penguins and various diving birds (Fajardo *et al.*, 2007, O'Connor, 2004, 2009). However, loss of plumage air due to wetting of feathers in cormorants leads to increased thermoregulatory and transport costs (Schmid *et al.*, 1995).

Overall, hydrodynamic design, propulsive efficiency, and stroke/glide patterns have made marine mammals efficient swimmers. The cost of transport (mass-specific metabolic rate/speed) for swimming marine mammals scales negatively with body mass and is indistinguishable from values for running terrestrial mammals, and flying bats (Williams, 1999). In other words, on a mass-specific basis, it costs the same for a marine mammal to swim a fixed distance as it does a terrestrial mammal to run or a bat to fly the same distance. Although the total costs of transport for swimming marine mammals and terrestrial runners are indistinguishable, the relative contributions of locomotion and body maintenance functions differ between the two groups (Williams, 1999, 2001). In marine mammals, 22–77% of the cost of transport is attributed to maintenance processes, whereas that value is only 12% in terrestrial mammals. This large maintenance component of the cost of transport in marine mammals is attributable to the cost of endothermy in the aquatic environment (see Chapter 8). Thus, the negative relationship of cost of transport in marine mammals to body mass should be primarily dependent on differences in maintenance costs and resting metabolic rates (Noren *et al.*, 2012b, Noren and Williams, 2000, Williams, 1999, 2001). In addition, a component of this negative relationship is probably also attributable to increased storage of elastic energy in tendons of larger mammals, and the lower rates of acto-myosin crossbridge cycling associated with the lower stroke rates of larger animals (Heglund *et al.*, 1982a, 1982b).

For semi-aquatic mammals such as muskrats, mink, and humans, the cost of transport is three to four times higher than that in marine mammals and running/flying mammals (Williams, 1999, 2001). This difference has been attributed to the increased drag of near-surface swimming and less aquatic specialization (increased hydrodynamic drag and decreased propulsive efficiency). Minimal cost of transport data for many penguin species are in the same range as that for swimming marine mammals (Baudinette and Gill, 1985, Culik *et al.*, 1994, 1996a, Hui, 1988b). Minimum costs of transport for foot-propelled avian divers such as cormorants are generally greater than those for penguins (Ancel *et al.*, 2000, Enstipp *et al.*, 2005, Schmid *et al.*, 1995). This increase in cost for cormorants in comparison to penguins has been attributed to differences in buoyancy, stroke style, and heat loss.

8 Thermoregulation

Thermoregulation during diving is an important physiological process in endotherms such as marine mammals and diving birds because the heat conductance and heat capacity of water are 24 and 3400 times greater, respectively, than those of air (Dejours, 1989). Thus, both convection and conduction are poised to remove heat from the body of a mammal or bird moving through water. Heat loss is decreased by (a) insulation in the form of subcutaneous fat (i.e., blubber) or pelage air (feathers in birds, fur in fur seals and sea otters) (Irving and Hart, 1957, Irving *et al.*, 1962, Kooyman *et al.*, 1976a, Liwanag *et al.*, 2012, Scheffer, 1964); and (b) decreased heat flow to the periphery via vasoconstriction in the skin and appendages (Chapter 5).

However, thermoregulation during dives is more than just insulation; it also involves rates of heat production and heat loss (Irving and Hart, 1957, Scholander *et al.*, 1950a, 1950b). Heat is produced within the body from metabolic processes, especially in active locomotory muscle. Only 20% of the energy released from adenosine triphosphate during muscle contraction is converted into muscular work; 80% is lost as heat (Smith *et al.*, 2005). In addition, specific dynamic action (SDA, the post-feeding increase in resting metabolism; also known as HIF, the heat increment of feeding) may contribute to heat production and maintenance of body temperature. In contrast, a decrease in metabolic rate of tissues secondary to decreased organ perfusion during dives would result in less heat production. Other possible mechanisms of heat production include the metabolism of brown fat and shivering. It has been proposed that the brown fat associated with the pericardial venous plexus of seals has a role in thermoregulation during diving activity in both seals and muskrats (Blix *et al.*, 1975, MacArthur, 1986). Shivering represents another route by which muscle produces heat. Seals do shiver as body temperature decreases (Kvadsheim *et al.*, 2005). However, the shivering response is inhibited or at least greatly reduced during experimental forced submersions (Kvadsheim *et al.*, 2005). Therefore, at least in seals, shivering during a dive is unlikely to occur regardless of how low core temperature is reduced.

Mechanisms of increased heat loss during dives include cold prey ingestion (Wilson and Culik, 1991), potential arterio-venous shunting in the skin and limbs (Chapter 5, Willis *et al.*, 2005), compression of the pelage air layer due to depth (Kooyman *et al.*, 1976a), water penetration of the feather–air layer in some birds (Elowson, 1984, Ribak *et al.*, 2005b, Rijke, 1968), and potential loss of heat through the poorly insulated brood patch of penguins (Handrich *et al.*, 1997, Schmidt *et al.*, 2006).

This chapter focuses primarily on thermoregulation during diving. The many thermoregulatory challenges that are faced on shore by pinnipeds or penguins will not be addressed. The role of metabolic processes in rates of energy/heat production, and early observations of temperature responses during forced submersions will be reviewed first. Then, basic anatomical and physiological thermoregulatory adaptations will be considered. These reviews will conclude with observed temperature profiles during diving in several species and assessment of various hypotheses of thermoregulatory mechanisms during diving.

8.1 Metabolism and heat production

Since Scholander's earliest forced submersion experiments with seals, it has been known that temperature decreased variably in tissues, and as much as 2.5 °C in the brain and blubber (Scholander, 1940, Scholander *et al.*, 1942b). These temperature declines were considered secondary to a decrease in metabolic rate during forced submersions. In forcibly submerged ducks, although deep body temperatures increased during submersion, temperatures decreased during the recovery period (Scholander, 1940, Scholander *et al.*, 1942b). Scholander interpreted these changes as evidence for both decreased metabolism during the submersion as well as for conservation of core temperature and cooling of the periphery (i.e., regional heterothermy) during the submersion, with subsequent rewarming of the periphery during the recovery.

Hypothermia, as demonstrated in Scholander's studies, is theoretically beneficial to a diver in two ways. First, the rate of oxygen store depletion could be depressed by a temperature-induced decline in tissue metabolic rate via the Q_{10} effect (Butler, 2004, Geiser, 2004). Second, even mild hypothermia of a few degrees can be beneficial during ischemia; neurological outcomes after cardiac arrest are improved by such therapy (Bernard *et al.*, 2002, Milde, 1992, Sessler, 2009). However, maintenance of body temperature in the normothermic range for an awake mammal or bird is important for optimal tissue function such as neural processing or muscle contraction (Bennett, 1984, Fischbeck and Simon, 1981, Mallet, 2002). Certainly, humans with mild hypothermia (32–35 °C) present with confusion, amnesia, dysarthria, and ataxia (Kempainen and Brunette, 2004, Mallet, 2002). On the other hand, spatial learning is conserved in rats cooled to as low as 32 °C (Moser and Andersen, 1994). Perhaps the temperature tolerance of the central nervous system of diving mammals and birds is more similar to that of the rat than the human.

