TECHNICAL REPORT

NO. T94-11

HOMEOSTATIC RESPONSES TO PROLONGED COLD EXPOSURE: HUMAN COLD ACCLIMATIZATION

by

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June 1994

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REPORT DOCUMENTATION PAGE

Form Approved
OMB No. 0704-0188

1. AGENCY USE ONLY (Leave blank)	2. REPORT DATE May 1994	3. REPORT TYPE AND DATES COVERED Technical Report

4. TITLE AND SUBTITLE

Homeostatic Responses to Prolonged Cold Exposure: Human Cold Acclimatization

5. FUNDING NUMBERS

6. AUTHOR(S)

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7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)

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Kansas Street
Natick, MA 01760-5007

8. PERFORMING ORGANIZATION REPORT NUMBER

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)

Same as Block 7.

10. SPONSORING/MONITORING AGENCY REPORT NUMBER

11. SUPPLEMENTARY NOTES

12a. DISTRIBUTION/AVAILABILITY STATEMENT

Approved for public release; distribution is unlimited.

12b. DISTRIBUTION CODE

13. ABSTRACT (Maximum 200 words)

This report reviews human physiological adjustments induced by chronic exposure to cold stress. Three broad types of adjustments are identified. The most commonly observed adjustment exhibited by humans chronically exposed to cold is a hypothermic habituation. Blunted shivering and vasoconstrictor responses to cold characterize this adjustment which enables maintenance of warmer skin during cold exposure. Metabolic acclimatization/acclimation has been observed in which shivering response to cold becomes exaggerated. Insulative acclimatization/acclimation has also been observed in which persons chronically exposed to cold vasoconstrict cutaneous vasculature more readily. The factors determining which pattern of adjustment occurs remain unidentified, although a theoretical explanation is presented which is based on the intensity of the cold stress experienced.

14. SUBJECT TERMS

Cold; Acclimation; Metabolism; Insulation

15. NUMBER OF PAGES

58

16. PRICE CODE

17. SECURITY CLASSIFICATION OF REPORT	18. SECURITY CLASSIFICATION OF THIS PAGE	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT
Unclassified	Unclassified	Unclassified	

NSN 7540-01-280-5500

Standard Form 298 (Rev. 2-89)

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FIGURE 14. Flowchart illustrating a theoretical scheme to explain the development of different patterns of cold acclimatization/acclimation which are observed in humans. The physiological effects of chronic cold exposure on humans have received much less attention from researchers than the effects to chronic heat stress. Compared to the effects of repeated heat stress, physiological adjustments exhibited by humans chronically exposed to cold appear to have less practical value in terms of ameliorating thermal strain, defending body temperature and preventing thermal illness and injury. None the less, the various thermoregulatory adjustments exhibited by humans chronically exposed to cold merit consideration because they are physiologically interesting and may provide insight concerning the nature and extent of human adaptability to environmental extremes.

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EXECUTIVE SUMMARY

This report reviews physiological effects of chronic cold exposure on humans, and speculates on mechanisms mediating these effects. Persons chronically exposed to cold exhibit adjustments in thermoregulation classified as cold acclimatization, cold acclimation, or cold habituation. Acclimatization refers to adjustments in response to changes in the natural environment, whereas acclimation refers to adjustments produced by exposure to artificial conditions in experimental chambers. Habituation refers specifically to adjustments that diminish physiological response to cold. Habituation is, by far, the most commonly observed adjustment to chronic cold exposure. Blunted shivering and cold-induced vasoconstriction are the hallmarks of habituation. These adjustments enable skin to be kept warmer, but contribute to a greater fall in core temperature, thus the term hypothermic habituation may denote this adjustment. Besides habituation, cold acclimatization and cold acclimation can heighten responses to cold, or induce responses not apparent in the unacclimatized state. These adjustments follow two patterns. Metabolic acclimatization/acclimation is characterized by a more pronounced thermogenic response to cold. An exaggerated shivering response may develop because of chronic cold exposure, and some evidence suggests that humans develop a nonshivering thermogenesis. Insulative acclimatization/acclimation pattern is characterized by enhanced mechanisms for conserving body heat during cold exposure. More rapid cutaneous vasoconstriction has been observed in chronically cold exposed persons, which may be mediated by enhanced sympathetic nervous responses. What determines which pattern develops is not known but a theoretical scheme can be proposed. Brief, intermittent cold exposures appear to induce habituation of shivering and vasoconstrictor responses to cold, even when only limited areas of body surface are exposed and whole body heat losses are negligible. More pronounced physiological adjustments appear to require exposure conditions severe enough that significant body heat is lost. Insulative adjustments appear to develop in response to cold exposures severe enough to cause deep body temperature to decline significantly. The stimulus for the metabolic pattern of cold adaptation may be prolonged exposure to conditions during which significant body heat is lost, but body heat production increases sufficiently to prevent a decline in deep body temperature. Compared to chronic heat stress, physiological adjustments to chronic cold exposure appear less practical in terms of relieving thermal strain, defending body temperature and preventing thermal illness and injury. Nonetheless, an understanding of these adjustments may provide insight concerning the nature and extent of human adaptability to environmental extremes.

INTRODUCTION

This chapter will review the thermoregulatory responses of persons chronically exposed to cold, and speculate on the determinants of the physiological adjustments exhibited. Consistent with conventions established earlier in this technical report, physiological adjustments produced in humans in response to chronic cold stress will be classified as acclimatization or acclimation, whereas the term adaptation will be reserved to describe genetic effects manifested as a result of natural selection. In the context of this chapter, the term habituation will be used to refer specifically to acclimatization or acclimation adjustments in which the physiological response to the cold stimulus is diminished in magnitude in the compared to unacclimatized state. Besides habituation, cold acclimatization resulting from living and working in cold environments, and cold acclimation induced by unusual or experimental alterations in environmental conditions, can result in physiological adjustments such that cold stress elicits either a more pronounced responses in the acclimatized than unacclimatized state, or a response not apparent in the unacclimatized state. These types of adjustments tend to follow two patterns. Metabolic acclimatization/acclimation is characterized by development of a heightened thermogenic response to cold. Insulative cold acclimatization/acclimation is characterized by enhancement of mechanisms for conserving body heat during cold exposure.

NATURALLY OCCURRING COLD ACCLIMATIZATION

Investigators have sought to document human capacity to acclimatize to cold by comparing thermoregulation in people regularly exposed to cold throughout their lives to that in people lacking this experience. For example, persons native to circumpolar regions of the world where temperatures are among the coldest of all inhabited regions have been studied, as well as scientific researchers and adventurers participating in polar expeditions into even colder areas. However, even in seemingly warm regions, nighttime temperature can fall below normal body temperature. People living in those areas under technologically primitive conditions, such that their clothing and shelter provided inadequate protection from the cold, have been studied for evidence of acclimatization. A third group of people who have been studied for signs of cold acclimatization are those whose occupations require them to regularly work while partially or wholly immersed in cold water. All of these people have demonstrated evidence of thermoregulatory acclimatization to cold.

CIRCUMPOLAR RESIDENTS

Circumpolar residents respond to whole-body cold exposure in the same general manner as persons from temperate climates. Inuits (2, 26, 29, 49), other Native Americans from the North American Arctic (17, 36, 49) and Norwegian Lapps (3, 49) all respond to acute cold exposure by increasing metabolic heat production through shivering and vasoconstricting peripheral blood vessels.

The most commonly observed thermoregulatory adjustment exhibited by circumpolar residents is a blunted shivering response. For example, Andersen *et al.* (2) reported that when Inuit subjects were moved from 25 to 5°C air temperature, their resting metabolic rate increased by 27%, as compared to more than a 60% increase in metabolic rate in unacclimatized control subjects. Andersen *et al.* (3) made similar observations when they compared thermoregulatory responses of Norwegian Lapps and non-acclimatized control subjects to cold overnight; these findings are shown in Figure 1. The Lapps exhibited a smaller increase in oxygen consumption and a more pronounced fall in rectal temperature during cold exposure than control subjects. This diminished shivering response compared to unacclimatized persons is an example of a habituation to repeated cold exposure.

The more pronounced fall in core temperature during cold exposure exhibited by the Lapps compared to control subjects is characteristic of the cold acclimatization in this particular ethnic group. However, this hypothermic habituation is not always observed in circumpolar residents. In contrast to the Lapps, studies of Inuits (1, 2, 26, 29, 58) and Native Americans from Arctic regions (35) do not indicate any consistent difference in their core temperature responses during cold exposure and those of unacclimatized control subjects.

Another observation often reported concerns skin temperature responses of circumpolar residents exposed to cold. As shown in Figure 1, the Lapps studied by Andersen *et al.* (3) tended to maintain warmer mean skin temperatures overnight than the control subjects. Likewise, Inuits appear to maintain higher mean skin temperatures than control subjects during cold exposure (1, 29, 58). Warmer skin in circumpolar residents than control subjects reflects a greater thermal conductance resulting from increased metabolism, altered vasomotor responses, decreased physical insulation associated with low subcutaneous fat, or all three factors.

In the absence of cold stress, both Inuits (1, 2, 13, 26, 29, 58) and Native Americans from the Arctic (13, 35) have been observed to have a higher resting metabolic rate than control subjects. The elevated basal metabolic rate allows them to sustain a greater rate of body heat loss and maintain warmer skin during cold exposure, with a smaller increment in shivering-induced metabolism than unacclimatized control subjects. However, the higher metabolic rate in circumpolar residents has been attributed to the effects of the high protein content of their diet (59), rather than a specific effect of chronic cold exposure.

Circumpolar residents appear to transfer heat from body core to shell more readily than unacclimatized persons. Whole-body thermal conductance depends on two components: a fixed conductive component in which thermal insulation is determined by the thickness of the subcutaneous fat and muscle layers comprising the body's shell; and a variable convective component in which heat flux is determined by peripheral blood flow. The latter is subject to thermoregulatory control mechanisms, whereas the former is not. Differences between Inuits and unacclimatized persons with regard to both components appear to provide the basis for greater thermal conductance in Inuits.

Under conditions in which peripheral blood flow was minimal (immersion in water cool enough to induce maximal vasoconstriction without eliciting shivering), Rennie *et al.* (58) observed that Inuits had a significantly higher thermal conductance than unacclimatized control subjects. However, as shown in Figure 2, most of the difference appeared to be due to differences in body composition, i.e. the fixed

FIGURE 1

FIGURE 2

conductive component. Therefore, these data (58) provide no evidence that residence in cold climates induces any thermoregulatory adjustments in circumpolar residents. Other investigations, however, suggest that the cutaneous vasoconstrictor response to cold is altered in circumpolar residents. For example, Brown and Page (9) measured hand blood flow in Inuits and unacclimatized control subjects during two-hour immersions in water at various temperatures ranging from 45 °C down to 5 °C. As shown in Figure 3, Inuits maintained higher hand blood flow than the control subjects at all water temperatures, but the difference was most pronounced at the colder temperatures. Similarly, Miller and Irving (52) observed that Inuits maintained higher finger temperatures during cold-air exposure than control subjects lacking significant cold-weather experience. Elsner *et al.* (18) observed that Native Americans residing in the arctic regions of Canada's Yukon Territory exhibited twice the hand heat loss of control subjects during immersion of the hand in cold water. All of these observations support the notion that cold-induced vasoconstriction in the hands of circumpolar residents is less pronounced than in unacclimatized persons. Furthermore, measurements of forearm blood flow during arm immersion in water of different temperatures also demonstrate that Inuits maintained higher peripheral blood flow during cold exposure than control subjects (8), suggesting the adaptation may not be limited to the hand circulation. Lastly, Miller and Irving (52) also observed that young Inuit boys did not exhibit the blunted vasoconstrictor response, suggesting that this habituation is an acclimatization acquired in time with repeated cold exposure, rather than an adaptation.

People native to temperate climates who sojourn in circumpolar regions reportedly experience cold acclimatization. Budd and Warhaft (10) reported that members of a research team exhibited an improved defense of rectal temperature during a standardized cold exposure after they had resided six months in the Antarctic. However, the improvement in this case was probably due to an increase in adiposity rather than an adjustment directly in response to chronic cold, since mean body weight of the subjects increased 2.5 kg during the study period. Other studies have reported that circumpolar sojourners develop similar responses as exhibited by life-long circumpolar residents. For example, a French physician who made a solo trek to the North Pole during the spring of 1986 exhibited a reduced metabolic heat production, more pronounced decline in rectal temperature, but maintenance of

FIGURE 3

warmer skin temperatures during a standardized cold-air exposure test compared to measurements made before he undertook the journey (6). Ambient air temperatures ranged from -12 to -52 °C during the trip. A similar pattern of acclimatization has been observed in soldiers living and working outdoors (air temperature range from -5 to -17 °C) during winter in Alaska (12).

Exposure to such severe cold conditions is not necessary to induce these adjustments. Members of scientific expeditions to the Antarctic have developed blunted metabolic and vasoconstrictor responses to cold despite living and working primarily indoors and being exposed to the extreme cold weather for only rare, brief periods (7, 11, 51). Apparently, repeated exposure of small areas of the body, such as the hands and face, to extremely cold temperatures is sufficient to stimulate a blunted vasoconstrictor response to cold, even when the exposures are fairly brief.

Overall, thermoregulatory adjustments experienced by circumpolar reside not appear to significantly improve their ability to defend body temperature during cold exposure. However, these people who live permanently or even temporarily in regions experiencing the most extreme cold weather on earth do become habituated to cold, in that cold-exposure elicits less shivering and a blunted vasoconstrictor response compared to persons from temperate climates. This acclimatization pattern probably reflects the type of cold exposure these people routinely experience. People living in these regions generally have adequate clothing and shelter to protect them from the cold and probably do not experience significant whole-body cooling, thus, explaining the lack of a more dramatic adjustments in thermoregulation. On the other hand, periodic short-term exposure of small portions of the body would be fairly common, such as when gloves are removed to complete a task requiring dexterity or when individuals moved through unheated corridors of a polar base. Indeed, a habituation of shivering and peripheral vasoconstrictor responses to cold is probably most advantageous for situations where whole body cooling is unexpected, since warmer skin and reduced shivering would conserve energy stores, improve comfort and help prevent peripheral cold-injuries.

