secondary to parasympathetic stimulation. This was demonstrated by a decrease in left ventricular dp/dt during forced submersion of the duck (Folkow and Yonce, 1967).

These hemodynamic findings in forcibly submerged ducks indicate that decreased heart rate and contractility are the primary mechanisms which serve to optimize myocardial oxygen supply and demand. In contrast to the seal, preload does not appear to be regulated during submersion of the duck; both filling pressures and ventricular volumes are increased. These factors potentially lead to increased wall tension and decreased gradients for coronary perfusion in the duck. There also do not appear to be any biomechanical adaptations, such as the aortic bulb in the seal, that would reduce afterload during the widespread vasoconstriction and elevated systemic vascular resistance during forced submersion of the duck. Hemodynamics during the bradycardias of emperor penguins may be different, but have not been investigated. Notably, preliminary studies indicate that the pulmonary artery of emperor penguins demonstrates hypoxic pulmonary vasodilation similar to that of the sea lion (K. Olson, personal communication).

# 7 Muscle and locomotory work

The biochemistry and energy metabolism of muscle is an essential component of the physiological basis of an animal's dive capacity. Despite the development of significant blood hypoxemia and muscle ischemia during a dive, muscle must continue to function to provide propulsion. And the work that muscle must perform during a dive is, in turn, dependent on hydrodynamics, drag, buoyancy, swim speed, and the pattern/efficiency of locomotion. Ultimately, hydrodynamics, swim patterns, and cost of transport are important because they increase the efficiency of diving and extend the duration of aerobic metabolism during a dive by decreasing the rate at which body oxygen stores are consumed. Therefore, this chapter will first review muscle fiber types and biochemistry in diving mammals and birds, and then outline the various factors that contribute to the locomotory workload of muscle during a dive.

In evaluating potential muscle adaptations and their significance to diving performance, it is most relevant to examine the muscles that are primarily responsible for underwater movement (see Table 7.1). An excellent review and reference source for the anatomy underlying the various locomotory styles of marine mammals is chapter 8 in Berta *et al.*'s 2006 textbook, as well as in Howell's classic text on the anatomy of marine mammals (Howell, 1930).

## 7.1 Muscle fiber types

The contractile properties and metabolic characteristics of a muscle are determined by its fiber type composition. Fibers are typically classified on the basis of myosin heavy chain isoforms and oxidative/glycolytic capacities into slow twitch oxidative (SO, Type I), fast twitch oxidative, glycolytic (FOG, Type IIa), and fast twitch glycolytic (FG, Type IIb) fibers (Zierath and Hawley, 2004). However, there are multiple heavy chain isoforms that can be expressed at different levels and even in different combinations in various muscles and species (Flück and Hoppeler, 2003, Rivero *et al.*, 1999). Hence, there were at least as many as five different Type II fiber subtypes in one study (Rivero *et al.*, 1999). It should also be remembered that myosin heavy chain isoforms are reflected in the contractile properties of muscle. Hence, myosin heavy chain immunohistochemistry classifies contractile fiber types, but not necessarily the metabolic capacities of the fibers. The expression of genes for enzymes in the oxidative and glycolytic pathways are under the influence of multiple signaling pathways (Flück and Hoppeler, 2003).

**Table 7.1** Underwater locomotory strokes and primary propulsive muscles of various divers.

| Diver | Locomotory stroke | Primary muscles | References |
|---|---|---|---|
| Cetaceans | Dorso-ventral oscillation of tail fluke | Epaxial/hypaxial muscles of the spine | A |
| Manatees | Dorso-ventral oscillation of trunk and tail fluke | Epaxial/hypaxial muscles of the spine | B |
| Otariids | Stroke of fore-limb flippers | Pectoralis, latissimus dorsi, shoulder muscles | C |
| Phocids | Lateral stroke of hind flippers | Longissimus dorsi-iliocostalis muscle complex | D |
| Walruses | Lateral stroke of hind limb flippers (primary) | Longissimus dorsi-iliocostalis muscle complex | E |
| Sea otters | Dorso-ventral undulation of hind trunk | Para-spinal muscles | F |
| Foot-propelled avian divers | Stroke of hind limbs | Leg muscles | G |
| Wing-propelled avian divers | Stroke of wings | Pectoralis and supracoracoideus muscles | G |

A: Fish and Hui, 1991, Fish *et al.*, 1988, Pabst, 1990, Strickler, 1980; B: Berta *et al.*, 2006, Kojeszewski and Fish, 2007; C: English, 1976, 1977, Feldkamp, 1987a; D: Bryden and Felts, 1974, Fish *et al.*, 1988, Pierard, 1971; E: Berta *et al.*, 2006, Gordon, 1981; F: Berta *et al.*, 2006, Williams, 1989, Tarasoff, 1972; G: Baudinette and Gill, 1985; Butler, 1991.