Given the challenges of thermoregulation in water, Scholander's documented temperature changes during forced submersions, and the potential benefits/risks of hypothermia, maintenance of proper body temperature is an important determinant of an animal's ability to dive. This optimization of body temperature is achieved through regulation of metabolic processes and regulation of heat conservation/heat loss mechanisms.

As already mentioned, heat production is associated with ATP breakdown during muscle contraction. Swimming activity and, presumably, the secondary heat production in muscle due to swimming, have been associated with maintenance of core temperatures in sea otters (Costa and Kooyman, 1984). Similarly, secondary heat production in exercising muscle may well account for the lack of an increase in metabolic rates in sea lions swimming in water temperatures below their thermoneutral zone (Liwanag *et al.*, 2009). It is also notable that muscle mitochondria from elephant seals, despite increased phosphorylation control, have a 50% greater respiratory mitochondrial leak, which may be related to thermogenesis in the diving seal (Chicco *et al.*, 2014). Exercise has also been found to decrease thermoregulatory costs in diving ducks (Kaseloo and Lovvorn, 2006), and wing flapping has been suggested to aid in warming of ingested prey in cormorants (Grémillet, 1995). In addition, the heat increment of feeding (HIF) may also contribute to heat production and maintenance of body temperature. HIF has been demonstrated in sea otters, seals, cormorants, ducks, penguins, and other birds (Bech and Praesteng, 2004, Costa and Kooyman, 1984, Enstipp *et al.*, 2008, Hawkins *et al.*, 1997, Janes and Chappell, 1995, Kaseloo and Lovvorn, 2006, Markussen *et al.*, 1994, Rosen and Trites, 1997).

However, it has also been questioned in some species and circumstances (i.e., low-protein diet) whether HIF can effectively substitute for thermogenesis and decrease the cost of thermoregulation during foraging/diving activity (Kaseloo and Lovvorn, 2003, Rosen and Trites, 1997, Rosen *et al.*, 2007). Indeed, Wilson and Culik have emphasized that the thermoregulatory costs to rewarm cold prey may be much greater in magnitude than HIF (Wilson and Culik, 1991). In addition, the digestive process may even be delayed until periods of relative inactivity so that the oxygen consumption associated with digestion does not compete for oxygen stores during foraging activity (Crocker *et al.*, 1997, Mitani *et al.*, 2010, Sparling *et al.*, 2007). In such cases, any contribution of HIF to thermoregulation might occur well after diving activity has stopped.

In terms of metabolic rate and heat production, mass-specific metabolic rates and thermoregulatory costs are higher in smaller-sized animals due to the well-known increased ratio of body surface area to volume in smaller animals (Kleiber, 1975). This relationship is also true in marine mammals, but in general the metabolic rates of marine mammals resting in water are typically elevated above that predicted by the Kleiber equation for mammals at rest (Lavigne *et al.*, 1986, Williams *et al.*, 2001b). This elevation has been attributed to both thermoregulatory costs and the carnivory of many marine mammals. Hence, the very high metabolic rates and food requirements of the smallest marine mammal, the sea otter (*Enhydra lutris*) (Kenyon, 1969, 1975, Morrison *et al.*, 1974, Yeates *et al.*, 2007).

Although the regulation of metabolic rate during free dives is debated and metabolic rates can be reduced during trained breath holds versus surface rest (Hurley and Costa, 2001), larger animals do appear to have lower rates of blood oxygen depletion, and, hence, lower metabolic rates during breath holds (Hudson and Jones, 1986, Noren *et al.*, 2012b). These lower metabolic rates are consistent with lower thermoregulatory costs in the larger divers, and confer an advantage in terms of the rate of oxygen store depletion. In addition, as discussed in Chapter 7, larger animals have lower locomotory stroke rates, and, thus, lower rates of heat production in muscle. Thus, the potential rate of mass-specific heat production by metabolic processes will be relatively lower in larger animals versus smaller animals. Interestingly, the potential effects of size and body design of minke whales (*Balaenoptera acutorostrata*) swimming in cold waters result in maintenance of an effective blubber insulation, a decrease in deep body temperature (35.1 °C), and a low estimated metabolic rate (Blix and Folkow, 1995, Folkow and Blix, 1992, Kvadsheim *et al.*, 1996).

8.2 Marine mammals: thermoregulatory anatomy and physiology

In marine mammals, blubber and fur serve as insulation during diving. Pinnipeds and sea otters both have fur, but fur is an effective insulator underwater only in the fur seals and sea otter (Kvadsheim and Aarseth, 2002, Liwanag *et al.*, 2012, Scholander *et al.*, 1950c). In adult harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*), thermal resistance of the fur decreased in water by 92% from that in air and was only 3% of total insulation, while the blubber contributed 85% to total insulation in water (Kvadsheim and Aarseth, 2002). Among phocid and otariid pinnipeds, only the fur seals retain an air layer upon immersion in water; blubber plays the primary role in the other species, even the sea lion, another otariid (Liwanag *et al.*, 2012).

In the Antarctic fur seal (*Arctocephalus gazella*), the difference between skin temperature below the fur and adjacent sea water can be as high as 20 °C at the surface, but that difference ranges between 4 and 0 °C during dives, decreasing with depth and increasing with ascent (Boyd, 2000). In the fur seal and sea otter, high hair density, elongation/flattening of the guard hairs, and interlocking underhairs facilitate air trapping (Kuhn et al., 2010, Liwanag *et al.*, 2012, Williams *et al.*, 1992a). Absent arrector pili muscles in pinnipeds also contribute to flattening of the fur layer in these animals (Kvadsheim and Aarseth, 2002, Liwanag *et al.*, 2012, Scholander *et al.*, 1950c).

The effectiveness of blubber as an insulator is considered dependent on its heat conductivity and thickness. It is important to note that heat conductivity correlates negatively with blubber lipid content, and that these parameters, as well as blubber thickness, can vary throughout regions of the body and with age (Dunkin *et al.*, 2005, Kvadsheim *et al.*, 1996, Ryg *et al.*, 1993, Worthy and Edwards, 1990). In pinniped and cetacean species with over a 4000-fold range in body mass, average blubber thickness ranged from 2 to 9 cm (Ryg *et al.*, 1993). Blubber thickness in different body regions ranged from 7 to 40 cm in one fin whale specimen (Lockyer and Waters, 1986).