PRIMITIVE PEOPLE LIVING IN TEMPERATE-WEATHER REGIONS

Even areas not noted for extreme cold weather can become quite cold, especially at night, and evidence for cold acclimatization has been observed in primitive people living in such climates. Primitive people are those whose geographic and/or cultural isolation from the mainstream of modern society has denied them the advantages provided by technological amenities. The ethnic and cultural heritage of the different primitive people which have been studied for cold adaptations varies, but, in contrast to circumpolar residents, they share the common disadvantage that their clothing and shelter are inadequate to provide them protection from cold weather. Therefore, it is not surprising that these persons appear to be have experienced different thermoregulatory adjustments than the pattern of cold habituation exhibited by circumpolar residents.

Among the earliest studies of thermoregulation in primitive people were those of C.S. Hicks and his co-workers (28) who studied the Aborigines living in the central Australian desert. Night-time low temperatures in the central Australian desert reach 0 °C in the winter and 20 °C in the summer; the low humidity and clear atmosphere enhance the potential for evaporative and radiative cooling. At the time that Hicks studied them (1930-1937), the central Australian Aborigines were nomadic tribes who lived out of doors and wore no clothing. They slept on the bare ground at night and their only protection from the cold was a small fire at their feet and windbreak made from light brush. Hicks reported that, in contrast to the increase in metabolic rate exhibited by unadapted subjects sleeping in the cold, the Aborigine's metabolic rate remained unchanged as ambient temperature fell at night (28). The Aborigines also exhibited a greater fall in skin temperature than did Europeans sleeping in comparable ambient conditions which, Hicks speculated (28) was due to a more pronounced cutaneous vasoconstrictor response to cold.

Subsequent studies of the Australian Aborigine by Scholander *et al.* (61) and Hammel *et al.* (24), confirmed Hicks' observations (28). Additionally, Hammel *et al.* (24) reported, as shown in Figure 4, that the Aborigine's rectal temperature also fell more than in control subjects. However, thermal conductance, calculated by dividing

FIGURE 4

the metabolic heat production by the core (rectal) to skin temperature gradient, was less in the Aborigine than the unacclimatized Europeans (24).

Hammel *et al.* (24) concluded that the lower thermal conductance of the Aborigine was evidence for a more pronounced vasoconstrictor response to cold than exhibited by unacclimatized persons. If this is indeed the mechanism, then the lower rectal temperatures exhibited by Aborigines sleeping in the cold must reflect a redistribution of body heat stores from the core to the shell while the reduced thermal conductance may reflect an insulative type of acclimatization to repeated cold stress. On the other hand, Hammel *et al.* (24) presented no evidence to demonstrate that a more pronounced cutaneous vasoconstrictor response was the mechanism for the reduced thermal conductance. Alternatively, the Aborigines may have exhibited a lower thermal conductance simply because of the lower metabolic heat production, i.e. their shivering response to cold had become habituated, but unlike the Inuits, their vasoconstrictor response had not.

Another primitive people who have been studied for signs of cold acclimatization are nomadic South African residents of the Kalahari desert. These people, who have been referred to as Bushmen, live in a desert environment very similar to that of central Australia. Like the Australian *Aborigines*, the Kalahari Bushmen employed minimal clothing or shelter, although they did wrap themselves in a cloak at night to protect themselves from the cold (67). Unlike the Aborigine, the Kalahari Bushman was observed to increase metabolic heat production as ambient temperature fell during the night (29, 66, 67).

Wyndham and Morrison (67) and Ward *et al.* (66) both reported that metabolic rate increased similarly during cold exposure in Bushmen and European control subjects. However, the Bushmen were smaller and leaner than the control subjects. This raises the possibility that if they had been compared to control subjects having similar subcutaneous fat thickness, the increment in metabolic heat production would have been found to be blunted in the Bushmen. Hildes (29) compared metabolic heat production measurements from Bushmen, Arctic Inuits and Caucasian control subjects made under similar standardized cold test conditions. Hildes (29) concluded that, compared to Caucasian control subjects, the Bushmen did exhibit a habituated shivering response to cold, but the increment in their metabolic heat production was similar to that of the Inuits. The Bushmen maintained lower skin temperatures during cold exposure than the Inuits (29), but not the Caucasians (66, 67). Therefore, metabolic heat production for a given skin temperature was lower in the Bushmen than the Inuits.

These observations suggest that the Kalihari Bushmen had become habituated with regard to shivering response to cold, but had not experienced the blunting of the cutaneous vasoconstrictor response to cold exhibited by Inuits. The absence of evidence for an insulative pattern of cold acclimatization as had been observed in the Australian Aborigine may reflect a milder environmental stress on the Bushmen. On the other hand, the possibility that the Aborigines had become (genetically) adapted cannot be ruled out.

The thermoregulatory responses to cold exhibited by the Alacaluf people studied by Hammel (22) in 1959 have been cited (23) as indicating the existence of the metabolic pattern of cold adaptation. These Native Americans lived nomadically on the islands off the coast of the southernmost tip of South America. The traditional clothing of the Alacaluf had been a loin cloth and cloak, but by the time Hammel undertook his studies they had begun wearing some modern garments. Nevertheless, their clothing provided only scant protection from the environment. The region's climate is very rainy, with mean low temperatures ranging from 0 to 8 °C and mean high temperatures ranging from 5 to 15 °C. Formerly, the Alacaluf slept on the ground in lean-tos constructed of brush, but by the time Hammel studied them, they had begun to build huts from scrap lumber and other construction materials they obtained from visitors. Further contributing to the cold stress to which they are subjected, the Alacaluf spent considerable time hunting for food, in and around the coastal waters. Overall, Hammel's description of them suggests that the Alacaluf followed a way of life similar to that of the coastal Inuits of the North American Arctic, and, while the environment was not as severe, the Alacaluf's clothing and shelter was less protective than that of the Inuits.

Hammel (22) measured thermoregulatory responses of the Alacaluf using the same standardized overnight cold exposure protocol used in many of the other studies of primitive people (2, 3, 17, 24, 35, 61). In contrast to the progressive rise in metabolic heat production exhibited by unacclimatized subjects during the overnight cold exposure, the Alacaluf subjects exhibited a progressive fall in metabolic heat production as they slept in the cold (22). However, metabolic heat production of the Alacaluf was over 50% higher than that of the non-adapted control subjects at the beginning of the cold exposure; therefore, by the end of the night the Alacaluf and non-adapted subjects had reached similar metabolic rates (22). The higher metabolic heat production throughout most of the cold exposure has been taken by some researchers as evidence of an enhanced thermogenesis, or metabolic acclimatization, induced by chronic cold exposure. However, it may be that these people were in fact only habituated to cold, as evidenced by the declining metabolic rate throughout the cold exposure similar to the response evidenced by the Australian Aborigine. The fact that the Alacaluf began the cold exposure with a higher metabolic rate than control subjects could simply reflect the effects of their diet as in the Inuits (59).

The thermoregulatory studies of the Kalihari Bushmen, Australian Aborigines and the Alacaluf people clearly indicate that their repeated cold exposure can result in habituation of the shivering response, as seen in the circumpolar residents. However, in contrast to the circumpolar residents, these primitive people exhibit no evidence of a blunted vasoconstrictor response. The possibility that repeated whole-body cooling can induce an insulative form of cold acclimatization, characterized by a more pronounced vasoconstrictor response is strongly suggested, but not confirmed, by the exaggerated fall in skin temperatures observed in the Australian Aborigines when they were exposed to cold. The study of the Alacalufs of Tierra del Fuego (22) has been cited as evidence for a metabolic form of cold acclimatization, but this interpretation of the data is tenuous at best.

The somewhat different acclimatization patterns exhibited by the Australian Aborigines, Inuits and Lapps may reflect the difference in the type of cold exposure that the groups experience. The circumpolar residents experience brief exposures of small body areas to extreme cold, while the Aborigines are exposed to less extreme temperatures, but the duration and extent (i.e. minimal clothing) are such that they experience prolonged periods of moderate whole-body cooling. Unfortunately, it is probably too late now to confirm and extend the studies of the primitive peoples. For the most part, they have been integrated into modern society and taken advantage of technological developments to improve their standard of living. As a result, they are no longer exposed to the chronic cold conditions which probably induced the thermoregulatory adjustment that they previously exhibited. However, there is other evidence demonstrating that repeated whole-body cooling is indeed the required stimulus to induce more significant cold acclimatization beyond habituation. The next section will review findings from studies of modern people who, as a result of occupation or endeavor are chronically immersed in cold water.

MODERN PEOPLE REPEATEDLY IMMERSED IN COLD WATER

Water has a much higher thermal capacity than air, and heat conductance from unprotected skin can be more than 70 times greater in water than air at the same temperature. For this reason, fishermen, divers and swimmers who frequently immerse part or all of body in water can experience considerable body heat loss, even when the water temperature is only mildly cool. A number of studies have documented evidence of cold adaptations in these people.

Persons whose occupations necessitate frequent immersion of the hands into cold water, exhibit alterations in the regulation of blood flow and skin temperature in the hands during localized cold exposure. The responses to cold that they exhibit are similar to those observed in the Inuits and other Circumpolar residents discussed earlier. For example, when their hands were immersed for 10-min in 2.5 °C water, Gaspe' fishermen of Quebec, Canada, maintained higher finger temperatures than unacclimatized control subjects (47). These fishermen spend several hours a day during fishing season (April through November) immersing their hands in water ranging from 9-12 °C. Fish filleters, who worked each day with one ungloved hand immersed in ice water, showed a similarly enhanced ability to maintain higher finger and hand temperatures during immersion of the hand in cold water compared to control subjects (54). Slaughter house workers who handle cold meat throughout their daily workshift showed a tendency for a similar adjustment, but differences between their responses and those of control subjects did not achieve statistical significance (19), possibly reflecting less severe hand cooling compared to the people who must immerse their hands in cold water.

To some extent, the maintenance of warmer skin during cold exposure is mediated by region-specific adaptations, that is, adjustments in local regulation of hand blood flow. This is demonstrated by the observation that when the fishermen mentioned above immerse their feet in cold water, foot temperatures fell to the same level as in control subjects (45). Presumably, the fishermen's feet are well protected from the cold, and therefore, do not exhibit the adjustments seen in the frequently exposed hands. Despite the fact that only the hands are exposed to the cold, centrally-mediated adjustments also appear to be involved in the blunting of the vasoconstrictor response to cold. As shown in Figure 5, besides maintaining warmer hand temperatures, the Gaspe' fishermen respond to immersing the hand in cold water with a smaller rise in systemic blood pressure than non-adapted control subjects (46). The blood pressure response to immersing the foot in cold water is also blunted in the fishermen compared to control subjects, even though there does not appear to any adjustment in regulation of blood flow and skin temperature in the feet. Furthermore, when the Gaspe' fishermen were exposed to whole-body cooling in cold air (60-min nude, resting exposure to 15 °C), the fishermen maintain higher skin temperature over their whole body, not just in the hands compared to control subjects (54).

The blunted vasoconstrictor response to cold exhibited by the fishermen and fish filleters is probably a form of cold habituation. Nelms and Soper (54), however, suggested that the warmer skin temperatures and higher blood flows maintained by these people reflects the development of a more significant cold acclimatization in that the cold-induced vasodilator response has become more sensitive or extensive. An increased whole-body thermal conductance would be a disadvantage in a cold environment if protective clothing were not worn to offset decreased physiological insulation. However, for the otherwise warmly dressed fishermen and filleters, an increased blood flow to skin of the unprotected hand would be beneficial for comfort and dexterity while working in the cold.

As pointed out elsewhere in this handbook, because of the very high heat capacity of water, the potential for body-heat loss and cooling is large during immersion in water, even when the temperature is only mildly cool. For that reason, several investigations have attempted to determine if swimmers or divers exhibit acclimatization to this repeated cold stress. Long-distance swimmers, surfers and scuba divers have all been reported to display blunted or delayed shivering during

FIGURE 5

cold-water immersion (15, 21, 63) suggesting that they have become habituated to the cold. Other data suggests that swimmers develop a more significant acclimatization.

Dressendorfer *et al.* (15) compared several physiological responses of highly trained long-distance runners and long-distance swimmers during a resting immersion in water cool enough to elicit maximal vasoconstriction (30 °C). Metabolic rates of the two groups, who had been matched for body mass, % fat and surface area, were the same during immersion (15). Therefore, cardiac outputs were probably similar in the two groups, since they were the same size and body composition. However, swimmers maintained lower systemic blood pressure and higher heart rates during immersion than runners (15). This suggests that, while cutaneous vasoconstriction was maximal in both groups, the swimmers maintained perfusion of more subcutaneous vascular beds than the runners. Thus, the swimmers appeared to minimize thermal conductance and body heat loss at the skin without compromising blood flow to subcutaneous muscle and internal organs. Such an altered pattern of physiological response, suggests that an insulative form of cold acclimatization may have developed in the swimmers.

Another group of individuals who repeatedly swim in cold water are the professional breath-hold divers of Korea and Japan, known as the Ama. The Korean divers, who are all women, work throughout the year, whereas in Japan there are both male and female divers, and they only work during the warm season. The Ama traditionally wore only a light-weight cotton bathing suit which offered little insulation, and they dove in water as cold as 10 °C in the winter and 25 °C in the summer (33, 34). During these dives, they experienced marked whole-body cooling. It was observed that the divers would terminate their work shift and leave the water to rewarm after their core temperature fell by about 2 °C (40, 41). Since skin temperature usually approaches water temperature during unprotected immersion in cold water, these people were subject to the greatest degree of cold stress, as reflected by repeated reduction in mean body temperature, of any of the groups considered thus far. It could be suggested that the willingness of these people to repeatedly subject themselves to such stressful conditions was itself evidence for their acclimatization and/or adaptation to the cold. However, the thermoregulatory responses of these divers, studied extensively over the last three decades by Drs. Suk

Ki Hong, Yang Saeng Park and numerous colleagues, provide a more physiological demonstration of cold acclimatization.