Classically, slow twitch fibers have been considered to underlie slow, prolonged activities such as marathon running, whereas fast twitch fibers contribute to rapid and/or powerful motions such as those in flight, sprinting, or weight lifting. Consistent with this concept, a larger percentage of slow twitch fibers predominates in the locomotory muscle of a large cetacean, such as the narwhal, in comparison to smaller dolphin species; based on size alone, the larger animal will probably have a lower stroke rate than its smaller counterparts (Sato *et al.*, 2007, Williams *et al.*, 2011b). However, this increase in slow twitch fiber composition is not the case in all large cetaceans; beaked whales, and fin whales have 50–75% fast twitch fibers (see Table 7.2).

With the exception of pilot whales and beaked whales (Velten *et al.*, 2013), fiber types in the primary locomotory muscles of diving mammals and birds are not unusual in comparison to non-diving species (Table 7.2). In slow-swimming beaked whales, the epaxial muscles had high myoglobin content, but had only 20% slow twitch oxidative fibers of small fiber diameter that were uniformly distributed among the more numerous large-diameter, fast twitch fibers with high glycolytic capacity (Velten *et al.*, 2013). The authors postulated that the slow twitch fibers provided routine stroke power and that these fibers utilized their own myoglobin-bound oxygen as well as that from the uniformly distributed surrounding fast twitch fibers. They also hypothesized that the 80% fast twitch fibers were utilized (a) during faster stroking rates and (b) after the myoglobin-bound oxygen depot was exhausted. The authors postulated that larger-diameter fibers allowed for relatively less metabolic demand due to a lower surface-to-volume relationship, fewer membrane ion pumps, and an overall slower muscle metabolic rate.

**Table 7.2** Muscle fiber type distribution in muscles of marine mammals and diving birds.

| Species | Muscle | %SO | %FT | %FOG | %FG | Reference |
|---|---|---|---|---|---|---|
| **Dolphins**<br>(3 species) | Longissimus dorsi | ~50 | ~50 | | | A |
| **Narwhal**<br>*Monodon monoceros* | Longissimus dorsi | 79 | 21 | | | B |
| **Pilot whale**<br>*Globicephala macrorhynchus* | Epaxial muscle | 62 | 38 | | | C |
| **Beaked whales**<br>(*Mesoplodon*, 4 species) | Epaxial muscle | 17–23 | 77–83 | | | C |
| **Pygmy sperm whale**<br>*Kogia breviceps* | Longissimus dorsi | 53 | 47 | | | D |
| **Fin whale**<br>*Balaenoptera physalus* | Longissimus dorsi | 46 | 54 | | | E |
| **Antarctic fur seal**<br>*Arctocephalus gazella* | Pectoralis | 10 | 90 | 28 | 61 | F |
| **California sea lion**<br>*Zalophus californianus* | Neck/shoulder muscle | 44 | 56 | 18 | 38 | G |
| **Grey seal**<br>*Halichoerus grypus* | Longissimus dorsi | 55 | 42 | 6 | 36 | F |
| **Harbor seal**<br>*Phoca vitulina* | Longissimus dorsi | 47 | 53 | 53 | | F, H |
| **Weddell seal**<br>*Leptonychotes weddellii* | Longissimus dorsi | 67 | 33 | 33 | | I |
| **Northern elephant seal**<br>*Mirounga angustirostris* | Longissimus dorsi | 100 | 0 | | | J |
| **Sea otter**<br>*Enhydra lutris* | Gastrocnemius | 56 | 44 | 2 | 42 | G |
| **Tufted duck**<br>*Aythya fuligula* | Gastrocnemius – red | 15 | 85 | 85 | 0 | K |
| | Gastrocnemius – white | 0 | 100 | 46 | 54 | K |
| **Atlantic puffin**<br>*Fratercula arctica* | Pectoralis | 0 | 100 | 100 | | L |
| **Cassin's auklet**<br>*Ptycoramphus aaleuticus* | Pectoralis | 0 | 100 | 100 | | L |
| **Emperor penguin**<br>*Aptenodytes forsteri* | Pectoralis | 0 | 100 | 100 | | M |

References: A: Bello *et al.*, 1985, Ponganis and Pierce, 1978, Suzuki *et al.*, 1983; B: Williams *et al.*, 2011b; C: Velten *et al.*, 2013; D: Kielhorn *et al.*, 2013; E: Hochachka and Foreman, 1993; F: Reed *et al.*, 1994a; G: Ponganis and Pierce, 1978; H: Watson *et al.*, 2003; I: Kanatous *et al.*, 2002; J: Moore *et al.*, 2014; K: Turner and Butler, 1988; L: Kovacs and Meyers, 2000; M: Ponganis *et al.*, 1997a.