Overall, heat loss to the environment through blubber is a function of surface area, blubber heat conductivity and thickness, and the temperature difference between the skin surface and the muscle–blubber interface (see above references). In such calculations, the temperature at the muscle–blubber interface is preferred over core temperature as the temperature gradient between the body core and environment is not necessarily confined to the blubber layer. As emphasized by Kvadsheim *et al.* (1996), use of an incorrect temperature may have caused errors in earlier estimations of metabolic requirements of whales based on calculations of heat loss to the environment. In addition, heat loss through the blubber layer is due to both conduction (the conductivity of the blubber) and also the magnitude of blood flow through the blubber (convective heat loss). These differences were well illustrated in young harp seals, in which blubber heat flux in water at 0 °C was equivalent to the calculated conductive heat loss through blubber, and to that of the blubber of a seal carcass, in which there was obviously no blood flow. However, at higher water temperatures, the calculated conductive heat loss was only 4–43% of the total blubber heat flux, which supports the concept that heat transfer via blood perfusion into the blubber accounted for the remainder (Kvadsheim and Folkow, 1997).

Heat conductivity in blubber tissues with similar total lipid content may also vary with lipid composition (Bagge *et al.*, 2012). The blubber of pygmy sperm whales (*Kogia breviceps*), with a similar total lipid content but higher wax ester content than that of short-finned pilot whales (*Globicephala macrorhynchus*), had 30% greater thermal conductivity.

Sirenians, as represented by manatees, have dense skin that is very low in lipid content; they do not have a true blubber layer (Gallivan *et al.*, 1983, Kipps *et al.*, 2002). Manatees do, however, have subcutaneous fat which presumably aids in insulation. In addition, there is a countercurrent heat exchanger in the tail vasculature (Rommel and Caplan, 2003). Minimum thermal conductance of the manatee has been reported to be similar to that of the seal, but that value is dependent on nutritional status and the quantity of subcutaneous fat (Gallivan *et al.*, 1983). In addition, the low metabolic rate of these animals limits their ability to maintain body temperature in colder water (Gallivan *et al.*, 1983). It has been argued that these factors limit the lower end of their thermoneutral zone and their geographical distribution to a water temperature of 20 °C (Irvine, 1983). Although the dense skin is disadvantageous in terms of heat retention, the high density of the skin as well as the pachyostotic bone of the manatee are considered to provide negative buoyancy in an animal with increased positive buoyancy due to its lung capacity (Kipps *et al.*, 2002).

Heat loss through the less-insulated appendages of diving animals has been estimated to represent 8–28% of total body heat loss in a modeling study of a large series of seals and whales (Ryg *et al.*, 1993). In the killer whale (*Orcinus orca*), 40% of total body heat loss may occur through the appendages, in part due to the larger percentage of body surface area represented by those structures (Kasting *et al.*, 1989). In young harp seals in 0 °C water, heat loss from the flippers was 2–6% of total body heat loss (Kvadsheim and Folkow, 1997). In contrast, in 24 °C water, flipper heat loss accounted for 19–48% of total heat loss in these animals, illustrating the importance of peripheral blood flow regulation under such conditions. A prior estimate of 84% of total body heat loss through the flippers of the free-diving harp seal (Gallivan and Ronald, 1979) was not consistent with these findings, but both studies emphasize the important role of the appendages in increasing heat loss during thermal stress.

In contrast to the role of insulation in conservation of body heat and temperature in an endotherm, blood flow regulation to the skin and appendages is considered the primary route of dissipation of excess heat generated through muscular exercise. It is here where the superficial arterio-venous anastomoses and blood vessels in the skin and appendages (see Chapter 5) potentially play an important role (Bryden and Molyneux, 1978, Molyneux and Bryden, 1975, 1978, Rommel and Caplan, 2003, Scholander and Schevill, 1955). Indeed, infrared imaging has revealed hot spots (skin temperatures above sea temperature) on the trunks of surfacing humpback whales (*Megaptera novaeangliae*), and the pectoral fins and dorsal fins of swimming minke whales and fin whales (*Balaenoptera physalus*) (Cuyler *et al.*, 1992). Localized heat flux from the dorsal fin is highest above superficial veins in the dolphin (Meagher *et al.*, 2002). Heat loss from the dorsal fin of the dolphin is highly variable. Heat flux decreased during diving, increased during ventilatory periods, and also increased as ambient water temperature declined (Meagher *et al.*, 2002, Noren *et al.*, 1999, Westgate *et al.*, 2007, Williams et al., 1999).

Although temperature regulation has been demonstrated to override the dive response in experimental studies (Hammel *et al.*, 1977), post-exercise heat flux at the surface was reduced at depth in diving dolphins (Noren *et al.*, 1999). Heat flux increased only slightly during ascent, but on return to the surface there was an immediate 80–100% increase in heat flux in the dorsal fin and tail fluke, presumably secondary to the surface tachycardia and peripheral vasodilation (Noren *et al.*, 1999). The occurrence of heat loss versus heat conservation responses at depth is most probably a function of the particular circumstances of a dive. It is notable that one exceptionally high measurement of heat flux occurred in the dorsal fin of a diving dolphin during submersion after it had performed an unusually strenuous exercise routine prior to the dive (Noren *et al.*, 1999). This increase in dorsal fin blood flow and heat loss would be consistent with Hammel *et al.*'s forced submersion observations that elevated body temperature may override the bradycardia and vasoconstriction of the dive response.

Besides an overriding of the dive response, there is another mechanism that could allow for external heat loss through the appendages. In two forced submersion studies of seals, Blix, Odden, and colleagues confirmed Scholander's findings of a 2.5–3.3 °C decrease in brain temperature during the submersion period (Blix *et al.*, 2010, Odden *et al.*, 1999). In the 2010 study, Blix also proposed a vascular anatomical basis to selectively cool the brain by examination of the brachial arterial and venous vasculature in the foreflipper. It was hypothesized that brachial artery blood flow through arterio-venous anastomoses in the foreflipper and then through large superficial veins in the flipper bypassed the heat-exchanging rete in the central flipper and allowed for the return of cooled blood to the heart, which would result in the lowering of aortic blood temperature and brain temperature. Such shunting through the hind flippers and pelvic plexus was also consistent with an observed decrease in rectal temperature.

Temperature regulation of organs within the body, especially the reproductive organs, can also be critical. There is both physiological and anatomical evidence for the role of countercurrent vascular heat exchangers in maintaining the temperature of reproductive organs in both cetaceans and pinnipeds (Pabst *et al.*, 1995, Rommel *et al.*, 1992, 1994, 1995).