One observation suggests the possibility that the diving women experienced a metabolic form of cold acclimatization. Kang *et al.* (39) observed a seasonal variation in the basal metabolic rate (BMR) of the Korean Ama. In the summer, when water temperatures were warmest, the Ama's BMR was lowest and equal to that of non-diving control subjects from the same community (39). Throughout the fall, the Ama's BMR increased, becoming highest in the winter when water temperatures were coldest; the non-diving control subjects exhibited no seasonal fluctuation in BMR (39). The physiological mechanism for the seasonal variation was not identified. Dietary factors were ruled out as causative (39). The development of a significant nonshivering thermogenesis was also thought to be unlikely since the thermogenic response to norepinephrine infusion was found to be minimal in winter and absent in summer (38). However, a pattern of seasonally-related increases in thyroid hormone utilization by peripheral tissues was observed (31). While the elevated BMR in the Ama during winter appeared to be in response to increased cold stress, the practical value of an increased BMR was negligible in terms of providing protection against whole-body cooling of the type the divers repeatedly experienced (33, 39).

Other observations are consistent with the development of a habituation type of cold acclimatization in the diving women. As shown in Figure 6, the shivering response to cold appeared to be blunted in the divers (30). Non-diving Korean women tolerated colder water without shivering than did non-diving Korean men presumably due to their greater subcutaneous fat thickness. However, the Korean diving women tolerated much colder water without shivering than non-divers of comparable fat thickness (30, 31). Although their shivering responses indicate that they had become cold-habituated like the Circumpolar residents and Australian Aborigines, the Ama's vasomotor responses and skin heat flow during cold exposure suggest that a more complex pattern of acclimatization had developed.

Considerable experimental evidence suggests that the Ama diving women had developed an insulative form of cold acclimatization; that is, mechanisms for conservation of body heat were enhanced. Hong (31) measured maximal tissue

FIGURE 6

insulation of Ama divers and non-diving Koreans from the same community. Maximal tissue insulation is the reciprocal of an individual's thermal conductance measured in water cool enough to induce maximal peripheral vasoconstriction without eliciting shivering; it is a measure of the individual's maximal ability to resist heat loss to a cool environment. Figure 7 depicts the relationship between maximal tissue insulation and subcutaneous body fat of the diving women and non-diving Koreans. The insulation derived from fat is quantitatively similar for divers and non-divers as indicated by the similar regression line slopes; however, maximal tissue insulation of the divers was greater than that of the non-divers with comparable subcutaneous fat thickness (31). Assuming a similar skin thickness in divers and non-divers, and that its contribution to insulation is negligible, the increased maximal tissue insulation in the divers must be derived from their muscular shell.

One determinant of the greater maximal tissue insulation in the divers is their blunted shivering sensitivity. Shivering causes an increase in muscle blood flow which facilitates convective heat transfer from body core to shell. Furthermore, movement of the skin surface disrupts stationary boundary layers above the skin surface, enhancing conductive heat transfer from skin surface to the environment. However, the increased insulation of the divers is not due solely to shivering habituation.

Development of an enhanced vasoconstrictor response to cold, improved countercurrent heat exchange mechanisms to conserve heat flowing into the musculature, or both could enable an increased maximum tissue insulation. Hong *et al.* (32) measured the forearm blood flow and forearm skin heat loss in six diving women and six non-diving control subjects from the same community while the individuals rested immersed in water at 30, 31 and 33 °C. As shown in Figure 8, the divers did not reduce peripheral blood flow as much in the cool water as did the control subjects (32). This would suggest that, rather than becoming more sensitive, the vasoconstrictor response to cold had become blunted or habituated, as observed in other cold-acclimatized people. However, whereas blunted vasoconstriction was accompanied by increased heat loss in the Lapps and Inuits, skin heat loss during immersion was the same or less for the Ama diving women compared to non-acclimatized control subjects (32). Clearly, the diving women had acclimatized such that they could reduce peripheral heat loss without as great a reduction in peripheral

FIGURE 7

FIGURE 8

blood flow as required in unacclimatized people. This pattern of acclimatization would be beneficial for swimming in cold water since it would allow oxygen and nutrient delivery to metabolically active tissue to be maintained economically with respect to body heat conservation. When the aforementioned studies were being completed, the divers wore cotton bathing suits while they worked. However, since 1977, the divers have been working in wet suits (56). In addition, the diving women had been rather lean when the initial studies of their thermoregulatory responses had been completed. However, by the early 1980s, the diving women had substantial amounts of subcutaneous fat (56). The added insulation from the wet suit and the adipose tissue enable the divers to tolerate longer work shifts while experiencing less severe body cooling than traditional divers had tolerated (56). When thermoregulatory responses to cold water immersion of the modern diving women were compared to non-diving controls, the insulative thermoregulatory acclimatization previously observed in the traditional cotton-suit diver are no longer apparent (56). This would suggest that the stimulus for the different pattern of cold acclimatization exhibited by the traditional divers as opposed to the Circumpolar residents and Aborigines was the faster, more substantial whole-body cooling experienced by the traditional divers.

EXPERIMENTALLY-INDUCED COLD ACCLIMATION

Thus far, this chapter has described how people routinely experiencing cold stress as a result of living conditions, occupation or avocation respond differently to an acute cold challenge than others lacking such a lifetime experience, thus they appear to be cold acclimatized. However, cross-sectional comparative studies of this type cannot readily distinguish physiological acclimatization from genetic adaptation (i.e. natural selection). Genetic factors do influence physiological responses to cold, possibly more due to inherited anthropometric differences than inherited thermoregulatory differences (20, 25, 55, 64, 65). Longitudinal studies demonstrate more clearly than cross-sectional comparisons what degree of physiological adjustments in response to chronic cold are possible in humans. This section will consider studies in which attempts were made to acclimate people to cold by artificially increasing the degree of cold stress to which they were subjected.

ACCLIMATION INDUCED BY REPEATED COLD-AIR EXPOSURE

Attempts to induce cold acclimation by repeatedly exposing subjects to cold air have employed a wide range of air temperatures and exposure durations. Table 1 summarizes the acclimation programs and resulting pattern of acclimation reported by several investigators. In the table, the studies are listed in order from the shortest to longest duration of exposure used to acclimate the subjects. Not surprisingly, the experiments which employed the coldest temperature used the briefest duration of exposure, while longer exposures were possible with warmer temperatures. As indicated in the table, the different approaches appear to yield different acclimation patterns. Brief (1 hour or less) daily exposures to cold air, repeated over a two-week period reportedly blunt the shivering response to cold (habituation) but have no effect on body temperature changes during the exposure (4, 27, 62). In studies employing longer exposure durations and a longer acclimation period (14, 42, 43, 50), both reduced shivering and more pronounced declines in body temperature during cold exposure have been reported; hence, this pattern of acclimation is termed hypothermic habituation. The distinction between the studies observing hypothermic habituation and those in which habituation of shivering and vasoconstriction occurred without apparent effect on regulation of core temperature is probably not physiological. Investigators observing hypothermic habituation have employed longer duration cold tests. Longer test periods would provide a greater opportunity for the imbalance between heat production and loss to be translated into a measurable fall in core temperature.

Only two of the cold-air acclimation studies demonstrated evidence for an acclimation pattern beyond a habituation. Mathew *et al.* (50) reported that, in addition to blunted shivering, daily four hour exposures to 10 °C produced altered vasomotor responses to cold. The cold-induced vasodilator response occurred more rapidly during cold exposure following acclimation, and palm rewarming was more rapid. These observations may indicate a form of vasomotor acclimation to the cold, or simply habituation of the vasoconstrictor response to cold. This remains to be determined.

TABLE 1

The other study reporting an acclimation other than habituation is that of Scholander *et al.* (60) which is classically cited as demonstrating a metabolic form of cold acclimation in humans. Scholander *et al.* (60) studied 8 students who had spent six weeks camping in the Norwegian mountains during autumn when ambient temperatures were moderately cold, especially at night, and rain, sleet and snow were frequent. To increase the subjects' cold stress, Scholander allowed the students to wear only lightweight summer clothing, and permitted only minimal shelter at night. Figure 9 shows the metabolic rate of these subjects while they rested in 20 °C air, compared to that of unacclimated control subjects. The campers exhibited a greater increment in metabolism upon cold exposure than did the control subjects. It is unfortunate that Scholander did not use a longitudinal design, i.e. measurement of the metabolic response to acute cold exposure in the campers before and after the acclimation period, since no other study has clearly demonstrated that individuals can develop an enhanced metabolic response to cold as a result of repeated exposure.

The development of a different type of metabolic acclimation reportedly occurred in two other cold-air acclimation studies. Davis (14), whose findings are depicted in the top panel of Figure 10, reported that subjects who acclimated by spending 8 hours per day in a cold room (T_{air} = 12 °C) for 31 days exhibited a reduction in both metabolic heat production, assessed by oxygen consumption measurement, and shivering, assessed by EMG activity of the upper arm and thigh. Davis (14) concluded that the decrease in shivering activity was more pronounced than the decrease in metabolic heat production; he interpreted this as demonstrating that nonshivering thermogenesis had developed to offset the reduced shivering thermogenesis. This interpretation is faulty since it assumes that changes in whole-body metabolic heat production will be matched by equivalent changes in shivering activity of the thighs and upper arms. Other muscle groups participate in shivering, and these muscles may have increased shivering to offset the decrease in the measured groups. Furthermore, in the lower panel Davis' data have been replotted to depict metabolic rate as a function of shivering activity, and it can be seen that changes in the recorded EMG activity do, in fact, closely correlate with the decrease in metabolic rate.

FIGURE 9

FIGURE 10

Joy (37) studied the effects of an acclimation program (exposure to T_{air} = 5 °C, 8 hours per day, for 25 days) similar to that used by Davis (14). After completing the program, 9 men responded to norepinephrine infusion with a more pronounced increment in metabolic rate than they did before acclimation. Joy (37) concluded that this demonstrated the development of nonshivering thermogenesis. However, the infusion experiments were done under thermoneutral conditions, and therefore provide no information concerning physiological responses to cold. While the possibility that humans can develop an enhanced thermogenic response, shivering or nonshivering, in response to repeated cold exposure cannot be dismissed, the human capacity for this pattern of adjustment remains to be clearly demonstrated.

ACCLIMATION INDUCED BY REPEATED COLD-WATER IMMERSION

One of the difficulties in acclimating people using cold-air exposure is that significant whole-body cooling is not usually achieved. When very cold air temperatures are used, skin temperature falls to freezing before core temperature declines substantially, and the exposure must be terminated to avoid inducing frostbite. When somewhat warmer air temperatures are used, frostbite can be prevented but the amount of time required to reduce core temperature becomes so excessive that few volunteers will either endure the discomfort or devote the time required to lower their core temperature significantly. These problems can be somewhat ameliorated by using cold water immersion to acclimate subjects, since body heat losses in cold water can result in rapid declines in body temperature. Furthermore, frostbite is not a problem with experimental cold water immersions, since skin temperature remains above freezing and nearly equal to water temperature. A summary of studies investigating the effects of repeated cold-water immersion is shown in Table 2.

As the studies of the Gaspe fishermen and fish filleters (47, 54) would suggest, repeated cold-water immersion of fingers, hands and forearms induces a blunting of the vasoconstrictor responses to cold in those regions (16, 48). Interestingly, when only one limb is subjected to repeated cold-water immersion, the blunted vasoconstrictor response can be demonstrated in the non-immersed contralateral limb

TABLE 2

as well as the immersed limb (16). This observation provides further evidence that habituation of cold-induced vasoconstriction is, to some, extent centrally-mediated.

Similar to the effects of repeated cold-air exposure, repeated whole-body immersion in cold water induces different patterns of cold acclimation, depending on the intensity of cold, duration of the exposure and length of the acclimation period. Brief cold-water immersions appear to induce habituation, even when the immersions are repeated relatively few times. For example, Lapp and Gee (44) had subjects immerse themselves twice a week, for one hour, in water that was 32 °C the first week and progressively cooler each week until, by the eighth week water temperature was 21 °C. Despite the progressive reduction in water temperature, self-reported bouts of shivering during immersion declined over the eight week period (44). A more systematic evaluation of the effects of repeated cold-water immersion was reported by Radomski and Boutelier (57) who had subjects immerse themselves in 15 °C water for 20-60 minutes a day for 5 days one week and 4 days the next week. Physiological responses of these subjects were measured during a standardized cold-air tolerance test (60 min at 10 °C), and compared to responses measured in control subjects who did not complete the repeated immersions in cold water. The unacclimated control subjects exhibited the usual responses after one hour of cold-air exposure: metabolic heat production increased, skin temperature decreased and rectal temperature increased. In contrast, the subjects who had been repeatedly immersed in cold water did not increase metabolic heat production, their skin temperature did not fall as much as that of the unacclimated subjects and their rectal temperature declined. These observations indicate that the repeated cold-water immersion had blunted the shivering and vasoconstrictor responses to cold. This hypothermic habituation was associated with a diminished sympathetic response to cold exposure, as evidenced by lower urinary norepinephrine excretion in the acclimated than unacclimated subjects during a two week sojourn in the Canadian Arctic (57).

When the immersion durations are increased and the immersions repeated over a longer acclimation period, patterns of cold acclimation besides habituation are induced. Young et al. (68, 69) studied the effects of an acclimation program consisting of 90 minutes of immersion in 18 °C water, repeated five days per week for eight weeks. During each immersion, the subjects, who wore only nylon swim trunks, experienced about a 1 °C decrease in rectal temperature. Physiological responses to cold-water immersion were unchanged by the acclimation program (68, 69). However, there was evidence indicating that the program induced adjustment in thermoregulatory responses to cold air.

Before and after completing the acclimation program, physiological responses were measured while the subjects were exposed to cold (5 °C) air. Some of the adjustments in responses to cold-air exposure appeared consistent with the development of hypothermic habituation to cold. For example, as shown in Figure 11, the fall in the subjects' rectal temperature during the cold-air exposure was greater and more rapid following the acclimation program. Also, metabolic heat production increased more slowly during exposure to cold air following the repeated cold-water immersions. However, by the 30th minute of cold exposure, metabolic heat production was the same as it had been before the immersion program, and for the remainder of the cold-air exposure there was a trend for higher metabolic heat production than before acclimation (68) raising the possibility of a metabolic acclimation to cold. Furthermore, other thermoregulatory adaptations suggested the development of an insulative type of cold acclimation.