The percentage fast twitch fibers are further subdivided into component fiber types where available. Abbreviations: SO: slow twitch oxidative fibers, FT: fast twitch fibers, FOG: fast twitch oxidative, glycolytic fibers, FG: fast twitch glycolytic fibers.

In contrast to the beaked whales, in pilot whales, which exhibit "underwater sprints" with high stroke rates, one-third of fibers were fast twitch, and two-thirds slow twitch, of which half were slow twitch oxidative fibers and half were a unique fiber type – slow twitch oxidative and glycolytic (Velten *et al.*, 2013). Fiber diameters were not enlarged as in the beaked whales. The authors postulated that slow twitch fibers were utilized for routine swimming, and that the fast twitch and more glycolytic fibers were for underwater sprints. And, of course, glycolysis was also possible in both fiber types when myoglobin-oxygen stores were depleted.

Among birds, the 100% FOG fiber composition of pectoral muscle in wing-propelled divers is characteristic of birds with flapping flight (Butler, 1991). Similarly, the fiber type distribution of the central, white portion of the gastrocnemius muscle and the lateral, red portion of that muscle in the legs of tufted ducks are also characteristic of other birds (Butler, 1991, Turner and Butler, 1988). However, differences in fiber type distribution can be associated with different locomotory patterns. For example, in contrast to a hummingbird or finch, which have 100% FOG fibers in their flight muscles, the pelican and albatross also have SO fibers in addition to FOG fibers (Meyers and Stakebake, 2005, Rosser *et al.*, 1994, Welch Jr. and Altshuler, 2009). The slow twitch fibers are considered to help maintain wing position during soaring of the pelican and albatross.

It is also worth noting that different distributions of fast twitch fibers into FOG fibers and FG fibers have been reported in harbor seal muscle (47% FG vs no FG fibers) (Reed *et al.*, 1994a, Watson *et al.*, 2003). Both studies, however, found the same proportion of total FT fibers (53%). This difference may, in part, be due to differences in histochemical staining techniques, and the probable range of oxidative capacities within FOG fibers. The earlier work utilized a myofibrillar ATPase stain dependent on acid/alkaline inhibition of ATPase isoforms in combination with serial oxidative enzyme stains, which allowed assessment of oxidative capacity based on subjective interpretation of the relative stain intensity. The latter study relied on immunohistochemical stains for the different myosin heavy chains, and therefore was specific for the contractile properties of the fibers (i.e., there were Type IIa, but not Type IIb fibers in the harbor seal). The fiber-specific oxidative and glycolytic capacities of those Type IIa fibers were not independently measured, but were assumed to be high (i.e., a FOG fiber) on the basis of enzyme activities in whole-muscle homogenates and on fiber type-specific findings in other species. These findings raise the issue of whether the terms, I, IIa, and IIb, should be used interchangeably with SO, FOG, and FG, especially in species in which characterization of individual fiber contractile properties and oxidative/glycolytic capacities have not been conducted. This issue was again exemplified in Weddell seal muscle (Kanatous *et al.*, 2002). By immunohistochemistry, 67% of fibers were Type I, and 33% Type IIa; there were no Type IIb fibers. By classic fiber type terminology, the Type I fibers would correspond to SO fibers, and Type IIa fibers to FOG fibers. One would predict high oxidative capacities in the muscle. Yet, muscle mitochondrial density and citrate synthase activities, both indices of oxidative capacity, were low in Weddell seal muscle, presumably as an adaptation for low aerobic metabolic rates during hypoxic conditions (Kanatous *et al.*, 2002). Therefore, readers must remember the complexities and limitations of fiber-typing techniques in interpretation of fiber type composition, especially in relatively exotic, non-standard species such as marine mammals and seabirds.

## 7.2 Muscle enzyme activities, energy substrates, and mitochondria

The oxidative and glycolytic enzyme activities measured in the muscles of these diving animals are consistent with the large percentages of oxidative fibers (SO and FOG) in their muscles, and, in general, are characteristic of non-divers (Baldwin, 1988, Baldwin *et al.*, 1984, Blix and From, 1971, Blix *et al.*, 1970, Butler, 1991, Castellini and Somero, 1981, Castellini *et al.*, 1981, Davis and Guderley, 1987, 1990, Hochachka and Foreman, 1993, Kanatous *et al.*, 1999, 2002, 2008, Mill and Baldwin, 1983, Polasek *et al.*, 2006, Ponganis and Pierce, 1978, Ponganis *et al.*, 1997a, Reed *et al.*, 1994a, Turner and Butler, 1988).