Other routes of external heat loss in divers include respiration and feeding. Respiratory heat loss in both dolphins and seals is minimized by apneic respiratory patterns and reduction of the temperature and water saturation of exhaled air (Coulombe *et al.*, 1965, Folkow and Blix, 1987, 1989, Kasting *et al.*, 1989). In the seals, the reductions in temperature and water vapor saturation are achieved through a nasal countercurrent heat exchanger. In dolphins, cooler tissue lining the cranial airway sinuses is considered to absorb heat from air prior to exhalation. It has also been proposed that compression of air below the blowhole prior to exhalation leads to water vapor condensation in the airway, thus decreasing the water content of exhaled air of the dolphin (Coulombe *et al.*, 1965).

Heat conservation during prey capture and feeding has not been investigated, although heat loss in the mouth of the mysticete whale is presumably minimized by a countercurrent, potential heat exchanging vasculature in the tongue (Heyning and Mead, 1997, Werth, 2007). Effects of cold prey ingestion on stomach temperatures are exemplified in stomach temperature pill studies of elephant seals and sea lions. After two prey ingestion events (unknown prey mass) in an elephant seal diving at sea, stomach temperature decreased from 36 to 33 °C, and then recovered to baseline within 40 minutes after the last feeding event (Kuhn *et al.*, 2009). In captive sea lions and elephant seals, ingestion of 1 kg of herring at an average temperature of 17.5 °C resulted in a decline of 4 °C in stomach temperature, which recovered to baseline within about 70 minutes in both species (Kuhn and Costa, 2006).

8.3 Marine mammals: body temperatures during dives

Before reviewing body temperatures in diving marine mammals, it is first important to consider the distribution of heat and temperature within the body. Temperature data from harvested whales documented temperature gradients with depth into the body as well as temperature variation within different regions of the body (Folkow and Blix, 1992, Morrison, 1962). The highest temperatures were near the heart and liver. Such regional heterothermy is not unusual, and this variation in temperature raises the question of the definition of core temperature, i.e., where should it be measured?

As an example of regional heterothermy in a living animal, temperature was 35 °C in superficial muscle during sleep apnea of elephant seals, while pulmonary artery temperatures during sleep apnea in the same animals were near 36.5 °C (Ponganis *et al.*, 2006b, 2008,). Even in humans, muscle temperatures at rest averaged 35 °C, with a range of 33.0 to 36.5 °C, and these muscle values were always less than simultaneous rectal temperatures (Saltin *et al.*, 1968). Indeed, it is the loss of vascular regulation during anesthesia and the redistribution of heat to cooler regions of the body that accounts for the initial decreases in core temperature during anesthesia (Sessler, 2000). And, in the other direction, it is probably the warming of the cooler blubber layer and other tissues of the dolphin that allows the animal to transiently move from cool off-shore water to near-shore water with surface water temperatures at or greater than body temperature (Heath and Ridgway, 1999). Because of the regional variation in body temperatures, core temperature is probably best represented by temperatures near the heart and liver, and in the blood of the central aorta, pulmonary artery, and/or vena cava.

Core body temperatures have not been measured during diving in cetaceans. Data from the whaling era revealed a mean post-mortem deep-body temperature of 35.8 °C, although pre-mortem deep muscle temperatures were above 38 °C in sperm (*Physeter macrocephalus*), humpback, and fin whales (Morrison, 1962). Post-mortem core temperature of harvested minke whales was 35.1 °C (Folkow and Blix, 1992). The closest available data from live cetaceans are stomach temperature and abdominal temperature profiles of captive spinner (*Stenella longirostris*) and Pacific bottlenose (*Tursiops gilli*) dolphins collected over the course of the day in the 1970s (Hampton and Whittow, 1976, McGinnis *et al.*, 1972). Abdominal and stomach temperatures in various animals were reported to range from 36 to 38 °C. Similarly, stomach temperatures of a captive manatee remained stable near 35.6 °C during daily activity (Gallivan *et al.*, 1983). Mean rectal temperature of captive sea otters during metabolic studies was 38.1 °C (Morrison *et al.*, 1974). In muskrats (*Ondatra zibethicus*), abdominal cavity temperatures decreased from a baseline of 38 °C to 34 °C after 15 min of diving activity in 10 °C water (Hindle *et al.*, 2006). Notably, in muskrats pre-chilled by 2 °C, diving behavior and dive oxygen consumption were unchanged.

It is in the pinnipeds that temperature profiles have been most successfully recorded during diving. Such profiles are important in that they are the end result of all the cardiovascular, metabolic, and thermoregulatory responses during the dive, and, therefore, provide insight into the nature of these responses during the actual dive. In addition, they address the question of the optimal temperature during diving, and whether lower body temperatures are critical to dive performance. The first evidence of hypothermia during free-diving were immediate post-dive arterial temperatures of 34.9 to 36.3 °C after five dives greater than 25-min duration in Weddell seals (Kooyman *et al.*, 1980). These post-dive temperatures were always lower than the final pre-dive temperature. It was also noted that shivering did not occur even with a temperature of 34.9 °C during the surface recovery period.

The first continuous arterial temperature profiles were reported in a single Weddell seal, and these data revealed mean dive temperatures between 35 and 37 °C for dives of 15–35-min duration and temperatures between 35 and 38.5 °C for shorter-duration dives (Hill *et al.*, 1987). These authors emphasized that temperatures did not change so much during the dive as prior to the dive. Temperatures were always less than 37 °C before dives longer than 15 min, and were less than 36.3 °C before dives longer than 30 min. Thus, Hill *et al.* concluded that the lower temperature prior to and during diving was not the result of a lower metabolic rate during the dive, but rather that the lower temperature was potentially the cause of a lowered metabolic rate. They also postulated that the pre-dive decrease in temperature was secondary to increased blood flow to the skin and flippers.

Continuous muscle temperature profiles in a free-diving Weddell seal revealed that muscle temperatures remained between 36 and 37 °C, with no obvious consistent trends up or down during diving (Ponganis *et al.*, 1993b). As in Hill *et al.*'s arterial temperature profiles, higher temperatures occurred during prolonged surface rest periods. Although hypothermia was not evident, it was still remarkable that these animals could perform muscular exercise during a dive without a significant increase in muscle temperature. Such a temperature profile in the primary locomotory muscle could be consistent with maintenance of some muscle blood flow during the dive. In addition, muscle temperature did decline a few tenths of a degree during the final segment of a 45-min dive, again suggesting that there could be some flow of cooler blood to muscle during the ascent tachycardia.

The range of internal body temperatures in seals at sea was also demonstrated in foraging studies utilizing stomach temperature pills. Although continuous temperature and depth profiles were not analyzed or extensively presented, it is notable that stomach temperatures prior to prey ingestion were near 36 °C in northern elephant (*Mirounga angustirostris*) seals and above 38 °C in gray (*Halichoerus grypus*) seals (Austin *et al.*, 2006, Kuhn *et al.*, 2009).