The fall in skin temperature observed by Young *et al.* (68) during the pre- and post-acclimation cold-air exposures is shown in Figure 12. Following the eight week program of repeated cold-water immersion, cold-air exposure caused skin temperature to fall about 4 °C lower than before acclimation (68). Although skin blood flow was not actually measured, the greater fall in skin temperature during cold exposure was similar to the adjustments noted by others studying the Central Australian Aborigine, and suggests that a more pronounced cutaneous vasoconstrictor response to cold had developed. Young *et al.* (68) also reported that the increment in plasma norepinephrine concentration elicited by exposure to cold air was more than two-fold greater following the acclimation program. This observation suggests that the acclimation had increased sympathetic nervous responsiveness to cold exposure. An increased sympathetic nervous responsiveness to cold is one mechanism which could mediate a more pronounced vasoconstrictor response to cold.

FIGURE 12

Similar effects of repeated cold-water immersion were reported by Bittel (5).[1] Bittel (5) compared thermoregulatory responses of nine men exposed to cold air (T_{air} = 10 °C) before and after completing a two month program of repeated cold-water immersions (4-5 times/week). In agreement with the findings of Young *et al.* (68), Bittel (5) observed a delayed onset of shivering during the standardized cold-air exposure following acclimation, but, subsequently, metabolic heat production tended to higher than during the pre-acclimation cold exposure. Also in agreement with the previous report, Bittel (5) observed that skin temperatures fell more during the cold-exposure test after than before acclimation. In contrast to observations of Young *et al.* (68), rectal temperatures did not fall as much during the post-acclimation cold-air exposure as before acclimation, but this may have reflected the warmer air temperature used for the standardized cold-air test. Bittel (5) calculated that the net effect of acclimation was a significant reduction in the heat debt that developed during cold-air exposure.

The lower skin temperatures during cold-air exposure following repeated cold-water immersion which were observed by both Young *et al.* (68) and Bittel (5) have two implications. First, at a given air temperature, lower skin temperatures reduce the thermal gradient for heat transfer between the skin and surrounding air, which contributes to improved insulation. Secondly, the magnitude of the acclimation effect on skin temperature maintained during cold exposure exceeds the magnitude of the acclimation effect on core temperature maintained during cold-air exposure (5, 68). Therefore, as shown in Figure 13, the core-to-skin thermal gradient in enlarged.

The larger thermal gradient between core and skin would favor redistribution of body heat from the core to the subcutaneous muscle shell, while the maintenance of

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[1]Bittel (5) refers to the repeated cold-water immersions as an acclimation procedure, although there is a comment in his paper stating that the immersions were performed as part of a diving course. Thus, this study (5) could arguably be considered as an acclimatization study, i.e. naturally occurring adjustments to chronic cold. However, since it is not clear whether the scheduling of the course was determined by the experimenters, and since the experimental approach used was very similar to that of Young *et al.* (68), the Bittel (5) study will be considered as an acclimation study for the purposes of this review.

FIGURE 13

lower skin temperature due to enhanced cutaneous vasoconstriction in cold air would limit heat loss from the body's shell. Muza *et al.* (53) reported that, in addition to the thermoregulatory adaptations, the subjects completing Young et al.'s (68) acclimation program experienced a smaller increment in blood pressure during cold exposure than observed before acclimation; cardiac output responses to cold were unaffected by acclimation. If the lower skin temperatures and greater increment in circulating norepinephrine observed following acclimation do reflect an enhanced cutaneous vasoconstrictor response to cold, then the concomitant blunting of the systemic pressure response to cold indicate that subcutaneous vascular beds must have been better perfused following acclimation. Thus, as was suggested to have occurred in the Korean diving women, acclimation by repeated cold-water immersion may enable better heat conservation by improved insulation at the shell surface, while perfusion of the subcutaneous shell is more optimally maintained than before acclimation.

DETERMINANTS OF THE ACCLIMATIZATION PATTERN

The findings from the studies reviewed demonstrate clearly that humans have the capacity for thermoregulatory adjustments in response to chronic or repeated cold exposure. The nature of the adjustments appears to differ depending on the type of the cold exposure. A theoretical schematic depicting the development of different patterns of cold adjustments is shown in Figure 14. Brief, intermittent cold exposures appear sufficient to induce habituation of shivering and vasoconstrictor responses to cold, even when only very limited areas of the body surface are exposed and whole body heat losses are probably negligible. Evidence for more pronounced physiological adjustments is observed only when the cold-exposure conditions are such that significant amounts of body heat are lost. Insulative adjustments appear to develop in response to repeated cold exposures which are sufficiently severe to preclude body heat loss from being offset by increased metabolic heat production; that is, when cold stress causes deep body temperature to decline significantly. The possibility that an enhanced thermogenic capability can develop in humans in response to chronic cold cannot be dismissed. It is tempting to speculate that the stimulus for development of this metabolic pattern of cold adaptation is prolonged periods during which significant body heat loss is experienced, but body heat production increases sufficiently to prevent a significant decline in deep body temperature. This speculation is not

FIGURE 14

unjustified, since the metabolic pattern of cold adjustments has only been reported in studies in which acclimatization/acclimation was induced by exposure to such conditions, i.e. prolonged exposure to moderately cold air.

Bittel (5) has suggested that factors other than the type of cold stress determine the pattern of thermoregulatory adjustments which characterize the acclimatization. As discussed above, Bittel (5) reported that repeated cold-water immersion induced an insulative of cold acclimation which mediated a lower heat debt during cold exposure. This conclusion was based on statistical analyses of physiological data from the entire subject group pooled together. However, Bittel (5) also examined each subject's data separately to identify the pattern of adjustments exhibited by that individual. Only four of the nine subjects clearly exhibited the unchanged metabolic response with enhanced insulation during cold exposure that was indicated by average responses of the group. One subject developed an enhanced metabolic response to cold but showed no sign of improved insulation following acclimation. Three subjects exhibited both a greatly increased metabolic response and an increased insulation after acclimation. Finally, one subject exhibited a decreased metabolic response to cold but enhanced insulation following the acclimation program. Due to the small number of subjects, Bittel (5) was unable to statistically relate individual factors to the pattern of acclimation, but he speculated that body composition and level of physical fitness were determinants of the type of acclimation experienced. Lean, fit individuals appeared predisposed to developing metabolic adjustments and fat, less fit individuals seemed predisposed to developing insulative adjustments.

Other evidence suggests that the different patterns of cold acclimatization/acclimation are not necessarily the result of different types of cold stress. Skreslet and Aarefjord (63) compared the thermoregulatory responses of scuba divers during a standardized cold-water immersion test performed before and at two week intervals throughout a 45 day period, during which the men were diving daily in 2-4 °C sea-water. Only 3 subjects were studied and statistical analyses were not attempted (63). Initially, the subjects all responded with an increase in metabolic heat production, which in two out of three subjects was sufficient to prevent rectal temperature from falling (63). After two weeks of cold-water diving all three divers exhibited a blunted metabolic heat production during cold-water immersion in comparison with the initial immersion, i.e., habituation (63). Also after two weeks, the two divers who had been able to tolerate the first immersion without a decline in rectal temperature now experienced a decline (63). After 45 days of cold-water diving, there was a trend for lower torso and thigh skin temperatures during immersion than during the initial test. Rectal temperatures tended to be maintained higher during immersion than they were after two weeks of diving.

Skreslet and Aarefjord (63) interpreted these observations as indicating that the different patterns of cold adjustments reportedly observed by others did not represent the development of mutually exclusive physiological states. Rather, they (63) hypothesized that the metabolic, hypothermic habituative, and insulative patterns of cold adjustments were actually different stages in the progressive development of complete cold acclimatization. Thus, their divers initially responded to whole-body cold exposure by shivering; eventually, however, this response disappeared and insulative adaptations developed to help limit body heat loss.

SUMMARY

Humans adjust physiologically to chronic cold exposure. This has been demonstrated in cross-sectional studies comparing cold responses of persons routinely exposed to cold during their daily activities with those of persons from who have avoided significant cold exposure. Longitudinal studies have demonstrated that these differences reflect, at least to some extent, physiological acclimatization, as opposed to genetic adaptation, since the adjustments can be induced by repeatedly exposing unacclimated persons from temperate climates to cold conditions. Three basic patterns of cold adjustments are observed. A metabolic pattern may develop in which cold exposure elicits a more pronounced increment in shivering or nonshivering thermogenesis than in the unacclimatized state. By far, the most commonly observed cold adjustment is a habituation in which shivering and cutaneous vasoconstriction is blunted; body temperature may decline more in the acclimatized than unacclimatized state. This habituation can be induced by exposure to conditions which result in superficial cooling of the body surface, even when exposure is brief and limited to small body regions. When individuals are repeatedly exposed to cold conditions severe enough to induce a significant decline in deep body temperature an insulative

type of acclimatization appears to take place. The exact determinant of which pattern will be induced by chronic cold exposure is unclear, but the nature of the cold stress (magnitude and extent of body cooling), the frequency of exposure and duration of the adaptive period, and individual factors all may influence the adaptive process.

The existence of processes of cold acclimatization in humans is interesting to physiologists since it contributes to our understanding of human adaptability in general and helps to explain differences between individuals in their responses to cold. However, the importance of cold acclimatization in providing the individual with an advantage in coping with the environment is less clear than with the acclimatization humans exhibit in response to chronic heat exposure. Habituation probably improves comfort and dexterity as well as reducing susceptibility to cold injury, but overall, the advantage provided by cold acclimatization, in terms of conservation of body heat and defense of body temperature, is considerably less than can be derived from modern protective clothing.

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TABLE 1. Acclimation programs employing cold air exposure.

STUDY	COMMENT	ACCLIMATION CONDITIONS USED			EFFECTS
		T_{air}	EXPOSURE DURATION	ACCLIMATION PERIOD	
Hesslink *et al.* (27)	chamber, shorts & T-shirts, 16 men	4.4 °C	30 min, twice daily	5 days/week for 8 weeks	shivering habituation
Armstrong and Thomas (4)	chamber, shorts & T-shirts, 4 women	4 °C	45 min/day	5 days/week for 2 weeks	shivering habituation
Silami-Garcia (62)	chamber, shorts, 5 women	10 °C	1 hr/day	10 of 14 days	shivering habituation
Mathew *et al.* (50)	chamber, shorts, 15 men	10 °C	4 hr/day	21 days	shivering habituation, vasomotor acclimation
Keatinge (42)	chamber, shorts, 5 men	6 °C	7.5 hr/day	17 days	hypothermic habituation
Davis (14)	chamber, shorts, 6 men in summer, 10 men in winter	12-14 °C	8 hr/day	31 days	hypothermic habituation
Kreider *et al.* (43)	chamber, shorts, 5 men	15 °C	24 hr/day	14 days	hypothermic habituation (metabolism not measured)
Scholander *et al.* (60)	living outdoors in Autumn, light summer clothes and sleeping bags	nighttime temperatures about 5 °C	24 hr/day	6 wks	metabolic acclimation

TABLE 2. Acclimation programs employing cold-water exposure.

STUDY	COMMENT	ACCLIMATION CONDITIONS USED			EFFECTS
		T_{water}	EXPOSURE DURATION	ACCLIMATION PERIOD	
Eagan (16)	immersion of one finger, cross-sectional study, 6 acclimated, 6 unacclimated men	"ice water"	10 min, 6 times/day	126 consecutive days	habituation of vasoconstrictor response to cold (observed in nonimmersed as well as immersed hand)
Leftheriotis *et al.* (48)	hand & forearm immersion, longitudinal study, 5 men	5 °C	20 min/day	30 consecutive days	habituation of vasoconstrictor response to cold
Lapp and Gee (44)	whole-body immersion, longitudinal study 3 men, 5 women	reduced progressively from 32 to 21 °C	1 hr/day	2 days/week for 8 weeks	shivering habituation
Radomski and Boutelier (57)	whole-body immersion, cross-sectional study, 3 acclimated, 8 unacclimated men	15 °C	20 to 60 min/day depending on individual tolerance	9 out of 14 days	hypothermic habituation
Young *et al.* (68)	whole-body immersion, longitudinal design, 7 men	18 °C	90 min/day	5 days/week for 5 weeks	insulative acclimation
Bittel (5)	whole-body immersion, longitudinal design, 10 men	10-15 °C, wet suits worn	1-3 hr/day depending on individual tolerance	4 or 5 days/week for 8 weeks	metabolic, insulative and mixed metabolic-insulative depending on individual subject anthropometric characteristics