The findings of normal glycolytic enzyme activities in these animals contrasts with earlier views that an enhanced glycolytic capacity underlied the diving abilities of marine mammals (George and Ronald, 1973, Simon *et al.*, 1974, Storey and Hochachka, 1974). It was even postulated that anaerobic pathways generating succinate and alanine contributed to diving ability (Hochachka *et al.*, 1975). Subsequent studies with documentation of non-elevated glycolytic enzyme activities in multiple tissues as well as demonstration of a lack of elevation of alanine in blood of diving seals (Castellini *et al.*, 1981, Guppy *et al.*, 1986) did not support these views.

This is not to say that glycolysis does not play a role in diving, but muscle of non-diving animals is already well-adapted for anaerobic energy production via glycolysis (Zierath and Hawley, 2004); hence, the lack of further elevation of glycolytic enzyme activities. Skeletal muscle glycogen concentrations are also not elevated (Groscolas, 1990, Kerem *et al.*, 1973, Williams *et al.*, 2012). However, there is enhanced buffering capacity in muscle of most marine mammals, up to 60% greater than terrestrial controls (Castellini and Somero, 1981, Lestyk *et al.*, 2009, Noren, 2004). Buffering capacity is also elevated in most penguin species, but in puffins and murres it lies between values for pigeons and pheasants (Castellini and Somero, 1981, Davis and Guderley, 1990, Mill and Baldwin, 1983). This buffering is considered secondary to histidine-containing dipeptides in the sarcoplasm (Castellini and Somero, 1981, Crush, 1970, Harris *et al.*, 1990), and it undoubtedly contributes to a more stable intracellular pH, especially during long dives.

Lastly, in regard to anaerobic energy sources, phosphocreatine concentrations are also not elevated in diving mammals and birds (Blix, 1971, Stephenson and Jones, 1992b, Stephenson *et al.*, 1997, Williams *et al.*, 2012). It is notable that despite the high myoglobin concentration in emperor penguin muscle (see Chapter 4), the "normal" glycogen and phosphocreatine stores of the emperor penguin can provide about six times more ATP than the myoglobin-bound $O_2$ (Williams *et al.*, 2012). However, due to the low metabolic rate of muscle during diving of emperor penguins, significant glycolysis and post-dive wash-out of lactate do not occur until after dives of about 6-min duration (Ponganis *et al.*, 1997b). In addition, after an 11-min dive with no muscle blood flow, it has been estimated that phosphocreatine would be only 56% depleted, and muscle glycogen less than 10% depleted (Williams *et al.*, 2012). Thus, there appears to be a large anaerobic energy reserve in emperor penguin muscle even without elevations in glycolytic enzyme activities, glycogen content, or phosphocreatine concentrations. The same argument has also been applied to Weddell seal muscle (Butler and Jones, 1997).

Muscle oxidative capacity has been assessed with examination of both enzyme activities and mitochondrial volume densities. It is notable that citrate synthase activity and mitochondrial volume densities were elevated in the upper mammalian range in two smaller pinnipeds (harbor seal, northern fur seal) and in the intermediate-sized Steller sea lion (Kanatous *et al.*, 1999, Watson *et al.*, 2007). However, in the Weddell seal, neither of these parameters were increased (Kanatous *et al.*, 2002, 2008). Differences may be secondary to a lower rate of energy demand in the Weddell seal, a larger, slower-stroking, longer-duration diver. Relatively low citrate synthase activities were also reported in two other large phocids, crabeater seals and leopard seals (Hochachka and Foreman, 1993). This latter reference also emphasized that higher pyruvate kinase/lactate dehydrogenase ratios favored pyruvate oxidation in large phocids, whereas lower ratios in dolphins and fin whales favored glycolysis (Hochachka and Foreman, 1993).

Remarkable among all the pinnipeds examined, however, is the relatively high activity of hydroxylacyl-CoA dehydrogenase, a key enzyme in fatty acid oxidation (Kanatous *et al.*, 1999, 2002, Polasek *et al.*, 2006, Reed *et al.*, 1994a). This enzyme pattern is consistent with the high free fatty acid turnover rate in flume-swimming seals (Davis *et al.*, 1991). In addition, muscle mitochondria from adult elephant seals demonstrated enhanced fatty acid utilization over pyruvate and increased phosphorylation control (Chicco *et al.*, 2014). Thus, these animals appear geared toward fat metabolism. Increased numbers of intramuscular lipid droplets have also been reported in several species of marine mammals (Kanatous *et al.*, 1999, 2002, Tulsi, 1975, Watson *et al.*, 2007), and in slow twitch versus fast twitch fibers of beaked whales (Velten *et al.*, 2013). Intramuscular triglycerides may serve as an important free fatty acid source because both the ischemia of diving (Chapter 5) and the relatively low capillary density in marine mammal muscle would decrease the potential for delivery of blood-borne fatty acids to muscle during dives (Kanatous *et al.*, 2001, 2002, Reed *et al.*, 1994a).