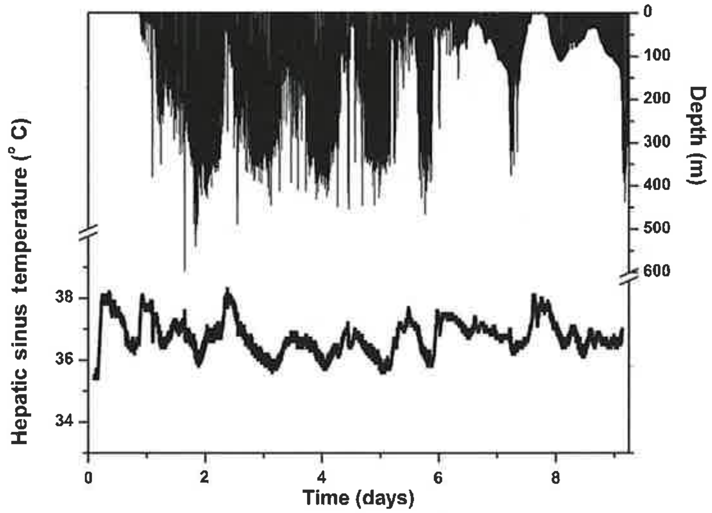

Figure 8.1 Hepatic sinus temperature of a young, translocated elephant seal (*Mirounga angustirostris*) varied between 36 and 38 °C during eight days of diving activity. There was no evidence of significant core hypothermia. Adapted from Meir and Ponganis (2010).

Almost 15–20 years after the last of the Weddell seal temperature studies, intravascular temperature profiles were obtained in juvenile, translocated northern elephant seals and in adult female California sea lions (*Zalophus californianus*) during maternal foraging trips to sea. In the elephant seal study, temperatures were recorded in the extradural vein, hepatic sinus, and aorta (Meir and Ponganis, 2010). There was a significant, albeit weak, negative correlation of mean dive temperature with dive duration in all but one of 13 seals. However, most temperatures were between 36 and 38 °C (Fig. 8.1). In only one seal were arterial temperatures consistently lower (between 34 and 36 °C). The lack of consistent, significant hypothermia (below 35 °C) in the hepatic sinus and aorta during dives as long as 25 min was taken as evidence that core hypothermia and a subsequent cold-induced decrease in metabolic rate were not required in such dives.

It was also notable that arterial temperature of elephant seals did not increase during what appeared to be routine, repeated foraging dives to 500–600-m depth (Fig. 8.2). However, during bouts of short-duration, shallow dives, temperatures could be more variable and higher (Fig. 8.2). Lastly, longer dives were occasionally associated with abrupt, transient decreases in either aortic and extradural vein temperature to as low as 30 °C (Figs 8.3, 8.4). The rapidity of the onset and recovery of these temperature declines argues for confinement of the temperature change to the blood, and for cooling through superficial arterio-venous shunts as described by Blix *et al.* (2010) in the flippers of the seal as the mechanism responsible for such a change.

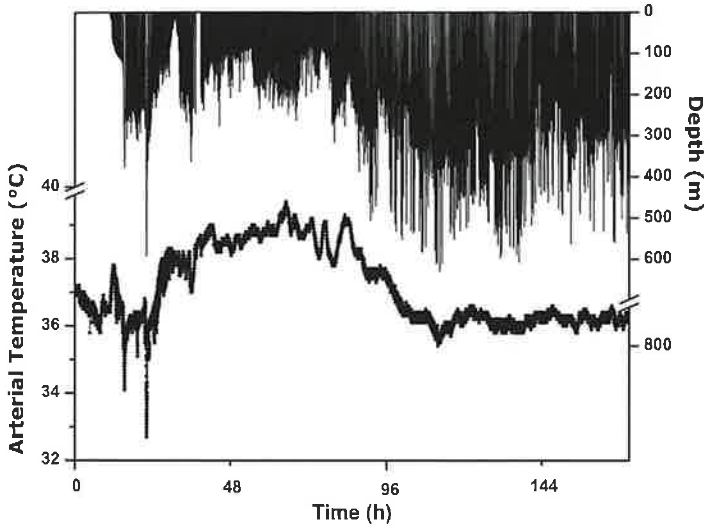

Figure 8.2 Aortic temperature of a young translocated elephant seal (*Mirounga angustirostris*) varied greatly during six days of diving activity. Higher temperatures to near 39 °C predominated during shallow diving activity while temperatures closer to 36 °C occurred during bouts of deeper dives.Adapted from Meir and Ponganis (2010).

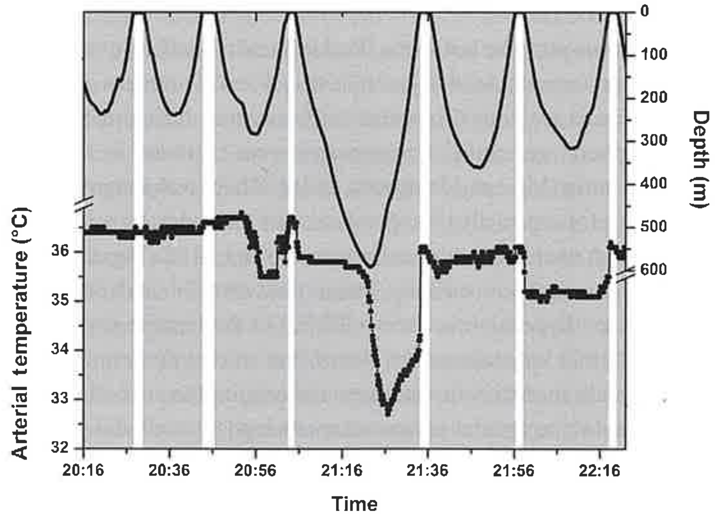

Figure 8.3 Transient decreases in arterial temperature can occur in longer dives of elephant seals (*Mirounga angustirostris*). The rapid decline to 32 °C and quick recovery to 36 °C suggest that such changes are probably confined to the blood and secondary to blood flow patterns. Shaded areas indicate dive periods in this and following figures. Adapted from (Meir and Ponganis, 2010).

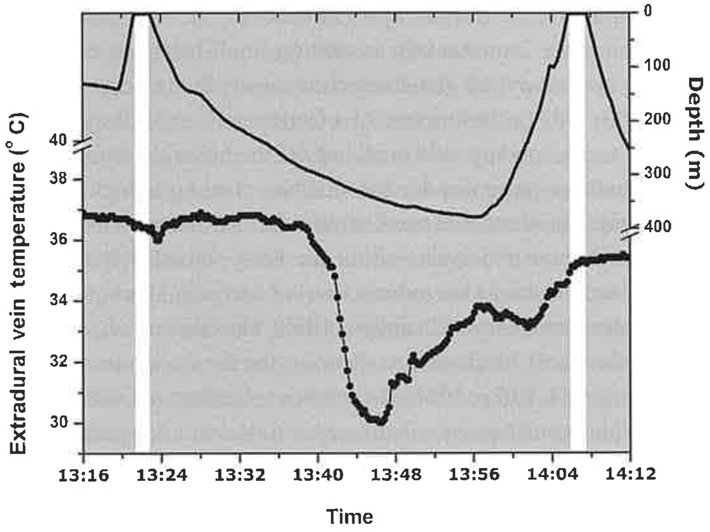

Figure 8.4 Transient decreases can also occur in extradural vein temperature during longer dives of elephant seals (*Mirounga angustirostris*). In this case, temperature declined almost 7 °C over four minutes, and then returned to near 35 °C by the end of the dive over the course of 22 minutes. Adapted from Meir and Ponganis (2010).

In Antarctic fur seals, intraabdominal temperatures have been reported to decline as much as 20 °C during a dive (Woakes *et al.*, 1992). In adult female California sea lions during maternal foraging trips to sea, vena caval temperatures remained between 36 and 38 °C, even during dives as deep as 400 m and long as 8 min (McDonald and Ponganis, 2013). Although temperature was again not elevated during diving activity, there was no evidence that significant core hypothermia was required in the sea lions to perform long dives.

In summary, temperature profiles during dives of Weddell seals, elephant seals, and sea lions reveal that core temperatures in the aortic and central veins primarily remain in the 36 to 38 °C range and that core hypothermia is not essential to perform routine and even long dives. Muscle temperature profiles in the diving Weddell seal and the dive behavior/oxygen consumption of pre-chilled muskrats support the same argument. On occasion, however, marked temperature changes can occur in blood, most probably related to selective shunting of blood to the periphery. Regional heterothermy, which has been demonstrated in marine mammals and terrestrial mammals at rest, most probably also occurs during diving, but regional temperatures have not been extensively examined in free-diving marine mammals. Certainly, however, data from harvested whales and forced submersion experiments support the concept of regional heterothermy.

8.4 Marine birds: thermoregulatory anatomy and physiology

Feathers and the air layer beneath them provide the major component of insulation in birds. Even in the emperor penguin (*Aptenodytes forsteri*) standing on ice, 86% of insulation is provided by the feather layer (Jarman, 1973). Maintenance of the air layer and water repellency are important for insulation in all birds, especially aquatic birds. Feather structure and uropygial gland secretions provide the basis of water repellency (Stettenheim, 2000). The basic structure of a feather consists of the main shaft with side branches (barbs) and secondary side branches off the barbs (barbules). Downy barbs at the base of the shaft are more slender and flexible, creating a thick, fluffy, air-trapping structure. In addition, there can be a small afterfeather associated with the shaft at its base.

A uniform distribution of feathers about the body, broad, flat shafts, and the size, spacing, density, and hooking (interconnection) of barbs and barbules are considered to contribute to water repellency (Chandler, 1916, Dawson *et al.*, 1999, Stettenheim, 2000), although the exact mechanisms allowing for the exclusion of water have been debated (Elowson, 1984, Rijke, 1968). In penguins, feathers are short, stiff, and capable of being "locked" into position by subcutaneous muscles; a long afterfeather and down provide insulation beneath (Dawson *et al.*, 1999). Mathematical modeling suggests that the small radius of the barbule and the barbule's geometric structure contribute most to the insulative properties of the feather layer (Du *et al.*, 2007).

In the cormorant, which is considered to have a partially wettable feather, the middle section of the feather is densely packed while the outer margins are more spaced (Grémillet *et al.*, 2005). In the center, hooklets on adjacent barbules interconnect with one another as in other feathers. This non-homogeneous arrangement in the cormorant feather allows water penetration on the periphery and air-trapping in the center. Water penetration of the feathers can account for observed weight gains in cormorants after diving, and lower feather air volumes than in other aquatic species (Grémillet *et al.*, 1998, 2005, Ribak *et al.*, 2005b, Wilson *et al.*, 1992b). Although water penetration of the feather layer decreases the cormorant's insulation, it also decreases buoyancy, a potential advantage for a diver. It is notable that in cormorant species adapted to colder regions, the feather air layer is larger, and in the deep-diving, sub-Antarctic blue-eyed shag (*Phalacrocorax atriceps*), the feather structure is reported to be homogeneous, like that of other aquatic birds, thus potentially making the feathers in this species water-repellent and preserving more air in the feather layer for insulation (Grémillet *et al.*, 1998). In general, mass-specific feather air volumes of carcasses were lowest in pursuit divers, intermediate in plunge divers, and highest in surface-feeding and flight-feeding birds, with the lowest values in cormorants, penguins, and divers (loons) (Wilson *et al.*, 1992b).

Water penetration of the feather layer has been assessed in ducks and cormorants, with assessment of an experimental index – the critical water penetration pressure (Grémillet *et al.*, 2005, Stephenson and Andrews, 1997). When they first developed this technique, Stephenson and Andrews found that the critical penetration pressure in duck and goose feathers was three times the pressure on feathers of a bird floating at the surface, and two times that of a partially submerged bird, thus providing experimental evidence of feather water repellency and protection of the feather air layer. Notably, critical penetration pressure of the dense, center portion of the cormorant feather was three times greater than that of the duck, again re-enforcing Grémilet *et al.*'s conclusion that the central section of the feather was resistant to water penetration, allowing for trapping of air beneath it.

The thermal conductance of birds in water has been evaluated with both carcasses and live animals. Cooling rates of carcasses of 14 species of aquatic birds revealed that thermal conductance increased two-fold with water contact and 4.8-fold with submergence (de Vries and van Eerden, 1995). Thermal conductances across gentoo (*Pygoscelis papua*) and Adélie (*P. adeliae*) penguin pelts increased 1.1–1.9 times on immersion into water, and 5.2-fold on compression to 10-m depth (Kooyman *et al.*, 1976a). However, during compression, unlike in live penguins, water penetrated the unwashed pelts. In a washed pelt free of oil, conductance on immersion alone increased 3.4-fold, supporting the role of feather oil in water repellency. In live little penguins (*Eudyptula minor*), and king penguin (*Aptenodytes patagonicus*) chicks, thermal conductance in water increased two- to four-fold, all consistent with compression of the air–feather layer (Barre and Roussel, 1986, Stahel and Nicol, 1982). Although total conductance in a live Adélie penguin increased three-fold on immersion in water, it did not increase further with compression to 10-m depth (Kooyman *et al.*, 1976a). In live thick-billed (*Uria lomvia*) and common (*U. aalge*) murres, calculated thermal conductances were low and did not decrease with decreasing water temperature (Croll and McLaren, 1993). The low conductance values of the murre were attributed to (a) buoyancy and minimal contact (including the wings) with water, (b) withdrawal of feet into the feather layer, and (c) maintenance of the feather air layer.

Besides compression of the feather layer, other potential routes of heat loss during diving are the appendages and the brood patch. For example, during flight of the herring gull (*Larus argentatus*), 80% of heat production is lost through the feet (Baudinette *et al.*, 1976). However, in the feet and wings of diving birds, the extensive countercurrent associations of arteries and veins discussed in Chapter 5 (Thomas and Fordyce, 2007, 2012) should promote heat conservation in the body core and cooling of the periphery even in the presence of some peripheral blood flow during diving. In addition, as already pointed out in this chapter, feet can be retracted into the feathers in birds such as murres. Superficial veins that bypass the countercurrent system in the wings of both diving and non-diving birds have been considered by most authors to provide a route for heat dissipation for periods of heat stress (in flight or on land) or during surface intervals. Hence, the flushed pink feet and inner wing surfaces of Adélie penguins exiting from the water.

Increased blood flow and heat loss through the brood patch during dives of king penguins has also been proposed as a mechanism of heat dissipation and thermoregulation (Schmidt *et al.*, 2006). As discussed in Chapter 5, blood flow through the arteriovenous anastomoses in the brood patch provides a mechanism of heat transfer to warm an incubated egg. In diving king penguins, although brood patch subcutaneous temperature always had a net decrease over the course of a dive, transient warming episodes of about 0.3 °C were recorded in 21% of dives. On this basis, Schmidt *et al.* hypothesized that fine peripheral blood flow adjustments could contribute to thermoregulation and observed temperature profiles during dives.

Cold prey ingestion represents another process that can contribute to lower body temperatures. Stomach temperature responses are highly variable and are dependent on the mass and temperature of ingested prey. Ingestion of a single prey item by a bank cormorant resulted in a 2 °C decrease in stomach temperature, with recovery to the baseline temperature of 40.5 °C in ten minutes (Wilson et al., 1995). In contrast, over a 50-minute feeding dive bout by the same species, stomach temperature could decrease as much as 5 °C (Wilson and Gremillet, 1996). In king penguins at sea, stomach temperature declined by as much as 20 °C over a ten-hour period of diving; the return to baseline temperatures of 36 °C took as long as another ten hours (Wilson *et al.*, 1995).

8.5 Marine birds: body temperatures during dives

Body temperature profiles during diving have been examined to both determine the effectiveness of the feather air layer underwater as well as to investigate the potential role of temperature in regulation of tissue oxygen demand during diving. In tufted ducks (*Aythya fuligula*), abdominal temperature increased during dive bouts in summer but decreased to about 40.5 °C during diving in colder winter waters, resulting in about a 1 °C difference in end-of-bout abdominal temperature between seasons (with a 15.5 °C lower ambient water temperature in winter) (Bevan and Butler, 1992b).

Further development of temperature loggers allowed application to diving birds in the wild, and documented 4–8 °C decreases in abdominal temperatures during dive bouts of gentoo penguins and South Georgian shags (Bevan *et al.*, 1997, Woakes *et al.*, 1992, 1995). In addition, variable but smaller temperature decreases were also reported in a king penguin, with thermistors located below the lower sternum (near the liver and stomach), in the mid-sternal region near the heart, and in the upper abdomen (Culik *et al.*, 1996b). On average, in both gentoo and macaroni (*Eudyptes chrysolophus*) penguins, abdominal temperature declined about 2.4 °C during dive bouts (Bevan *et al.*, 2002, Green *et al.*, 2003).

The most remarkable decreases in abdominal temperature were reported in king penguins, in which lower intraabdominal temperature (between the brood patch wall and stomach) decreased as much as 20 °C during dive bouts (Handrich *et al.*, 1997). These reports all raised issues of regional heterothermy, effects of cold prey ingestion, effectiveness of insulation, and the potential role of diving cardiovascular responses in the distribution and loss of heat, i.e., decreased heat production due to perfusion-related decreases in organ oxygen consumption, decreased muscle blood flow and subsequent transfer of muscle heat to the rest of the body, and possible heat loss through the well-vascularized brood patch and through the wings. In particular, the potential savings in oxygen costs due to hypothermia were highlighted. As an example, it was calculated that, if the temperature of the entire body of a gentoo penguin decreased the average 2.4 °C found in the abdomen, then, based on the Q_{10} effect, the duration of aerobic metabolism would be increased by 29%, and all recorded dives of the gentoo penguin would be within its calculated aerobic limit (Butler, 2004).

The question remained, however, whether temperature did indeed decline in the whole body or, for that matter, at least in the highest O_2-consuming organs (brain, liver, kidneys, muscle). This question was particularly relevant because many of the abdominal temperature sensors in these studies were implanted near the brood patch wall and/or near the stomach, the former poorly insulated, the latter a reservoir for ingested cold prey items, and neither an organ of high oxygen consumption. This question was addressed in a series of investigations of emperor penguins voluntarily diving at an experimental dive hole (Ponganis *et al.*, 2001, 2003b, 2004).

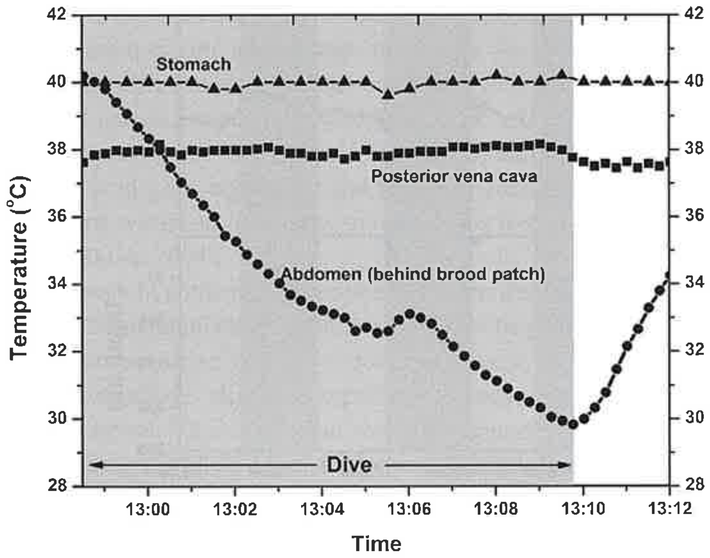

Figure 8.5 Regional heterothermy and preservation of core temperature occurred during this 11.3-min dive of an emperor penguin (*Aptenodytes forsteri*) at an isolated dive hole. Both stomach and posterior vena caval temperature are preserved while the intraabdominal temperature behind the brood patch declines almost 11 °C during this dive. Decreased peripheral perfusion and heat loss through the less-insulated brood patch probably contributed to the decline in abdominal temperature. Adapted from Ponganis et al. (2003b).

The dives of emperor penguins at the experimental dive hole were interspersed with surface periods out of the water on the sea ice and were usually only to about 50-m depth due to prey distribution (Ponganis *et al.*, 2000). Nonetheless, despite this behavioral difference with other penguin species that stay in the water and dive continuously at sea, the temperature inside the abdomen behind the brood patch of the emperor penguin declined to as low as 19 °C, confirming the previous findings in king penguins. However, these declines did not correlate with dive duration, and, in addition, simultaneously recorded vena caval temperatures showed only minor fluctuations (Fig. 8.5), and usually increased during the dive period (Ponganis *et al.*, 2001). In addition, during deep dives to 225-m depth, aortic temperatures actually increased about one 1 °C (Fig. 8.6). Lastly, during the second longest dive currently reported for an emperor penguin, vena caval temperature remained near 36.7 to 37.0 °C (Fig. 8.7). Because vena caval and aortic temperatures were considered more representative of both core temperature and the temperature of central organs, it was concluded that central hypothermia and an associated decrease in organ metabolic rate did not occur despite the large changes in abdominal temperatures behind the brood patch. Rather, the temperature

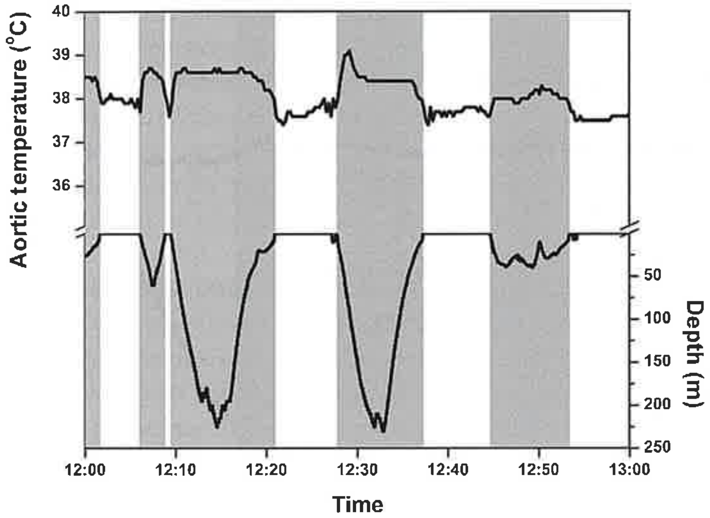

Figure 8.6 Maintenance and even elevation of arterial temperatures occurred during >10-min, 225-m deep dives of an emperor penguin (*Aptenodytes forsteri*) at an isolated dive hole. Thus, core hypothermia is not essential to make deep, long-duration dives. Adapted from Ponganis et al. (2004).

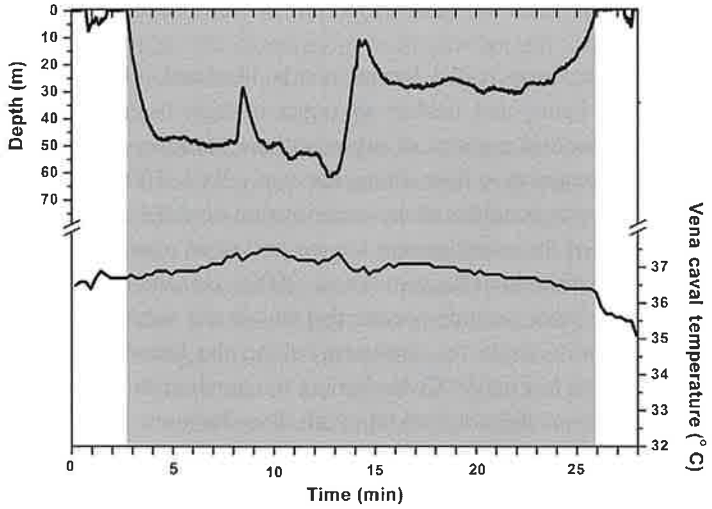

Figure 8.7 Posterior vena caval temperature was preserved at 36.5–37.0 °C during this 23.1-min dive of an emperor penguin (*Aptenodytes forsteri*). Vena caval hypothermia did not occur in one of the longest dives reported for an emperor penguin. Although regional heterothermy may occur, whole-body and core hypothermia were not essential to such dive performance. Adapted from Ponganis et al. (2007, 2010a).

profiles were considered consistent with a model of regional heterothermy based on conservation of core temperature, peripheral vasoconstriction, and cooling of an outer body shell. This model was also consistent with elevations in aortic temperatures and pectoral muscle temperatures during dives as well as with (a) conservation of intradive temperatures in the large central limb veins, and even in the stomach (despite documented cold prey ingestion); and (b) large decreases in intradive temperature in the peripheral wing and foot veins, subcutaneous tissues, and sub-feather space (Ponganis *et al.*, 2003b, 2004).

Although hypothermia in peripheral regions during a dive can decrease the metabolic cost of thermoregulation, in that heat need not be generated to maintain those peripheral temperatures during a dive, it does not appear, at least in emperor penguins at an isolated dive hole, that core hypothermia leads to a decrease in the metabolic rate of central organs. This conclusion was also supported by the lack of correlation of dive temperature and dive duration in these animals, and the maintenance of vena caval temperature even during a 23.1-min dive (Fig. 8.7), one of the longest recorded dives of any emperor penguin (Ponganis *et al.*, 2010a). Although deep body temperatures of other penguin species have not been measured during diving, it is notable that, although pectoral muscle temperature of king penguins at sea also increased during dives, muscle temperature did decrease gradually throughout an entire dive bout due to declines during surface intervals (Schmidt *et al.*, 2006). During dive bouts with mean durations of 4.8–12.4 hours, mean pectoral muscle temperatures declined 0.5–4.0 °C. However, it is unknown whether longer dives were associated with lower muscle temperatures in these king penguins as correlations between dive duration and intradive pectoral muscle temperature were not reported. As previously reviewed in seals, it is also remarkable that penguins were able to perform continuous diving for up to 12 hours without significant elevations in locomotory muscle temperature.

Central temperature profiles have also been recorded in an alcid diver, the guillemot; core hypothermia did not occur during diving (Niizuma *et al.*, 2007). Core temperature (beneath the right lobe of the liver, adjacent to the heart and lungs) was conserved and even increased as much as 1 °C during dives, while peripheral temperature (subcutaneous abdominal wall) decreased as much as 2.5 °C during a dive and 8 °C during a dive bout. Thus, in the guillemot, a bird weighing less than 1 kg, there does not appear to be a hypothermia-associated reduction of metabolic rate in central organs during dives.