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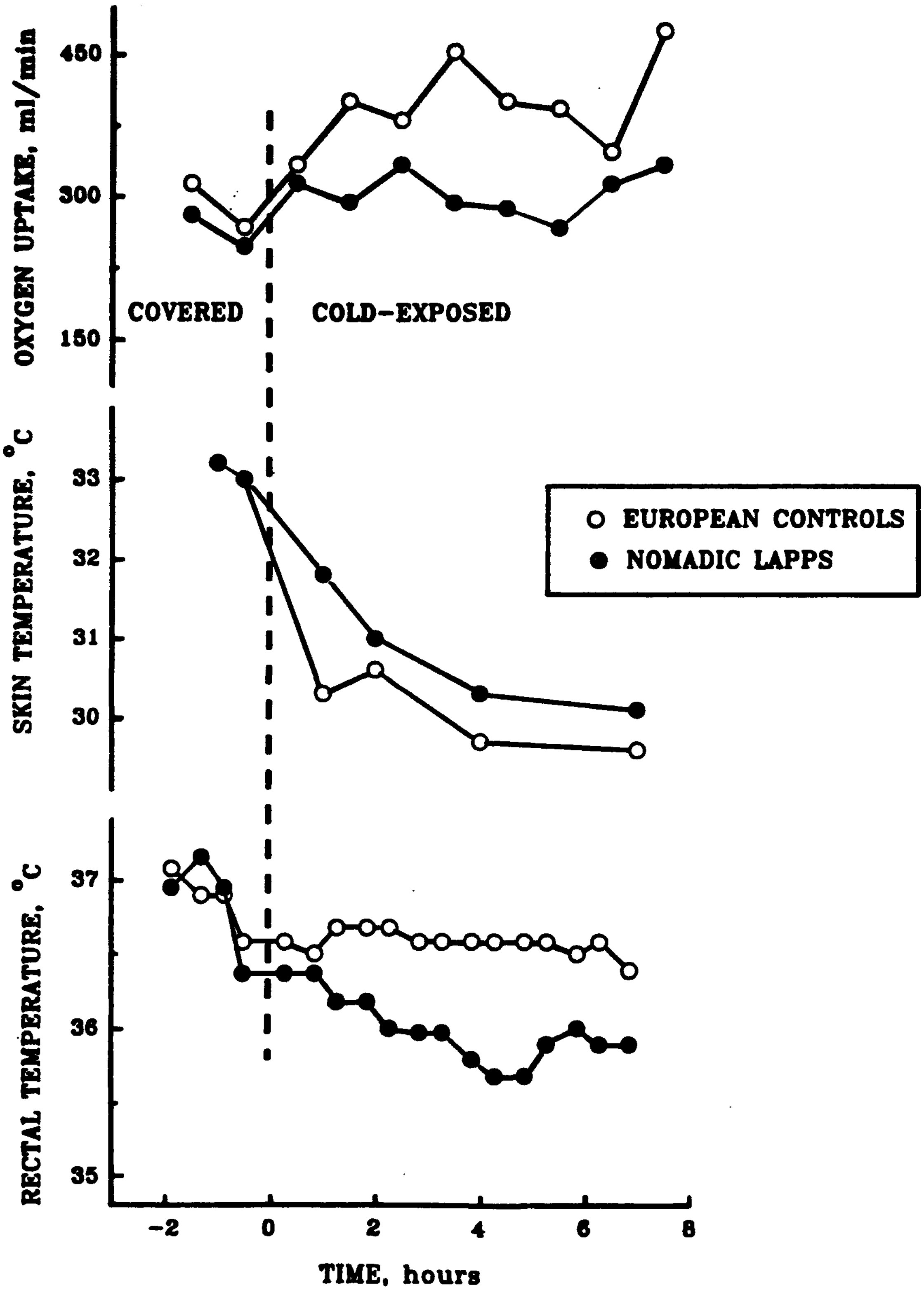
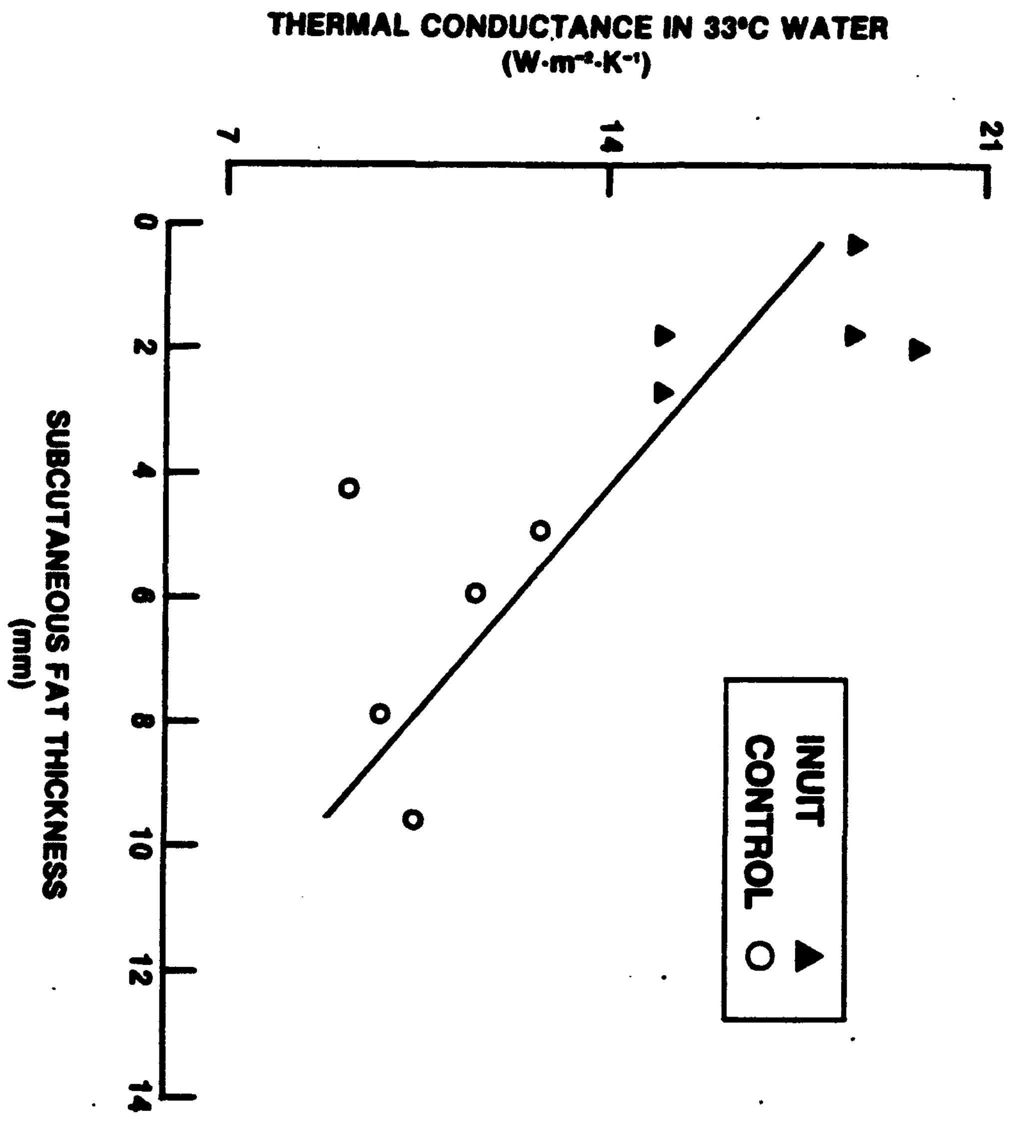
Fig 1



OXYGEN UPTAKE, ml/min
450
300
150
COVERED
COLD-EXPOSED
SKIN TEMPERATURE, °C
33
32
31
30
EUROPEAN CONTROLS
NOMADIC LAPPS
RECTAL TEMPERATURE, °C
37
36
35
-2
0
2
4
6
8
TIME, hours

Fig 2



THERMAL CONDUCTANCE IN 33°C WATER
(W·m⁻²·K⁻¹)
7
14
21
0
2
4
6
8
10
12
14
SUBCUTANEOUS FAT THICKNESS
(mm)
INUIT
CONTROL

Fig 3

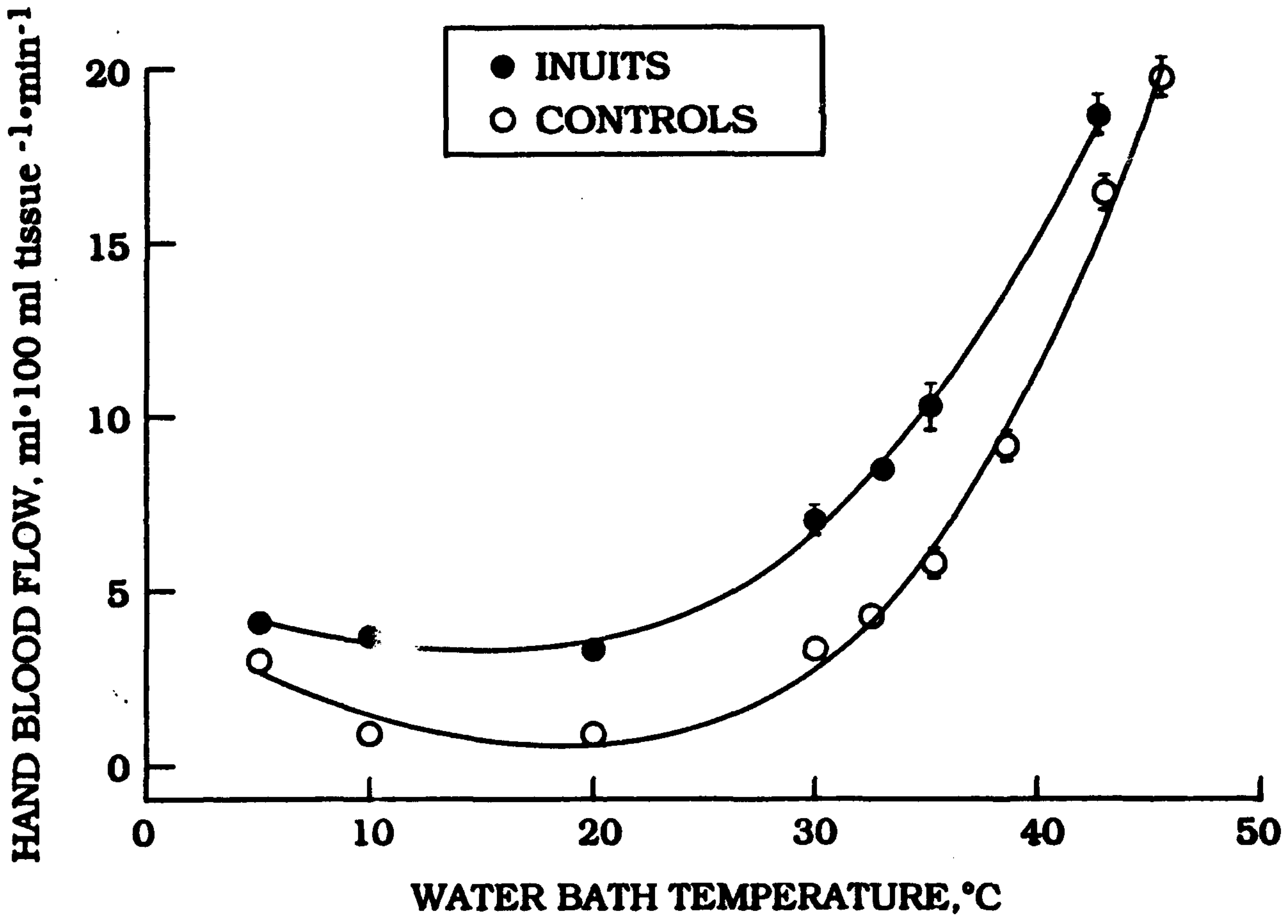
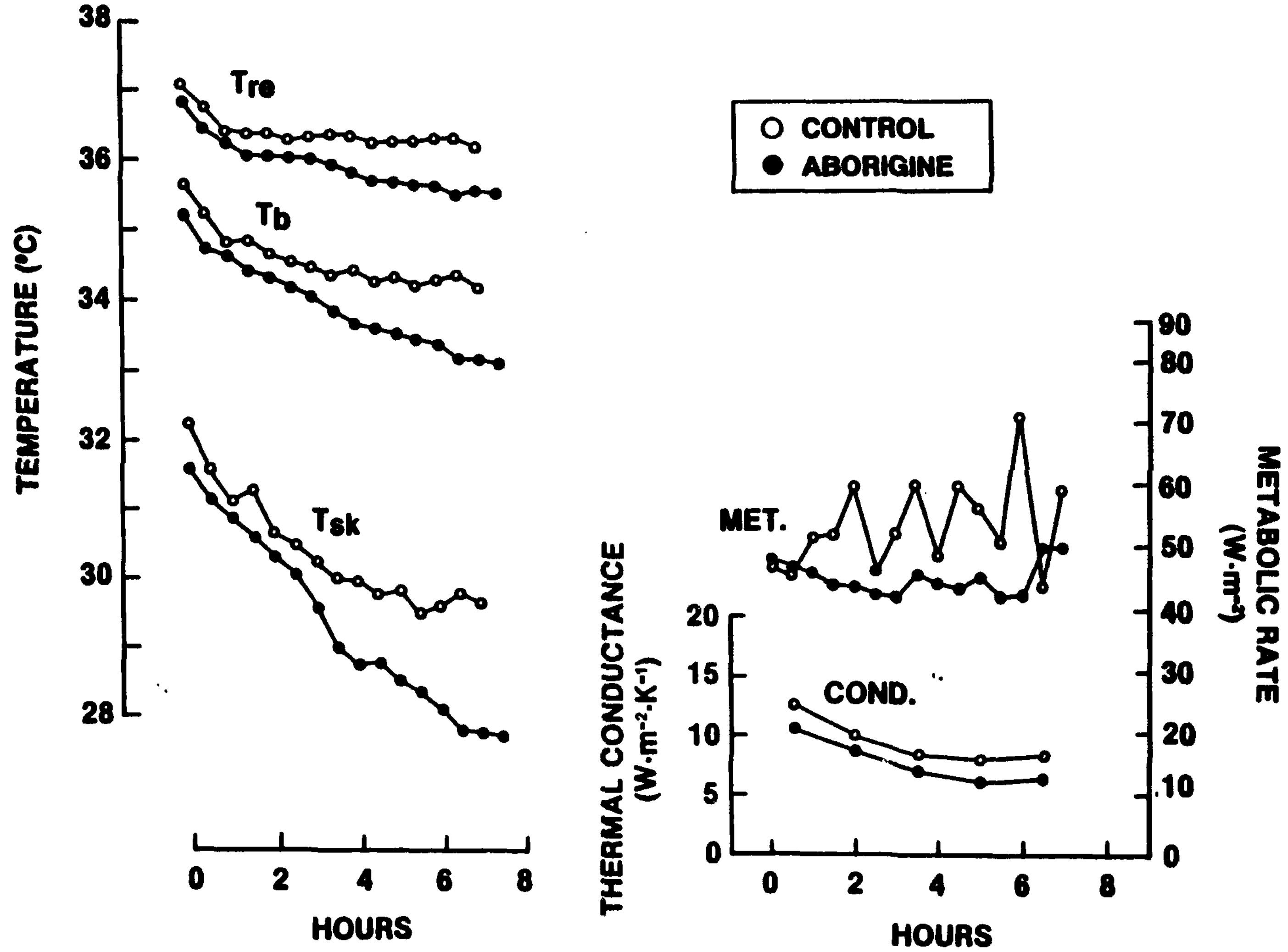

INUITS
CONTROLS
HAND BLOOD FLOW, ml•100 ml tissue -1•min-1
20
15
10
5
0
0
10
20
30
40
50
WATER BATH TEMPERATURE,°C

Fig 4



TEMPERATURE (°C)
38
36
34
32
30
28
Tre
Tb
Tsk
0
2
4
6
8
HOURS
CONTROL
ABORIGINE
MET.
COND.
THERMAL CONDUCTANCE (W·m⁻²·K⁻¹)
20
15
10
5
0
METABOLIC RATE (W·m⁻²)
90
80
70
60
50
40
30
20
10
0
HOURS

Fig 5

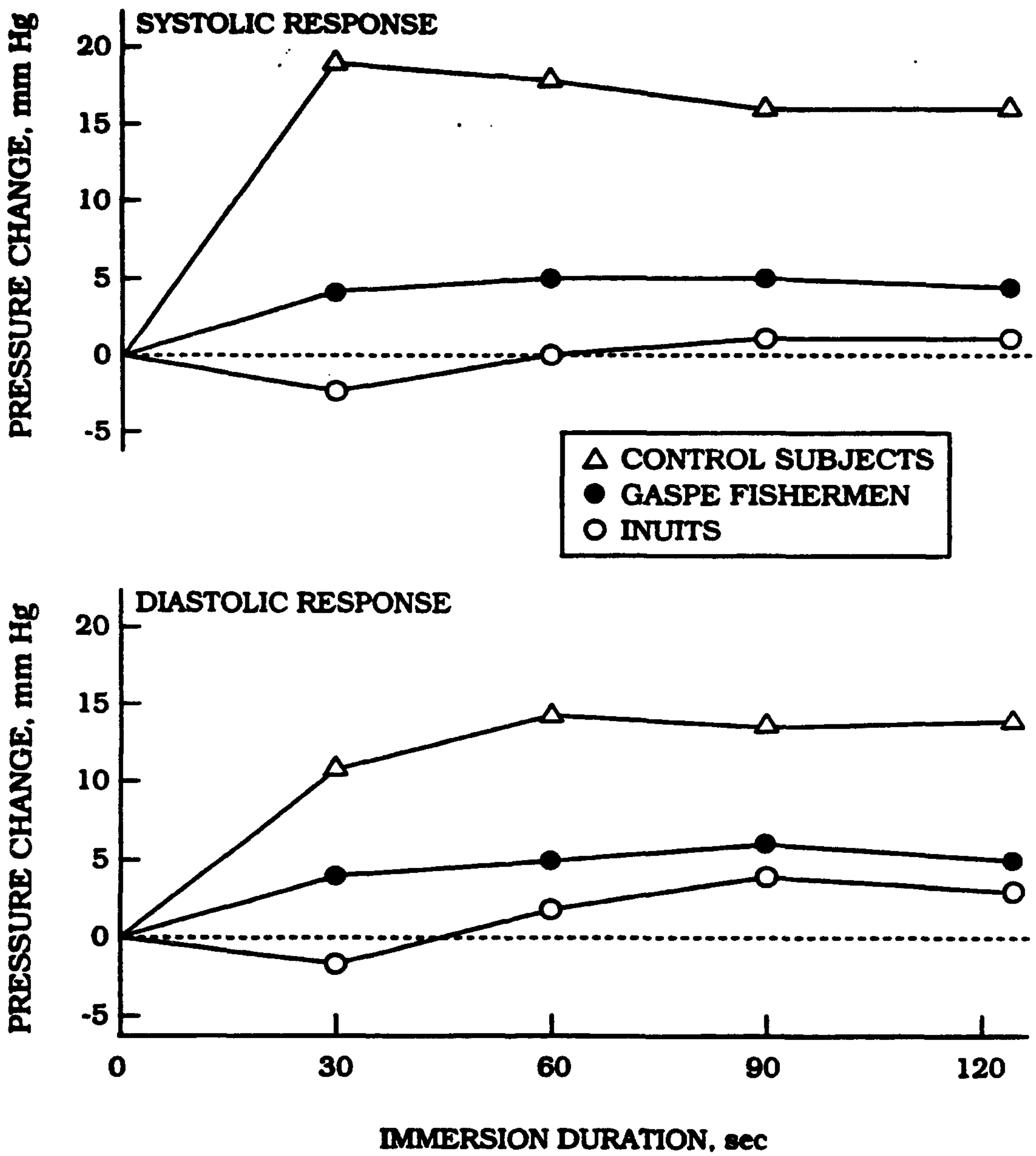

SYSTOLIC RESPONSE
DIASTOLIC RESPONSE
PRESSURE CHANGE, mm Hg
20
15
10
5
0
-5
CONTROL SUBJECTS
GASPE FISHERMEN
INUITS
0
30
60
90
120
IMMERSION DURATION, sec

Fig 6

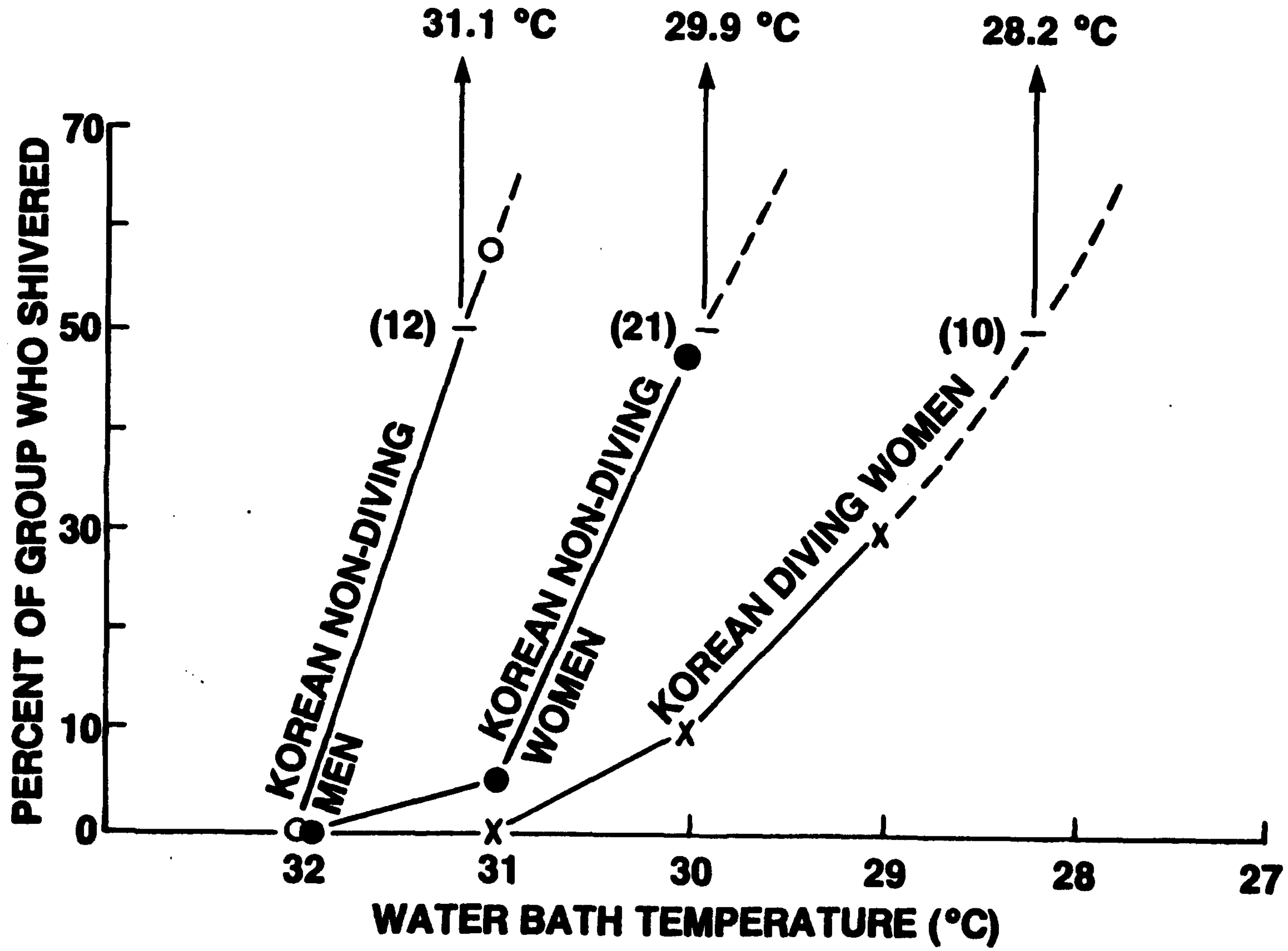

PERCENT OF GROUP WHO SHIVERED
0
10
30
50
70
31.1 °C
29.9 °C
28.2 °C
(12)
(21)
(10)
KOREAN NON-DIVING MEN
KOREAN NON-DIVING WOMEN
KOREAN DIVING WOMEN
32
31
30
29
28
27
WATER BATH TEMPERATURE (°C)

Fig 7

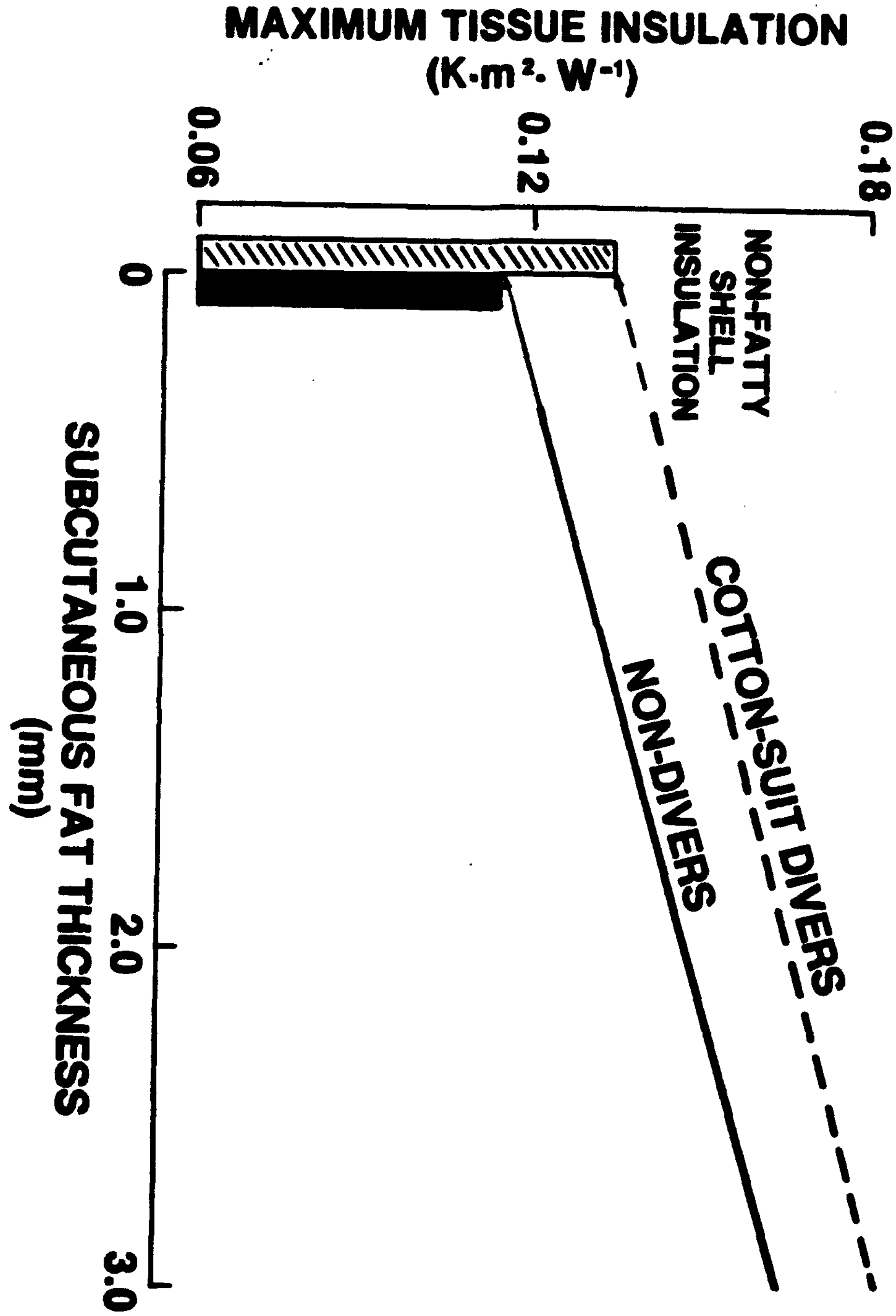

MAXIMUM TISSUE INSULATION
(K·m²·W⁻¹)
0.06
0.12
0.18
NON-FATTY
SHELL
INSULATION
COTTON-SUIT DIVERS
NON-DIVERS
0
1.0
2.0
3.0
SUBCUTANEOUS FAT THICKNESS
(mm)

Fig 8

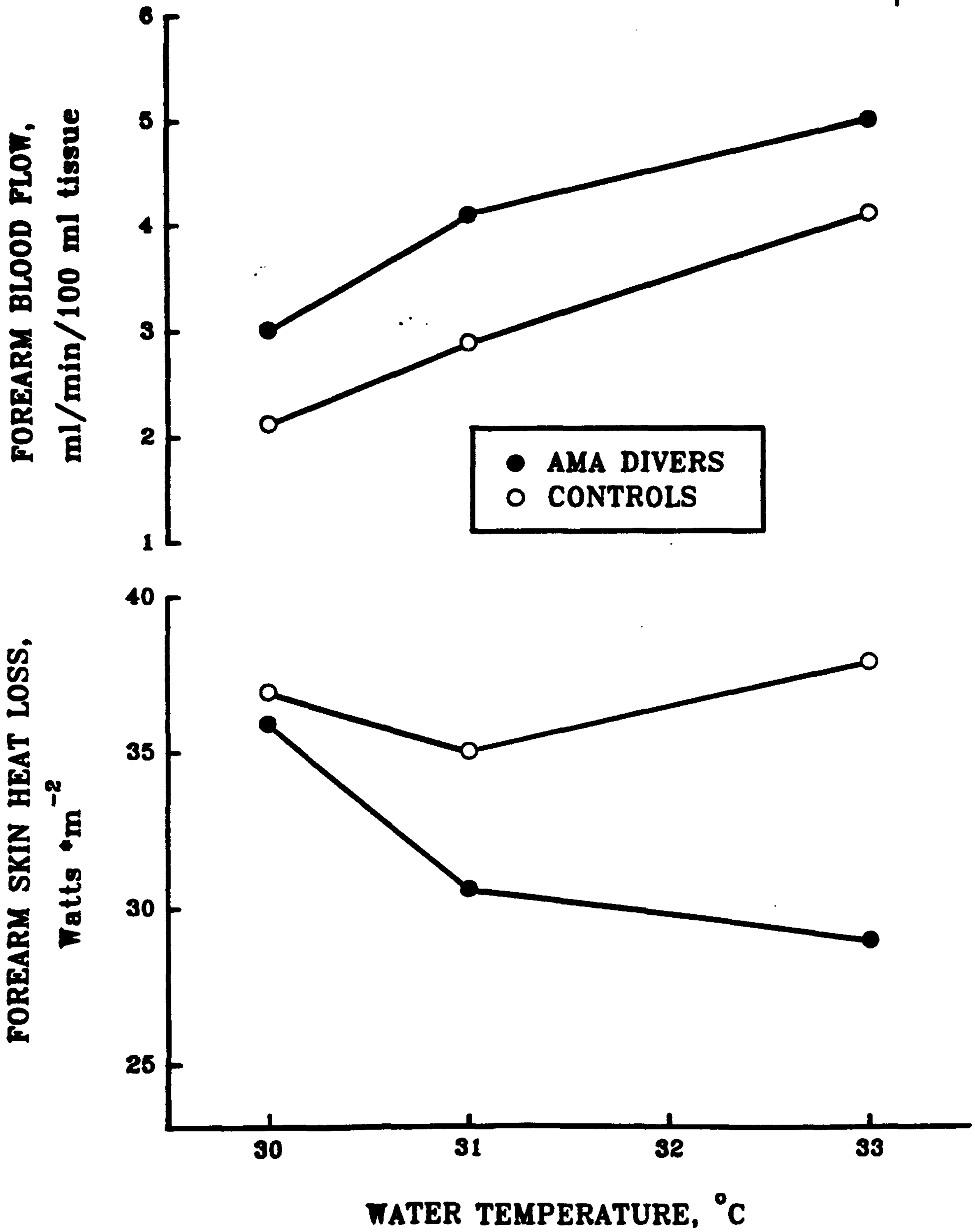
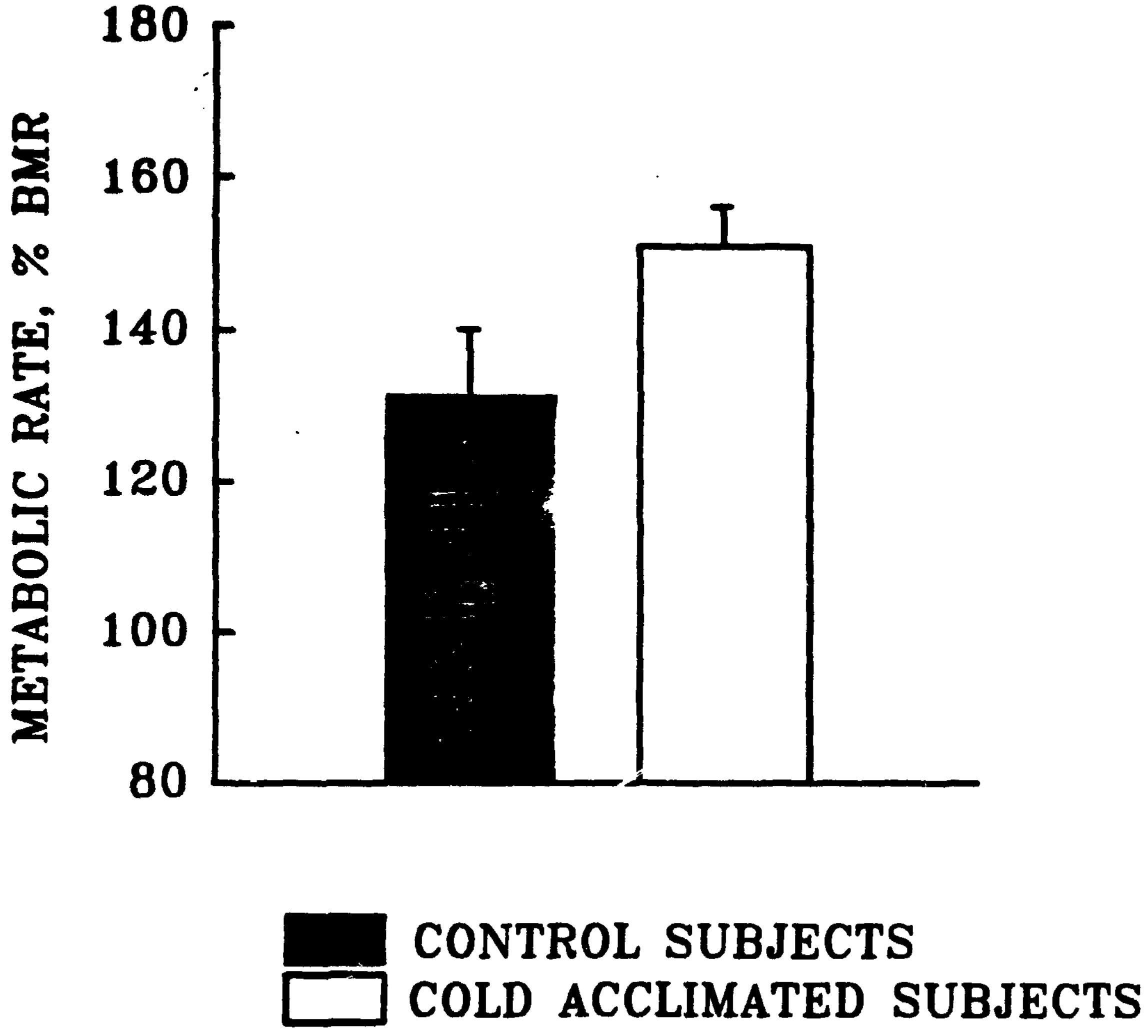
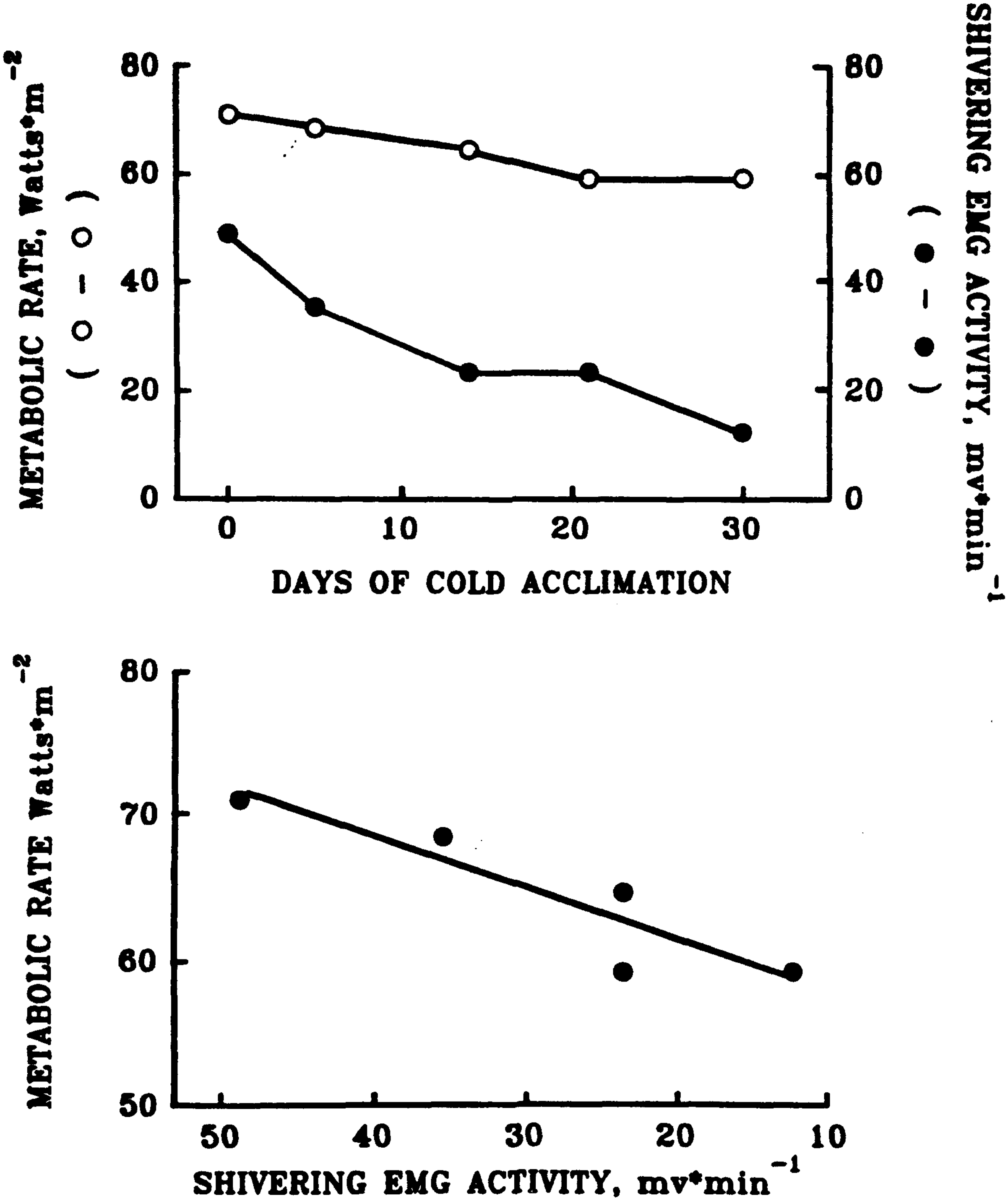

FOREARM BLOOD FLOW, ml/min/100 ml tissue
1
2
3
4
5
6
AMA DIVERS
CONTROLS
FOREARM SKIN HEAT LOSS, Watts *m⁻²
25
30
35
40
30
31
32
33
WATER TEMPERATURE, °C

Fig 9



180
160
140
120
100
80
METABOLIC RATE, % BMR
CONTROL SUBJECTS
COLD ACCLIMATED SUBJECTS

Fig 10



METABOLIC RATE, Watts*m^-2 (○ - ○)
SHIVERING EMG ACTIVITY, mv*min^-1 (● - ●)
80
60
40
20
0
0
10
20
30
DAYS OF COLD ACCLIMATION
METABOLIC RATE Watts*m^-2
80
70
60
50
50
40
30
20
10
SHIVERING EMG ACTIVITY, mv*min^-1

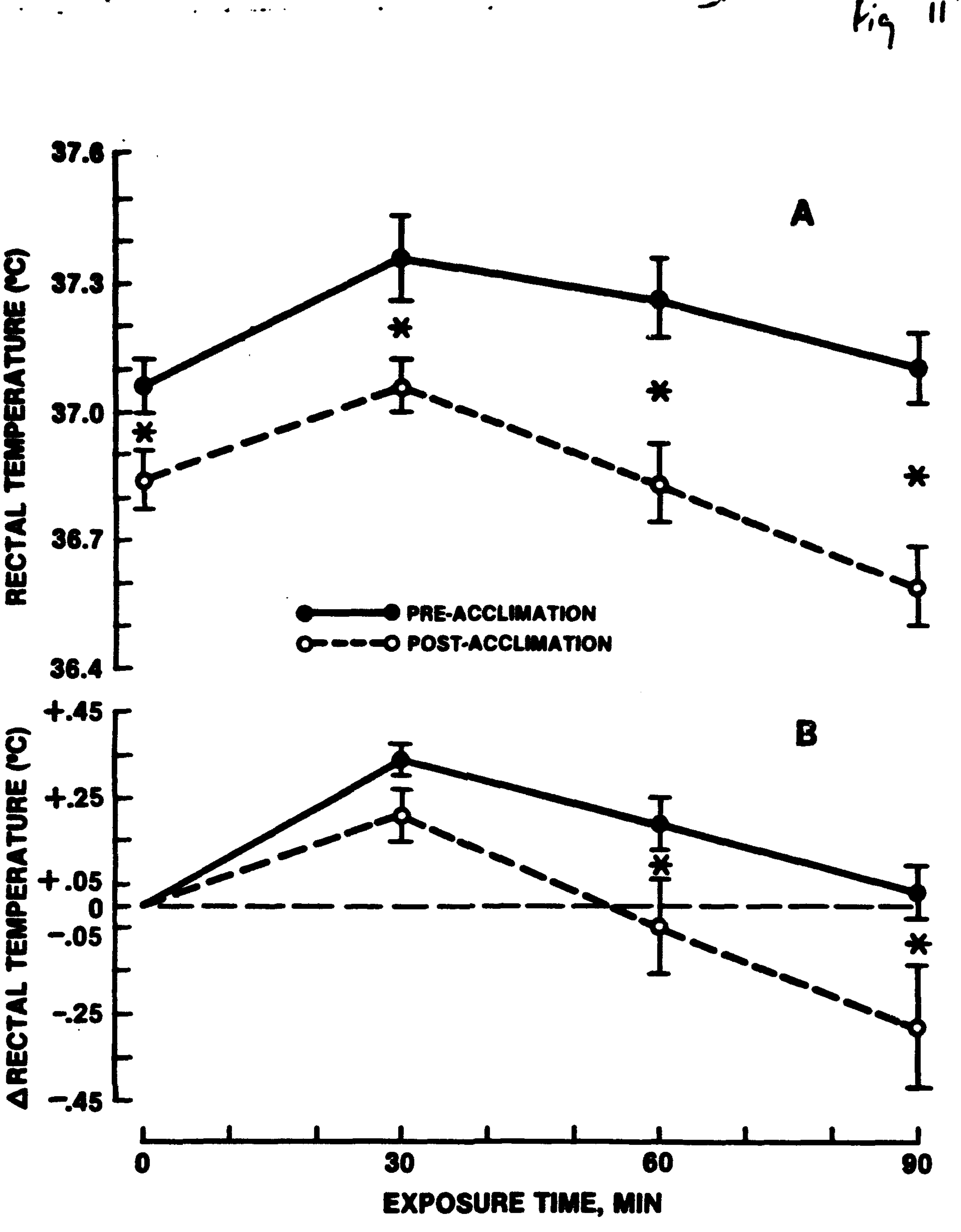
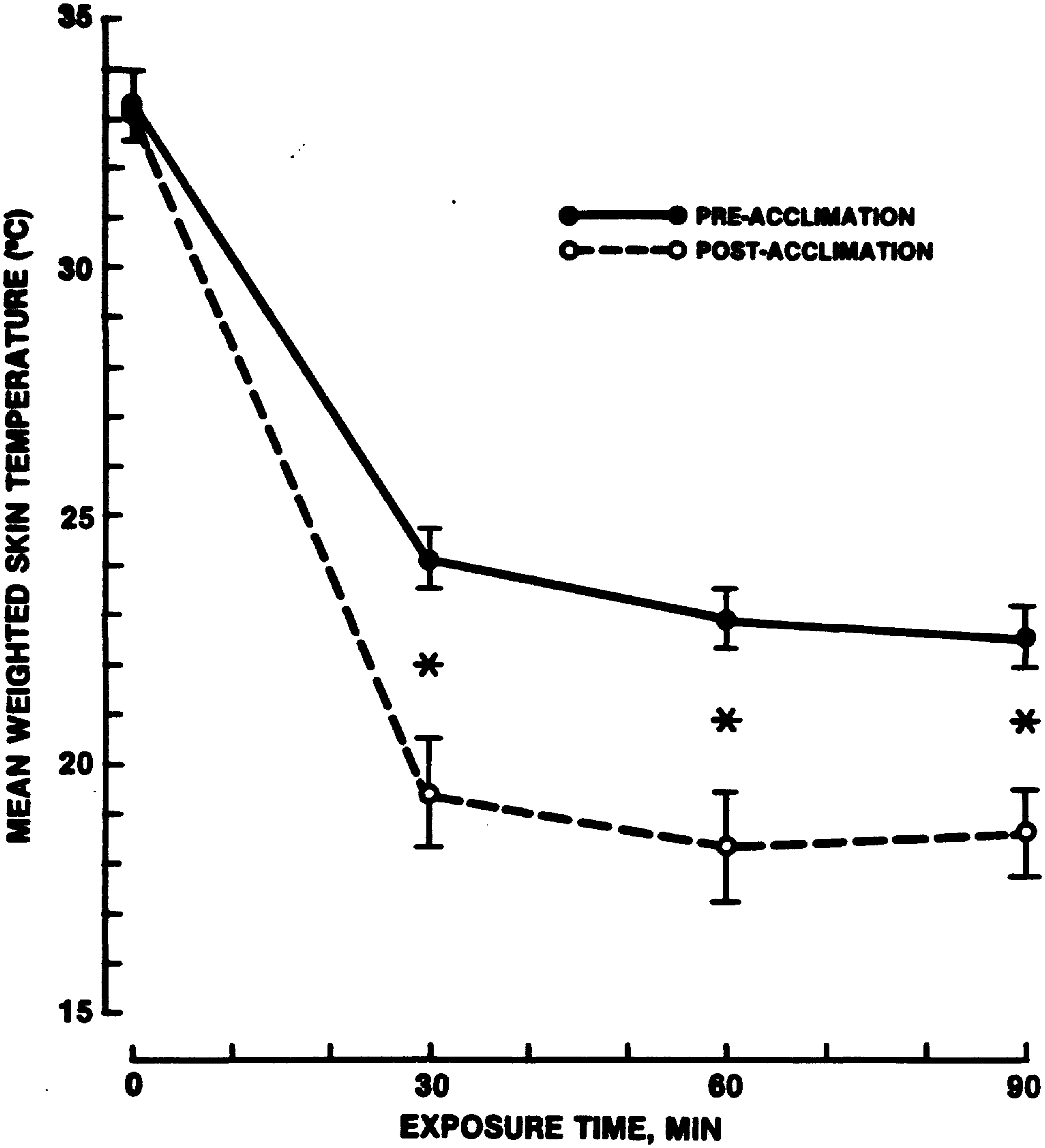


Fig 11
A
B
37.6
37.3
37.0
36.7
36.4
RECTAL TEMPERATURE (°C)
PRE-ACCLIMATION
POST-ACCLIMATION
+.45
+.25
+.05
0
-.05
-.25
-.45
ΔRECTAL TEMPERATURE (°C)
0
30
60
90
EXPOSURE TIME, MIN

Fig 12



35
30
25
20
15
MEAN WEIGHTED SKIN TEMPERATURE (°C)
PRE-ACCLIMATION
POST-ACCLIMATION
*
*
*
0
30
60
90
EXPOSURE TIME, MIN

Fig 13

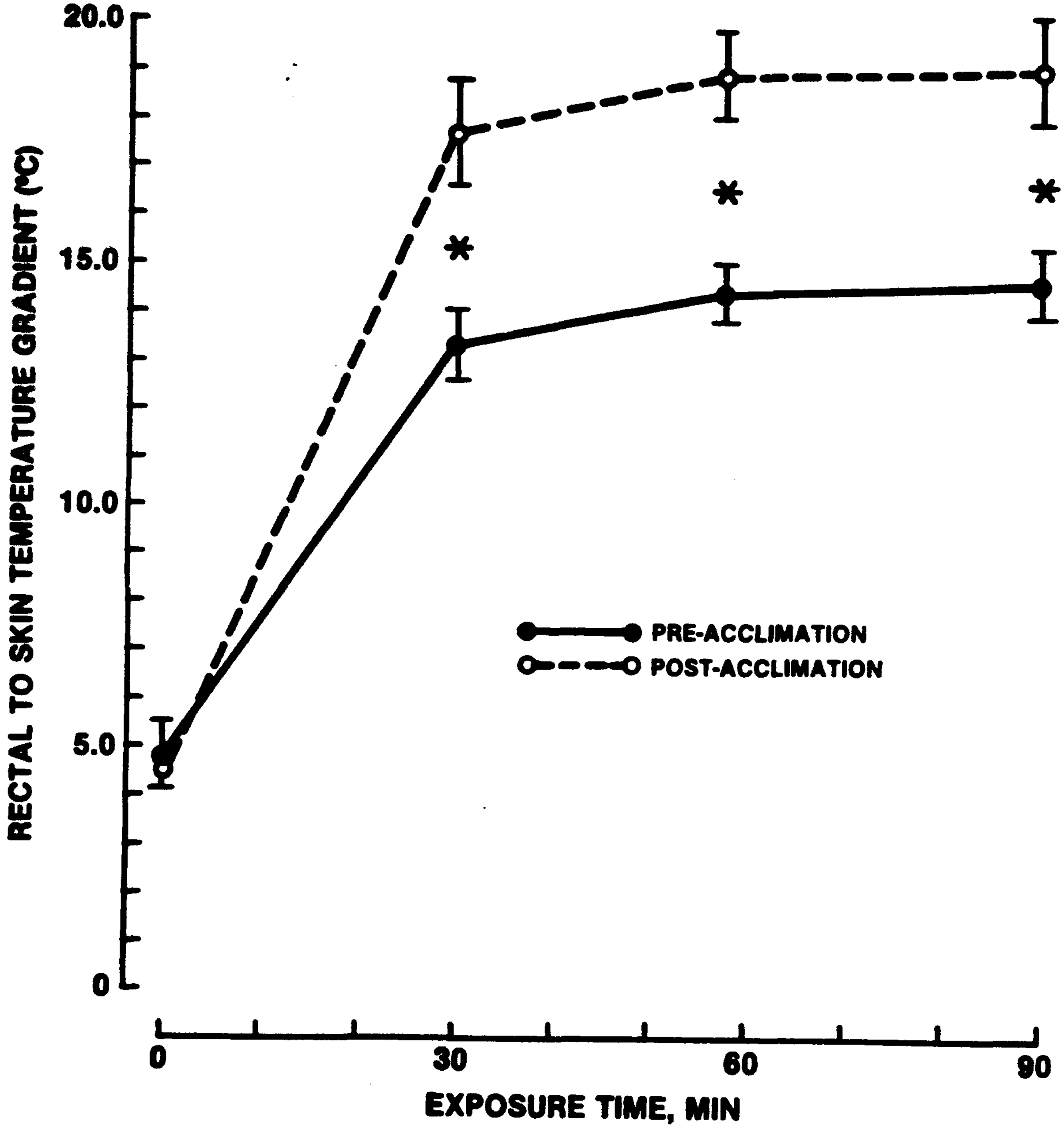
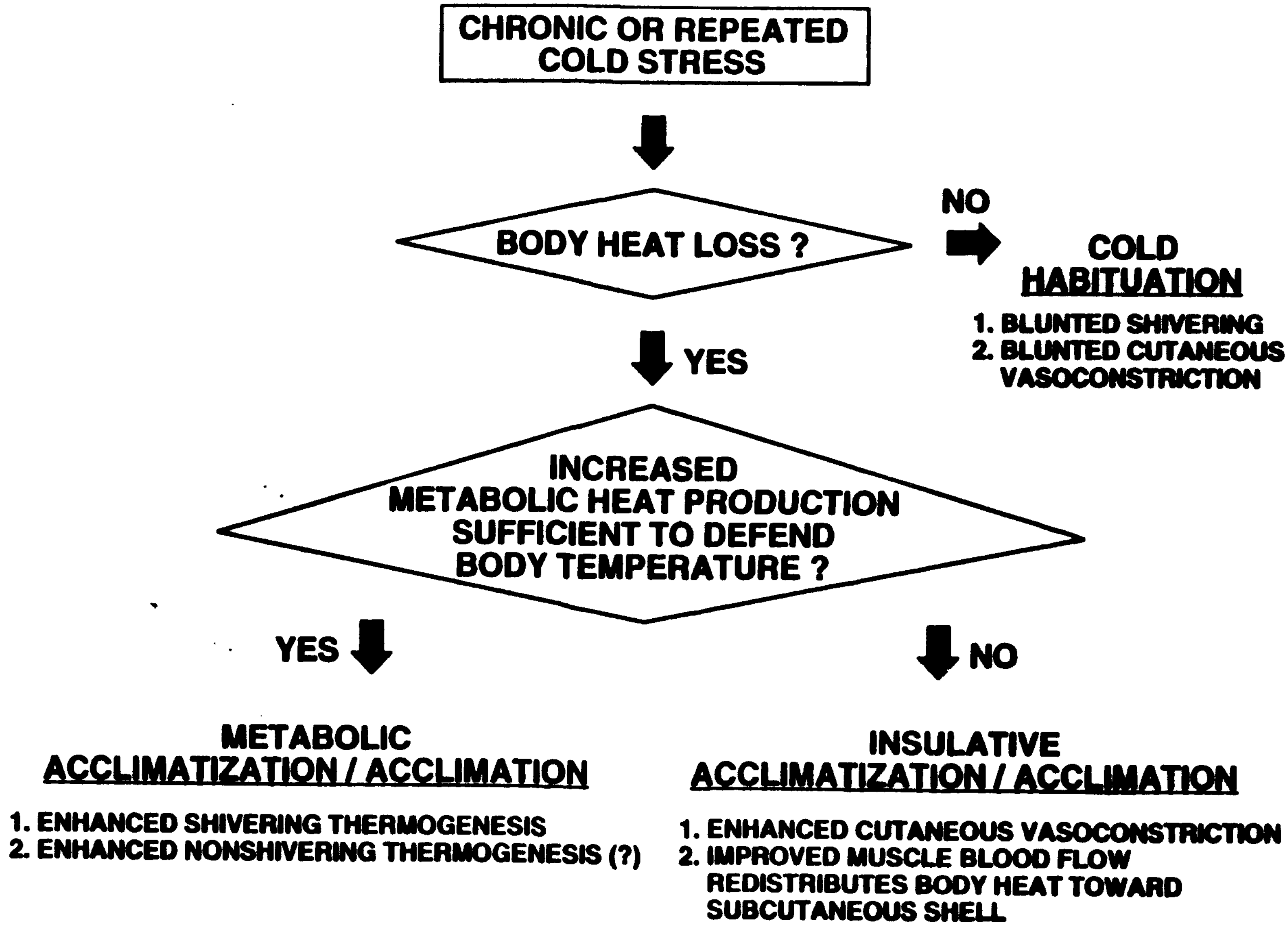

20.0
15.0
10.0
5.0
0
RECTAL TO SKIN TEMPERATURE GRADIENT (°C)
*
*
*
PRE-ACCLIMATION
POST-ACCLIMATION
0
30
60
90
EXPOSURE TIME, MIN

Fig 14


CHRONIC OR REPEATED COLD STRESS
BODY HEAT LOSS ?
NO
COLD HABITUATION
1. BLUNTED SHIVERING
2. BLUNTED CUTANEOUS VASOCONSTRICTION
YES
INCREASED METABOLIC HEAT PRODUCTION SUFFICIENT TO DEFEND BODY TEMPERATURE ?
YES
NO
METABOLIC ACCLIMATIZATION / ACCLIMATION
1. ENHANCED SHIVERING THERMOGENESIS
2. ENHANCED NONSHIVERING THERMOGENESIS (?)
INSULATIVE ACCLIMATIZATION / ACCLIMATION
1. ENHANCED CUTANEOUS VASOCONSTRICTION
2. IMPROVED MUSCLE BLOOD FLOW REDISTRIBUTES BODY HEAT TOWARD SUBCUTANEOUS SHELL