Much less is known about the potential for fatty acid metabolism in diving birds. In the tufted duck, capillarity of the leg muscle fibers is 70–80% that of the pectoralis (Turner and Butler, 1988), but, as reviewed in Chapter 5, most of the cardiac output during diving is delivered to the leg musculature. The ratio of hydroxyacyl-CoA dehydrogenase to citrate synthase in the leg is similar to that in pectoral muscle, indicating similar propensity for fatty acid oxidation in the two muscles (Turner and Butler, 1988). In emperor penguins, the density of lipid droplets in the pectoral muscle was about three times that in the leg muscles (Ponganis *et al.*, 1997a).

Another ultrastructural observation on muscle mitochondria in marine mammals is that most of the mitochondria (greater than 80%) are interfibrillar (Kanatous *et al.*, 1999, 2002, Velten *et al.*, 2013, Watson *et al.*, 2007). In contrast, 20% or more of mitochondria are subsarcolemmal in terrestrial mammals. The authors have proposed that the increased mitochondrial volume and interfibrillar distribution of mitochondria increase mitochondrial surface area and decrease distances for diffusion of $O_2$ from myoglobin, thus maintaining aerobic metabolism under hypoxic conditions. High mitochondrial volumes and homogeneous mitochondrial distributions have also been found in the liver, kidneys, and stomach of seals, which the authors again propose supports aerobic metabolism under hypoxic conditions (Fuson *et al.*, 2003). In diving birds, much less is known about mitochondrial distribution, although 75–90% of mitochondria were interfibrillar in both the chest and leg muscles of emperor penguins (Ponganis *et al.*, 1997a).

The potential role of hypometabolism in prolongation of muscle function during periods of hypoxia and ischemia (low or no blood flow) has been considered since the forced submersion experiments of Scholander (Scholander, 1940, Scholander *et al.*, 1942a). Oxygen consumption of muscle does decrease during muscle ischemia in many mammals (Duran and Renkin, 1974, Gutierrez *et al.*, 1988, Mizuno *et al.*, 2003). Such a decrease in muscle oxygen consumption may account for the maintenance of myoglobin oxygen saturation during sleep apnea of seals despite a calculated decrease in muscle $O_2$ extraction (Ponganis *et al.*, 2008).

Hypothermia and various hypoxia-linked mechanisms (ion channel arrest, a reversed Pasteur effect (lack of increased glucose consumption and lactate production during hypoxia), and decreased protein synthesis; see Chapter 8) have been proposed to decrease metabolic rate in muscle of diving mammals and birds (Butler, 2004, Hochachka, 1988, Hochachka and Guppy, 1987, Scholander *et al.*, 1942b). These hypoxia-linked mechanisms of metabolic suppression have been documented extensively in turtle tissues and, to some extent, in seal hepatocytes (Hochachka and Lutz, 2001, Hochachka *et al.*, 1988). However, as regards hypothermia, muscle temperature remained near 37 °C or even increased during dives in free-diving Weddell seals, emperor penguins, and king penguins (Ponganis *et al.*, 1993b, 2003b, Schmidt *et al.*, 2006). In regard to metabolic suppression, the muscle ATP turnover rate did not decline during forced submersion of ducks, but was maintained through depletion of myoglobin-bound oxygen, and breakdown of phosphocreatine and glycolysis (Stephenson and Jones, 1992b). In addition, the contribution of phosphocreatine breakdown could account for the energetic shortfall calculated in Scholander's forced submersion experiments (Kooyman and Ponganis, 1998). Thus, there is still no evidence of a unique mechanism of metabolic suppression in muscle of marine mammals and diving birds.

After reviewing all these investigations into muscle fiber type distribution, enzymes activities, energy substrate concentrations, buffering capacities, and mitochondrial distributions, the most consistent, outstanding feature of muscle in divers is the elevation of myoglobin concentration (Chapter 4). By far, the increase in myoglobin content is the predominant adaptation in the muscle of diving mammals and birds. The duration of aerobic metabolism in muscle is extended not only by that increase in myoglobin concentration, but also by a low muscle metabolic rate, which is due to the low energy cost of underwater locomotion in these animals.

## 7.3

## Locomotory work

In contrast to a terrestrial mammal, which works primarily against gravity during locomotion, a marine mammal or deep-diving seabird primarily works against drag (resistance in water to movement) (Williams, 1999). In this respect, the cost of underwater locomotion is potentially increased because the density and viscosity of water are 800 and 60 times greater than those values in air, respectively (Dejours, 1987). Thus, efficient locomotion is essential to the success of diving mammals and birds. Minimization of the cost of underwater locomotion is achieved through several mechanisms. Perhaps most significant is hydrodynamic design and drag reduction. Other cost-saving measures include stroke and glide locomotory patterns, and utilization of buoyancy changes to decrease stroke effort.

### 7.3.1 Hydrodynamics and drag

The hydrodynamics of diving mammals and birds are based on their streamlined body shapes and the consequent reduction in drag. Excellent articles and reviews on hydrodynamics are available for cetaceans (Fish, 1994, Fish and Hui, 1991, Fish *et al.*, 2008), pinnipeds (Feldkamp, 1987b, Stelle *et al.*, 2000, Williams and Kooyman, 1985), sea otters (Williams, 1989), and diving birds (Lovvorn and Liggins, 2002, Lovvorn *et al.*, 2001). Readers with particular interest in hydrodynamics are referred to these citations.

Key components of body design relative to hydrodynamics include a fusiform shape, the location of maximum width relative to body length, and the design of limb appendages. These factors contribute to drag reduction through maintenance of a boundary layer (a layer of water extending from the body surface to a point at which it is moving at 99% of full speed; see Fish and Hui, 1991 for full details). Flow in the boundary layer may either be laminar (thereby reducing the frictional component of drag), turbulent (which is more stable, causing boundary layer separation to occur further down the length of the body and decreasing the size of the pressure wake, thus decreasing the pressure component of drag), or transitional (Fish, 1994).

Flow properties within the boundary layer vary according to the non-dimensional Reynolds number ($R_e$). $R_e = vl\rho/\mu$, where $v$ is swim speed, $l$ is body length, $\rho$ is water density, and $\mu$ is water viscosity (Webb, 1988). Boundary flow is laminar, turbulent or transitional at $R_e < 5 \times 10^5$, $> 5 \times 10^6$, or between those two values, respectively (Fish, 1994). As of 2008, there was still no conclusive evidence that laminar flow occurs in the boundary layer of dolphins (Fish *et al.*, 2008). Therefore, as emphasized by those authors, it is the maintenance of a boundary layer over as much of the body length as possible, and not necessarily laminar flow, which contributes most to drag reduction.

The fineness ratio (ratio of body length to maximum width) serves as an index of the fusiform shape; a value of 4.5 has been considered optimal in that it represents maximal volume, minimum surface area, and, thus, the lowest drag for a given volume. However, optimal fineness ratios and drag reduction may vary with swim speed, swim style and body size; most values of fineness ratios in marine mammals have ranged between 3 and 8 (Fish *et al.*, 2008). It has been proposed that a fineness ratio of 6.3 contributes to the ability of spinner dolphins (*Stenella longirostris*) to perform their aerial spins (Fish *et al.*, 2006).

The location of maximum width along body length (usually the shoulder) is also important because it is at this point that laminar flow is most likely to become turbulent, or where boundary layer separation will occur. The shoulder occurs at 35–40%, 40%, and 50–60% of body length from the tip of the rostrum or nose in cetaceans, otariids, and phocids, respectively (Fish *et al.*, 2008). The appendages, the movement of which has been estimated to contribute to 28% of drag in a dolphin (Lang and Pryor, 1966), are also streamlined, promoting maintenance of a boundary layer over their surface. One of the most remarkable appendage modifications are the foreflippers of the humpback whale. The tubercles along the scalloped leading edge of the flipper contribute to increased lift and prevention or delay of stall during high-speed underwater turns (Fish and Lauder, 2006, Fish *et al.*, 2008).

Lastly, the bare skin of cetaceans and the hair properties (flat fur pelage) of other marine mammals also contribute to streamlining (Fish *et al.*, 2008). However, drag reduction through turbulence dampening by dolphin skin properties has never been demonstrated (Fish and Hui, 1991). Presumably the flat feather layer of penguins also contributes to streamlining. Notably, it has been recently proposed that release of air microbubbles from the feather layer of penguins contributes to a reduction in drag during high-speed exits onto sea ice (Davenport *et al.*, 2011).

Drag is proportional to body size and swim speed, and its relationship to these and other parameters is determined by the drag equation: $D = \frac{1}{2}(\rho v^2 A)C_D$, where D is drag, $\rho$ is density of the fluid, $v$ is swim speed, $A$ is the reference area, and $C_D$ is the drag coefficient, a dimensionless constant related to the body geometry and flow around it. Because of this relationship, drag is proportional to body size and it increases curvilinearly with swim speed. Drag force can be measured by towing frozen carcasses, models, or even trained, live animals, or it can be calculated from deceleration rates of gliding animals (Feldkamp, 1987b, Lovvorn and Liggins, 2002, Lovvorn *et al.*, 2001, Williams and Kooyman, 1985).

Two additional features of drag are especially relevant to diving. First, the drag of an object at the surface is greater than that at depth due to the creation of wave drag at the surface (Fish, 1994, Williams and Kooyman, 1985). Drag of a towed harbor seal was 2.5 times greater at the surface than at depth (Williams and Kooyman, 1985). At depth, the sea otter can swim at higher speeds and with up to 41% less oxygen consumption than at the surface (Williams, 1989). And, in penguins, oxygen consumption during submerged swimming is less than that during surface swimming (Hui, 1988b). Thus, the metabolic demand and physiological responses of an animal swimming at the surface in a flume may be quite different from those of an animal during a dive. Second, drag measurements are usually determined when an animal is gliding. Drag during the stroking phase of locomotion is increased due to resistance against the propulsive limbs and early disruption of the boundary layer (Fish, 1994, Williams and Kooyman, 1985). In the swimming harbor seal, it was estimated that drag increased nearly two-fold during the stroke phase versus the glide phase of swimming (Williams and Kooyman, 1985). Drag also increased three-fold during the stroke phase of the cormorant (Ribak *et al.*, 2005a). Hence, the advantage of a stroke–glide pattern of swimming and the importance of the design and thrust development of locomotory appendages.

The design and function of locomotory appendages in the production of thrust in diving mammals and birds have been examined in multiple species and described in several reviews (Feldkamp, 1987a, 1987b, Fish, 1994, 1998, Fish and Lauder, 2006, Fish *et al.*, 1988, 2006, 2008). A recent novel analysis and thorough review of thrust production in the dolphin is highly recommended (Fish *et al.*, 2014).

The cetacean tail fluke acts as a flexible hydrofoil and has propulsive efficiencies (0.75 to 0.90 in different species), which are greater than those (<0.70) of propellers of commercial ships (Fish *et al.*, 2008). Further increasing the efficiency of locomotion in the dolphin are (a) the anatomical levering by long spinous and transverse processes and chevron bones on their vertebrae, and (b) the attachment of epaxial muscles to a subdermal connective tissue sheath, allowing transmission of force to caudal vertebrae (Fish and Hui, 1991, Pabst, 1990, 1993, Pabst *et al.*, 1999).

The hind flippers of seals also act as hydrofoils (Fish *et al.*, 1988). In the sea lion, due to the design of the foreflipper and anatomy of the shoulder, the foreflipper acts as both a hydrofoil and a paddle, generating thrust in all phases of the stroke cycle (English, 1976, 1977, Feldkamp, 1987a). Penguins, guillemots, and puffins fly through water with their wings acting as hydrofoils with thrust production in both phases of the stroke (Clark and Bemis, 1979, Hui, 1988a, Johansson and Aldrin, 2002, Lovvorn *et al.*, 2004). In foot-propelled avian divers such as grebes and cormorants, the motion of the webbed feet is considered to transit from drag-based to lift-based propulsion throughout the stroke cycle (Johansson and Lindhe Norberg, 2001, Johansson and Norberg, 2003, Ribak *et al.*, 2004). The power output of a stroke in all these animals is also potentially affected by the amplitude and velocity of the stroke as well as the angle of attack of the appendage.

Lastly, the behavior of an animal during a dive may also affect drag. An excellent example is the lunge feeding of rorqual whales. Although these animals have a streamlined body shape, feeding involves opening the mouth to about 80°, engulfment of a large mass of water, distention of the buccal cavity, and creation of an "engulfment" drag as water is pushed forward in the mouth (Goldbogen *et al.*, 2011, Potvin *et al.*, 2009). This engulfment drag forms about 90% of the increase in drag during the mouth-opening phase. The increased drag and cost of lunge feeding is thought to limit the dive durations of these large whales (Croll *et al.*, 2001, Goldbogen *et al.*, 2007, 2008, 2011, 2012, Simon *et al.*, 2012).

### 7.3.2 Locomotory patterns and costs

The basic locomotory pattern of all diving mammals and seabirds is a stroke and glide pattern (Clark and Bemis, 1979, Johansson and Aldrin, 2002, Johansson and Lindhe Norberg, 2001, Johansson and Norberg, 2003, Lovvorn, 2001, Lovvorn *et al.*, 1999, 2001, 2004, Miller *et al.*, 2004b , Ribak *et al.*, 2004, 2005a, Sato *et al.*, 2003, van Dam *et al.*, 2002, Watanuki *et al.*, 2003, 2005, 2006, Williams, 1989, 2001, Williams *et al.*, 2000, Williams *et al.*, 2012, Wilson and Liebsch, 2003). As reviewed earlier in this chapter, this pattern of locomotion is optimal in that there is decreased drag during the glide phase. Although the thrust and amplitude of a stroke have not been examined as closely as stroke rate in these divers, it appears that change in stroke rate primarily contributes to changes in propulsive effort and swim speed.

Stroke rates vary considerably during diving and among divers and are probably governed by (a) minimization of drag (body size, drag coefficient, swim velocity), (b) swim speed requirements for prey pursuit, and (c) buoyancy (see references in prior paragraph). During diving, changes in buoyancy secondary to air volume compression play a particularly significant role in determination of the rate and pattern of stroking (Enstipp *et al.*, 2006, Lovvorn *et al.*, 1991, Lovvorn *et al.*, 1999, 2004, Skrovan *et al.*, 1999, Watanuki and Sato, 2008, Watanuki *et al.*, 2003, 2005, 2006, Williams, 2001, Williams *et al.*, 2000, Wilson *et al.*, 2010).

Stroke rates are usually highest at the start of a dive when the animal is most shallow and air spaces are least compressed. As the animal descends, air volume in the respiratory system and the air layer in the outer pelage (if present, as in birds, fur seals, sea otters) are compressed and buoyancy decreases. The decrease in buoyancy allows many animals to either decrease stroke rate or begin prolonged gliding during descent. For example, in deep dives of elephant seals, Weddell seals, and dolphins, glides began at a mean depth of 86 m and comprised 80% of descent time (Williams *et al.*, 2000). In blue whales, prolonged glides began at 18-m depth (Williams *et al.*, 2000). Prolonged gliding during descent has not been observed in diving birds, although most species decrease their stroke rate below 20-m depth (Watanuki *et al.*, 2006, Wilson *et al.*, 2010). Another species which does not glide during descent is the right whale (*Eubalaena glacialis*), which is especially buoyant due to its large percentage fat composition (Nowacek *et al.*, 2001).

During ascent, however, most species must increase stroke rate and even stroke amplitude to overcome negative buoyancy at depth (Williams, 2001). As air within the body re-expands later during ascent, many animals can again take advantage of increased buoyancy to decrease stroke rate and eventually glide to the surface during the final phases of the dive (Nowacek *et al.*, 2001, Sato *et al.*, 2002, 2011, Watanuki and Sato, 2008, Watanuki *et al.*, 2006, Williams, 2001, Williams *et al.*, 2012, Wilson *et al.*, 2010). In shallow-diving cormorants, the entire ascent is a passive glide (Kato *et al.*, 2006, Watanuki *et al.*, 2005).

Prolonged gliding and lower stroke rates secondary to buoyancy changes in diving animals translate into lower metabolic costs and potentially into lower rates of oxygen store depletion. For equidistant dives of Weddell seals, deep dives with prolonged gliding had 35% less recovery oxygen consumption in comparison to shallow dives with continuous stroking (Williams, 2001, Williams *et al.*, 2000). Thus, decreased buoyancy secondary to air compression provides an advantage to deeper divers. During the long foraging trips of pregnant elephant seals, increased body weight and fat deposition throughout the trip resulted in the achievement of neutral buoyancy, with decreased stroke rates, more ascent glide time, and increased bottom time during dives (Adachi *et al.*, 2014). In comparison to negative buoyancy, neutral buoyancy may result in decreased locomotory effort and metabolic rate, thus contributing to the long-duration dives of these seals.

The increased buoyancy of a flying bird versus that of a neutrally buoyant penguin may also account for lower metabolic costs of penguins even during shallow dives (Butler and Woakes, 1984, Culik *et al.*, 1991, 1994, Schmid *et al.*, 1995). This is especially evident in shallow-diving ducks, in which oxygen costs are 21% greater than that of ducks surface swimming at maximum speed; most of that work is to overcome buoyancy (Butler, 2000, Lovvorn and Jones, 1991, Lovvorn *et al.*, 1991, Stephenson, 1993, 1994, 1995, Stephenson *et al.*, 1989a, Woakes and Butler, 1983). Decreased buoyancy may be achieved by reduced plumage air in deeper diving, flighted birds (Wilson *et al.*, 1992b), as well as by differences in the pneumatization of bones in 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).