc} when wearing protective clothing, given that we lack information about temperatures between 0°C and 10°C, and that 28°C marks the T_{lc} in naked subjects.

The practical implication of this study is that cockpit temperature in Sea King helicopters should be regulated to lie between 10°C and 14°C (T_a) in order to prevent heat stress in pilots when wearing aircrew protective clothing. Pilot discomfort will increase at cockpit temperatures above 18°C, as a result of increases in metabolic rate, MST and sweating.

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Paper II

Paper III

Paper IV

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook *Corvus frugilegus.*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.
1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit *Parus montanus.*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988	Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
1988	Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
1988	Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
1988	Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.).
1989	John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989	Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
1989	Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990	Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
1990	Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990	Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
1991	Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway.
1991	Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
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1992	Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
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1993	Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.
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1995	Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
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1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
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1996	Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.
1996	Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996	Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.
1996	Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
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1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.

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1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
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1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998	Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999	Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*

1999 Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999 Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999 Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999 Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.
1999 Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999 Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999 Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999 Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999 Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999 Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999 Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999 Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000 Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000 Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000 Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000 Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000 Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000 Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000 Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001 Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations.
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania

2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Bilogy	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease

2009 Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009 Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009 Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009 Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009 Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009 Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010 Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments -Focus on formulated diets
2010 Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010 Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010 Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania
2010 Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010 Anders Lyngstad	ph.d Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation