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SWIMMING PERFORMANCE AND HYDRODYNAMIC CHARACTERISTICS OF HARBOR SEALS PHOCA VITULINA[1]

T. M. WILLIAMS[2] AND G. L. KOOYMAN

Physiological Research Laboratory, Scripps Institution of Oceanography, University of California,
San Diego, La Jolla, California 92093
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Hydrodynamic characteristics, including fineness ratios, coefficients of drag, and the influence of body size, shape, and position on drag were examined for harbor seals (*Phoca vitulina*). Drag for towing animals increased curvilinearly with velocity over the range 0.7 to 3.5 $m \cdot s^{-1}$ and was described by the equations: $Drag(N) = 6.49$ velocity $(m \cdot s^{-1})^{1.79}$ for a submerged adult seal, and $Drag(N) = 1.29$ $e^{1.9 \text{ velocity } (m \cdot s^{-1})}$ for the seal towing at the water surface. The importance of streamlining was demonstrated by comparing these values with those of a towing human subject. At 2.0 $m \cdot s^{-1}$ drag for a submerged human was 113 N, representing a 5.0-fold and a 1.9-fold increase in drag over submerged and surface towing seals, respectively. Coefficients of drag (*Cd*) followed this trend and were three times greater for the human subject. Alterations in body configuration of the seals, as occurs during stroking movements, resulted in an increase in body drag. From our calculations, body drag during gliding phases may more than double during active swimming by seals and influences the swimming performance of these animals.

INTRODUCTION

Aquatic activity by pinnipeds is aided by a streamlined body shape that reduces both resistance (drag) in the water and the power output needed for forward motion. Despite many reports concerning the hydrodynamic properties of small fish (Gray 1968; Webb 1975), little has been known about the streamlining and hydrodynamics of large aquatic vertebrates until recently. Drag measurements of gliding penguins and porpoises allude to the importance of body design for movement through the water. The drag coefficient (*Cd*) for a solid body, such as the emperor penguin (*Ap-*

tenodytes forsteri), is less than half the lowest values presented for fish at comparable Reynolds numbers (Clark and Bemis 1979). Furthermore, gentoo penguins (*Pygoscelis papua*) achieve lower frontal drag coefficients (*Cdf*) than any designed vehicle (Nachtigall and Bilo 1980). In a series of papers, Lang (Lang 1963, 1966, 1974) investigated the hydrodynamic properties of three species of porpoises. These studies have demonstrated that (1) the *Cd* of a gliding porpoise is equivalent to a rigid body with a near-turbulent boundary layer, (2) there are no unusually low drag characteristics for the porpoise in comparison to other streamlined bodies such as penguins, and (3) the maximum power output per body weight may exceed humans' by as much as 2.5 times (Lang 1974).

Even less information is available regarding the hydrodynamic properties of pinnipeds. Only descriptive texts concerning the seal's body form and propulsion methods (Mordvinov 1968, 1972) and the damping role of fur on body drag in seals (Mordvinov and Kurbatov 1972) provide a few limited insights. With this in mind, in the present study we examined a variety of hydrodynamic characteristics in the harbor seal (*Phoca vitulina*). Total body drag and the effects of body size, shape,

and position relative to the water surface were investigated. Drag measurements were obtained at various controlled velocities using trained seals and avoided problems inherent with using rigid models. Indices of swimming performance included top swimming speed, preferred glide speeds, and maximum thrusting power measured for the same animals. In addition, some of the major areas of turbulence on the seal were qualitatively assessed by videotaping a seal swimming through bioluminescent water. To obtain a better appreciation of the adaptations of seals for aquatic performance, total body drag and maximum thrust were determined for a human subject using identical methods. The results of this study permit an examination of the variability of hydrodynamic properties, performance capabilities, and optimum swimming speeds of seals.

MATERIAL AND METHODS

ANIMALS

Swimming ability and hydrodynamic characteristics were determined on one adult and one immature male harbor seal (*Phoca vitulina*). The adult seal (S1) was a captive-raised animal taken from Cold Bay, Alaska, as a suckling pup. At the time of the study this animal was 8 yr old and weighed 70–90 kg. Total body length of S1 was determined from the gliding configuration of the seal by means of photogrammetry after the method of Van Sciver (1972) (fig. 1*A*). Length measurements were also made by marking nose and flipper tip positions of the seal in a resting posture signaled by a trainer. Body lengths from the two different methods agreed to within 2%. S2 was an immature, 27-kg harbor seal originally rescued, as an orphaned pup, from a San Diego beach. Body length of S2 was determined in a similar manner to S1. The human subject (SF) was a 25-yr-old, athletic male, chosen for his similarity in body weight to S1.

SWIMMING PERFORMANCE

Top swimming speed of the adult seal was determined by training the animal to leap toward a target suspended over the water. The seal swam a prescribed course approximately 10 m long requiring an average of 2.5 s to traverse from a resting start. Over a period of several months, the height of the target was progressively raised until the limits of the animal were reached. At this maximum height, the underwater velocity of the animal prior to the upward turn preceding the leap was taped with an underwater video camera (RCA TC2000 and 8-mm lens). The camera was centrally positioned 4.3 m from an underwater grid. The distance of the seal from the camera was determined using a second grid pattern on the bottom of the tank. Relative grid length was calculated by correcting for the distance of the swimming path of the seal from the camera. Swimming velocity of the seal was then determined by videotaping the run and counting the number of timed cycles that occurred as the animal traversed the grid. A GYYR VTR TV system that cycled at 60 frames $\cdot$ s^{-1} was used for the swimming tests. Cycling rate of the VTR was calibrated by taping the sweep second hand of a clock.

Truth measurements of the seal's speed were made by videotaping the passage of an underwater missile along the swimming path of the seal. Rate of movement of the missile was controlled by a weighted line attached to the missile. As the weighted line descended, four evenly spaced photoelectric cells were tripped and recorded on a Brush 220 strip chart recorder. The rate of passage of the missile determined by the photoelectric cells and by the VTR system agreed to within 5%.

Leap height of the seals, taken as the distance of the center of gravity above water, was recorded simultaneously with the videotaped speed tests. This was accomplished by photographing seals against a grid background during the peak of the leap. Both seal length and center of gravity were determined from the photographs. Treating the seal's body as two differently sized cones, we placed the center of gravity at the point of equal volume between two cones. From these data the velocity of the leap was calculated according to the equation

$$V = \sqrt{2gh_2 - h_1}, \qquad (1)$$

where V = velocity, g = gravity acceleration, h_1 = initial height of the center of

gravity above the water when the flipper tips are at the water surface, and h_2 = maximum height of the center of gravity above the water. Velocity calculations made in this manner were consistently lower than the underwater determinations. Therefore, speeds determined from the underwater videotaped tests are reported exclusively.

BODY DRAG

Drag force was measured over a range of speeds for S1 at a body weight of 85 kg and for S2 at both 27 kg and 33 kg. The animals were passively towed behind a variable speed, electrically driven cart that traveled the perimeter of a ring tank.

Outer and inner tank diameters were 21 m and 14.5 m, respectively. Water depth of the tanks was 3.5 m. The seals were trained to be towed in a gliding body configuration while biting a soft neoprene mouthpiece that conformed to their head profile. Tow duration ranged from 4 to >15 s, with the shortest tow periods occurring at the highest velocities. The animals were towed both on the water surface (fig. 2) and while submerged at a depth of approximately 1 m. This depth represents 2.8 body diameters of the adult seal and, therefore, approximates the three-body diameter depth required for the avoidance of surface drag effects. Recordings were continuously made and drag measurements taken from steady-state drag traces
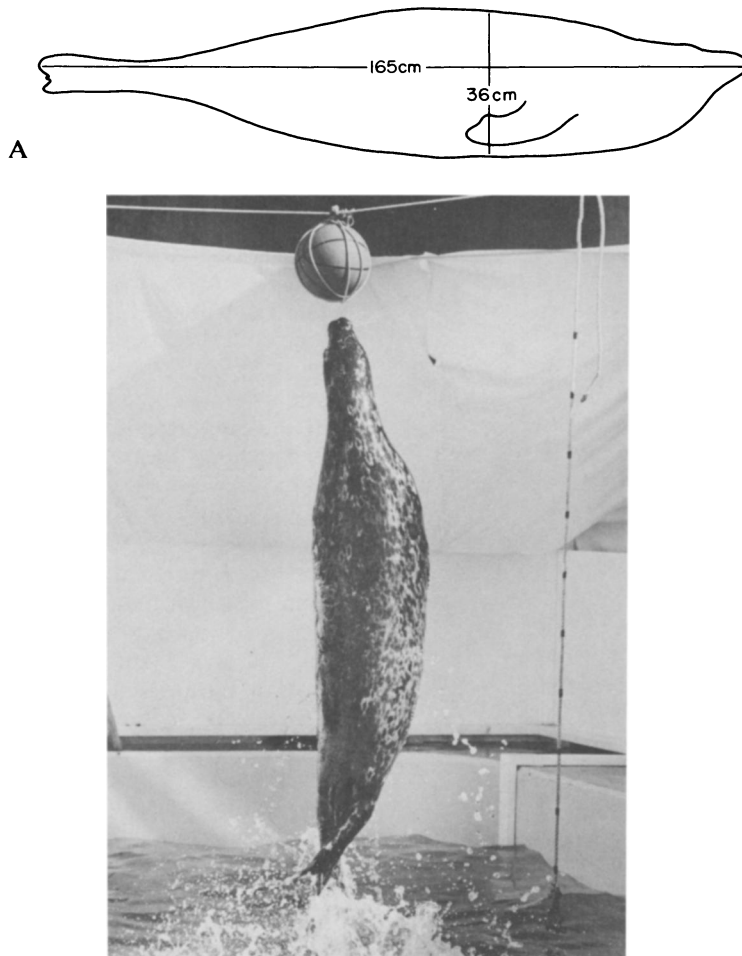

FIG. 1.—A, Outline and physical dimensions of the adult harbor seal as traced from an underwater gliding sequence. B, Body configuration and position of the adult harbor seal during a trained leap.
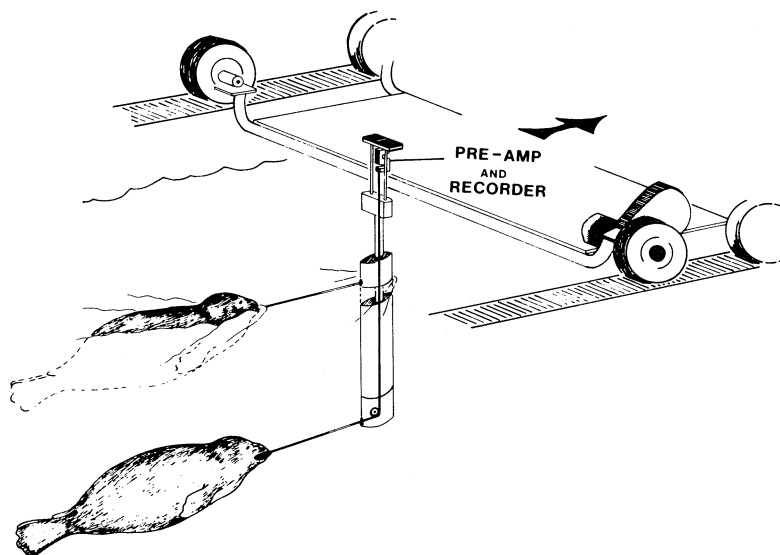
FIG. 2.—Ring tank cart and apparatus used in the determination of total body drag during towing. Measurements were made as the trained seals were towed either on the water surface or submerged. In the latter case a strut was added in order to position the seals approximately 1 m below the water surface.

held for a minimum of 4 s. Flipper movements or changes in body orientation were noted on the trace. Test speeds were varied each day, and no more than 11 individual tows were conducted per session.

Body drag of the towed seals was obtained by measuring resistive forces with a calibrated load cell (Western Scale, Inc.). The shaped mouthpiece was attached to the load cell with a braided nylon towrope. The line was passed over a pulley situated at the level of the animal. Following a 90° turn at the pulley, the line was passed through a 2.5-cm diameter pipe and connected to the end of the load cell. The pulley was housed in a fiberglass strut shaped to reduce water turbulence directly in front of the towing seal. During the submerged towing tests, the fiberglass housing was attached to the bottom of an 89-cm-long metal hydrofoil. Total depth was 100 cm.

Total length of the towline from the pulley to the mouthpiece was approximately 1 m and therefore avoided some of the interfering turbulence created by the strut. Particular care was also taken to permit water turbulence created by the towing animals to subside between tows. Electrical signals from the load cell were recorded on the strip chart recorder (Brush

220) after preamplification (UFI, Inc.). The load cell was calibrated against a hand-held dynamometer (Weigh and Test Systems) prior to each towing session. A correction factor, determined for the dynamometer by calibrating it against known weights, was used to correct the load cell recordings. Force tracings were converted to drag in newtons by multiplying the kilogram force reading by the acceleration of gravity. Drag values of the rope and mouthpiece alone, measured over the range of test speeds, were insignificant. Body drag for the human subject was determined in the identical manner with the exception of the mouthpiece. In this case, the towline was held with both hands. The arms were positioned overhead and the body maintained in a prone position with the head facing the tank floor.

Speed of the cart was determined simultaneously by recording the rotation rate of the outside cart tire. A magnet mounted on the hub of the tire tripped a mercury switch with each complete tire revolution. Each trip was recorded using the second channel of the chart recorder. A correction factor for the speed of the animal was made by noting the position of the towing seal relative to the outside wheel.

TABLE 1

Summary of physical dimensions of harbor seals *Phoca vitulina*

	Seal 1	Seal 2		Human Subjects	
Dimension	8 yr	6 mo	12 mo	SF	PT
Body length (m)	1.65	1.10	1.30	1.72	1.82
Length/diameter (*FR*)	4.6	3.8	4.4	. . .	. . .
Mass (Kg)	85	27	33	75	79
Surface area (m²)	1.20	.67	. . .	1.90[a]	2.00[a]
Frontal area (m²)	.101	.065	.069	. . .	. . .
Flipper area (m²):					
Fore—total of both	.09	.04	.04	. . .	. . .
Hind—part closed (glide)	.09	.07	.05	. . .	. . .
Hind—open	. . .	. . .	.10	. . .	. . .

[a] From Mathews and Fox 1976.

COEFFICIENTS OF DRAG

Drag coefficients were calculated from the force of the towing seals according to the equation

$$Cd = 2D/\rho AV^2, \qquad (2)$$

where ρ = water density, A = surface area, V = velocity, and D = drag force. Variations of this equation presented by Bilo and Nachtigall (1980) were used to calculate coefficients of drag based on body surface area and frontal area of the animal. The body dimensions used to make these calculations (table 1) and other Cd calculations for frontal and total surface area were obtained for the seals from TV images, similar to the method of Nachtigall and Bilo (1980). In this method the profile is divided into a series of thin cross sections. Surface area is calculated assuming that each section is a cylinder. The sum gives total body surface area.

Cd was also determined from deceleration rates during a glide, using the equation

$$D = ma \qquad (3)$$

or

$$D = m(V_1 - V_2)t^{-1}. \qquad (4)$$

While general theory holds that D is proportional to V^2, equation (4) is correct for instantaneous measurements and, in practice, for brief periods of time and small changes in velocity. In this equation D

= force(N), V_1 and V_2 = initial and final velocity (m · s⁻¹), and t = total time from beginning to end of the glide (s). Deceleration measurements were taken as seals glided past stationary markers on the long wall of a rectangular holding tank. The locations of the markers were such that natural glides occurring during routine swimming patterns were videotaped. Two markers 3–5 m apart for S1, and 2 m apart for S2, were placed along the glide path of the seals. Centered on each marker line was a submersible video camera. Each camera was coupled to a GYYR VTR through an RCA image splitter. As the seal approached the first marker, camera 1 transmitted to the whole television screen. When the seal passed from the view of camera 1, the splitter was switched to camera 2, which then transmitted to the entire screen. Together with an observer above water, swimming or gliding patterns of the seal were noted over the entire course. Only runs in which no apparent stroke activity occurred were used to determine the rate of deceleration. Since the total length of each seal was known, V_1 and V_2 could be determined by counting the total number of frames required for the seal to pass from nose to flipper tip past each marker line. Velocity equaled seal length divided by the time for one body length to pass the mark. Accuracy of the measurement was determined by calculating the known distance (L) of the glide from the determined values of total time of glide and the velocity changes:

TABLE 2

SUMMARY OF VELOCITIES FOR A MATURE AND IMMATURE HARBOR SEAL

Seal	Velocity (m·s^{-1})	bl·s^{-1}	Re ($\times 10^6$)[a]
S1:			
Routine	1.4 ± .13 ($n = 24$)	.9	1.9
Peak[b]	4.9[$\bar{X} = 3.9 \pm .46$]($n = 16$)	3.0	6.7
S2:			
Routine	1.9 ± .32 ($n = 10$)	1.7	1.7

[a] $Re = -\dfrac{\rho L V}{\mu} = \dfrac{(1025 \text{ Kg·m}^{-3})\,(L)(V)}{1.232 \text{ Kg·m}^{-1}\text{·s}^{-1} \times 10^{-3}}$ (Vogel 1981).

[b] Peak velocity achieved in a burst, starting from 0 velocity at the surface and ending in a leap 2.6 s later and 8.2 m down the pool.

$$L = V_1 t + \tfrac{1}{2} a t^2, \qquad (5)$$

where V_1 = the initial velocity, t = time interval of the velocity change, and a = deceleration during time t. Using these methods, the calculated L agreed to within 5% of the known L.

THRUST MEASUREMENTS

Thrust generation by the adult seal (S1) was determined by training the seal to swim along a prescribed course with a harness around its neck. The harness was attached by a 5-m line to a calibrated spring scale. Like the towing line used for the drag experiments, the line was situated at the level of the animal and passed through a pulley. Once the line was taut, the animal was encouraged by the trainer to touch a target located directly in front of the animal. In this way maximum thrusting efforts were measured as the animal continued to swim. Care was taken to avoid jerking motions on the line. Similar measurements were made for a human subject (*PT*) wearing the harness across the chest.

BIOLUMINESCENCE

Periodic occurrence of high concentrations of bioluminescent plankton in the seal holding tanks permitted visualization of the flow patterns around the body and flippers of the swimming animals. On these occasions, swimming and towing performances were videotaped using a GYYR VTR TV system and a light-sensitive camera (Cohu). Tapes were analyzed frame by frame and representative sequences traced from the television screen for estimates of boundary layer thickness.

RESULTS

Physical dimensions of the subjects are presented graphically in figure 1*A* and are summarized in table 1. Area measurements included total surface, flipper surface, and maximum frontal area. Fineness ratios (body length/maximum body diameter) ranged from 3.8 for the 6-mo-old seal to 4.6 for the 8-yr-old (S2).

SWIMMING PERFORMANCE

Routine velocities of S1 and S2 were obtained during steady swimming back and forth in a 12-m rectangular pool (table 2). The routine values of 1.4 m·s^{-1} and 1.9 m·s^{-1}, respectively, for S1 and S2 were obtained just as the seals began to glide the length of the tank. In contrast to the upright position of S2, routine swimming by the adult seal was performed in an inverted position less than 1 m from the pool floor. During the glide the velocity declined about 0.2–0.5 m·s^{-1} before the seals began stroking and proceeded to reverse directions.

The peak velocity of 4.9 m·s^{-1} for S1 was obtained after much training and many trial runs (table 2). Top speeds required good technique by the seal, such as a porpoising start near one end of the pool and immediate, vigorous, thrusts of fore and hind flippers throughout the run. Swimming speed from the peak speed
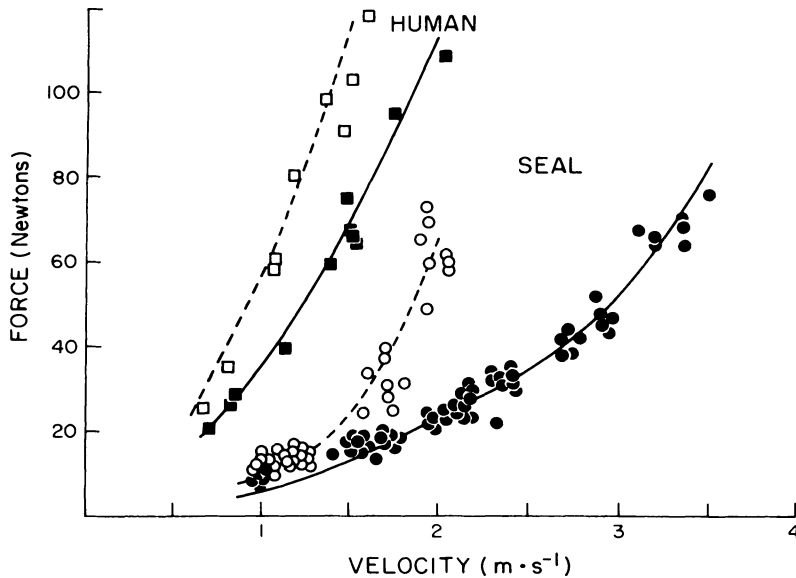
FIG. 3.—Total body drag of the towed adult seal and human subject in relation to velocity. □ = surface tow, human, $y = 55.9x^{1.72}$, corr = 0.99, $n = 9$; ■ = submerged tow, human, $y = 36.3x^{1.64}$, corr = 0.99, $n = 15$; ○ = surface tow, seal; ● = submerged tow, seal. See text for statistics on the seal data. Dashed and solid lines represent the least-squares fit of the data. Each symbol indicates a single towing bout lasting a minimum of 4 s.

trials averaged 3.9 ± 0.46 (SD) m·s^{-1}. At the top speed S1's relative velocity was three body lengths per second (bl·s^{-1}) in comparison to 0.9 bl·s^{-1} at routine velocity. Routine velocity for S2 was 1.7 bl·s^{-1} (table 2).

BODY DRAG

Drag forces obtained while towing S1, S2, and SF increased nonlinearly with speed (figs. 3, 4). Best-fit equations for S1 were

$$\text{Drag}(N) = 6.49 \text{ velocity (m·s}^{-1})^{1.79}$$

$$(\text{corr} = 0.97, n = 94) \quad (6)$$

for submerged drag, and

$$\text{Drag}(N) = 1.29 \; e^{1.9 \text{ velocity (m·s}^{-1})}$$

$$(\text{corr} = 0.96, n = 66) \quad (7)$$

for surface drag in relation to velocity (fig. 3). Over the range of 0.9 to 3.5 m·s^{-1}, body drag of the submerged seal increased from 5.1 to more than 65.0 N. Towing on the surface resulted in a sharper increase

in drag with velocity. At the highest surface tow speed of 2.0 m·s^{-1}, drag was 2.5 times the submerged value at the identical speed.

Submerged and surface drag of the human subject (SF) showed similar trends with speed as found for the seals. At all comparable speeds the surface drag of SF was greater than submerged drag as well as considerably greater than both surface and submerged drag of the adult harbor seal. For example, at 2.0 m·s^{-1}, SF submerged drag was 113 N. This was 5.0 times the value for the submerged seal drag and 1.9 times the drag of the seal towing on the water surface at this speed.

Submerged drag was also affected by the size of the seal (fig. 4A). Over the overlapping test range of 1.0–2.8 m·s^{-1}, drag was consistently greater for the larger seal, with the greatest differences observed at the highest tow speeds. These differences are seen both for an individual animal at two body weights and when comparing adult and juvenile animals. However, if scaled on a mass-specific basis, the drag of the larger, adult animal is lower than

for the smaller seal (fig. 4B), and differences between the different-sized seals are reduced.

COEFFICIENTS OF DRAG

Drag coefficients for frontal area and surface area during glides are presented in the upper portion of table 3. The average glide speed was 1.2 $m \cdot s^{-1}$ and 1.8 $m \cdot s^{-1}$ for S1 and S2, respectively. At these velocities, the concurrent drag forces were calculated to be 6.6 N for S1 and 4.1 N for S2. Drag coefficients based on surface area and frontal area were determined

A

B
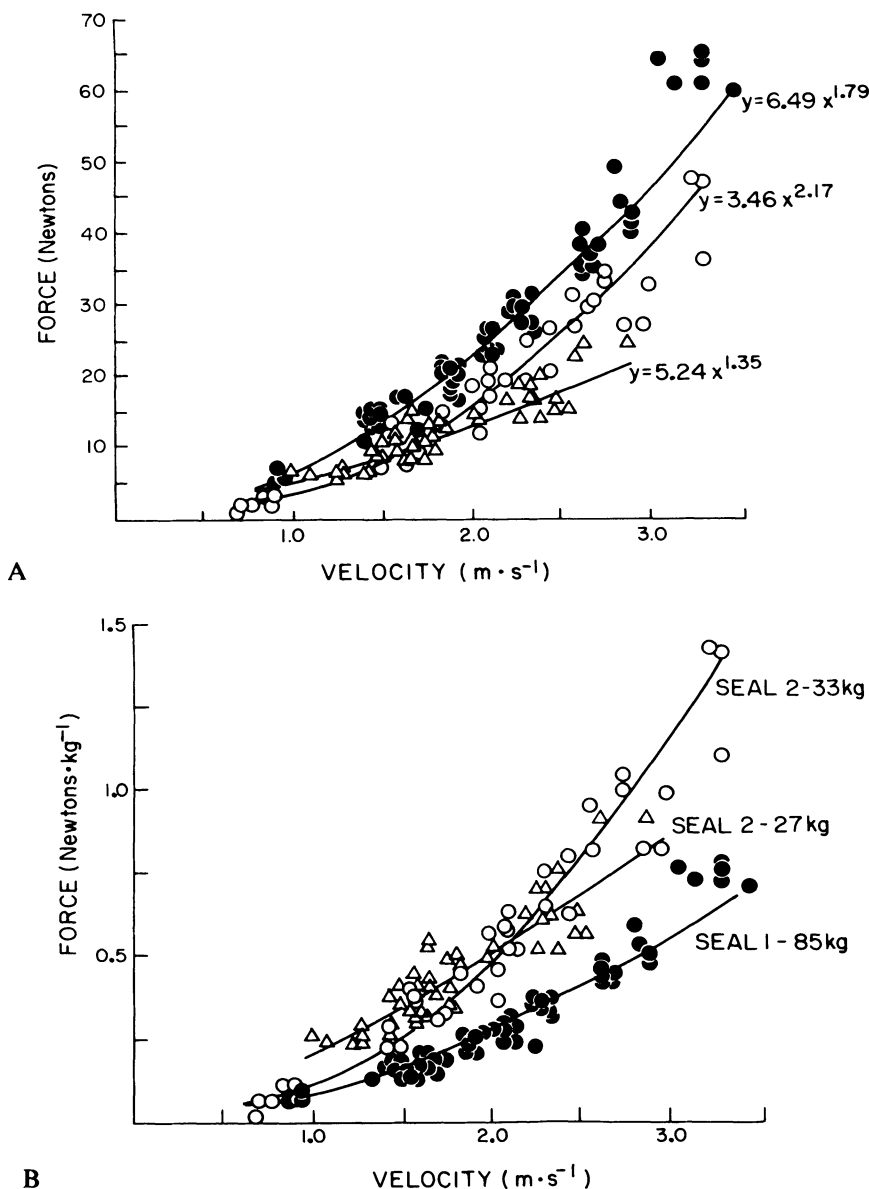
FIG. 4.—A, Total body drag in relation to towing velocity for three submerged harbor seals weighing 27 kg (△), 33 kg (○), and 85 kg (●). Best-fit curves are presented and indicated by the solid lines through the data points. Corresponding correlation coefficients are 0.90 (n = 53), 0.96 (n = 46), and 0.97 (n = 94). B, Transformation of the data presented in A to weight-specific drag as a function of towing velocity. Symbols are the same as for A.

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TABLE 3

SUMMARY OF DRAG COEFFICIENTS DURING SUBMERGED GLIDES AND TOWS FOR TWO HARBOR SEALS
AND ONE HUMAN SUBJECT

	Seal 1		Seal 2		SF	
Glide:						
Glide Va (m·s^{-1})[a]	1.2		1.8		. . .	
Drag force (N)	6.6		4.1		. . .	
Re (×10^6)	1.6		1.6		. . .	
$Cd_A = \dfrac{2\text{ Drag}}{\rho A_T V^2}$	.007		.004		. . .	
$Cd_F = \dfrac{2\text{ Drag}}{\rho F V^2}$	.088		.038		. . .	
Tow:						
Tow V (m·s^{-1})	1.2	1.8	1.2	1.8	1.2	1.8
Drag force (N)	9.1	18.6	6.7	11.6	48.9	95.2
Re (×10^6)	1.6	2.5	1.1	1.6	1.7	2.6
Cd_A	.010	.009	.013	.010	.035	.030
Cd_F	.122	.111	.140	.107	. . .	. . .

[a] Va = average velocity during the glide.

from these drag estimates. Each coefficient based on glide drag was found to be greater for S1 than for S2.

Drag coefficients calculated from tow drag forces were also determined at 1.2 and 1.8 m·s^{-1} for comparison with the glide drag coefficients (table 3, bottom). Based on the best-fit drag equations for submerged tows, the drag forces at 1.2 m·s^{-1} were 9.1 N and 6.7 N for S1 and S2 and 48.9 N for SF. The respective drag coefficients were greater for the towed seals than for the glide estimations. For example, the towed Cdf at the same speed was 2.8 times the glide value for S2 and 1.4 times that for S1. This suggests that S2 was not as well trimmed during tows. Variability in drag and the lower correlation coefficient for the drag versus velocity relationship for S2 (fig. 4) supports this explanation. Thus, in general, S2 had higher drag coefficients during towing experiments than S1 but lower coefficients during glide conditions. SF's drag coefficients, representing those of a nonhydrodynamically designed body, were much higher than the seals'.

MAXIMUM THRUST PRODUCTION

Thrust measurements from S1 showed a range of values from 107 N to 490 N

(fig. 5). The average value for this animal was 392 N. In comparison, a human subject of 79 kg (PT) using the front crawl had a much narrower range of thrust development and was limited to the lower limits of the range for S1. The average
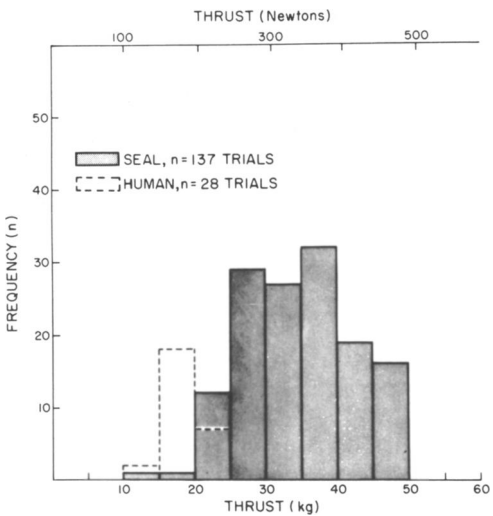

FIG. 5.—Frequency distribution of thrust measured for a human subject and the adult seal. Duration of the efforts were variable and presumably led to the observed distribution in thrust development. Note in particular the discrepancy in the magnitude of thrust presented here and total body drag in fig. 3.

thrust measured for *PT* was 157 *N*. This value was 60% lower than measured for the corresponding measurement of the seal.

BIOLUMINESCENT STUDY

Three major areas of disturbance were found along the body of S1 during swimming bouts through bioluminescent plankton (fig. 6). These were located at the facial whiskers, along the trunk caudad to the shoulders, and surrounding the
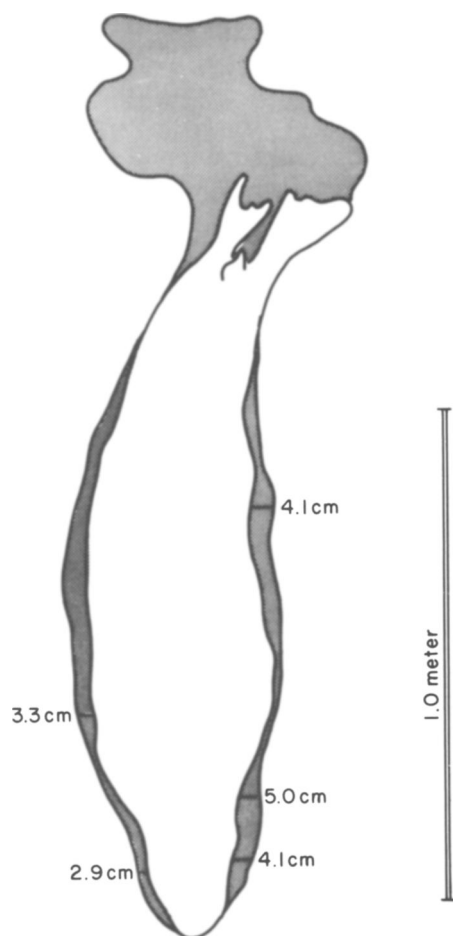

FIG. 6.—Overhead view of the harbor seal swimming at approximately 2.0 m·s⁻¹ and a depth of 1 m through bioluminescent water. The figure was traced from a television screen and represents a composite of such drawings. A transition in disturbance appears to occur at the shoulders. Similarly, the transition of the boundary layer from laminar to turbulent conditions has been placed by Aleyev (1977) immediately cephalic to the maximum diameter of seals and within the shoulder region.

hind flippers. The thickness of the areas of disturbance varied with the site and was less than 5.0 cm along the length of the body. Calculation of boundary layer thickness along the trunk based on a flat plate under turbulent conditions (Vogel 1981) was 56% lower than the measured thickness of the bioluminescence around the seal.

DISCUSSION

Swimming performance by seals, like other animals utilizing aquatic locomotion, is influenced by the hydrodynamic design of the swimmer's body. Resistive forces, termed drag, that must be overcome in order to move forward in water are dependent on three major variables and a dimensionless constant that take into consideration physical characteristics of the body and the fluid medium. These are (1) swimming velocity, (2) physical properties of the water such as density and viscosity, (3) body size, and (4) the drag coefficient, a term dependent on the peculiarities of water flow around the body (Vogel 1981). The resultant formula conventionally used to estimate drag (eq. [2], rearranged) takes these factors into account.

Because it enters directly into equation (2), body size has a profound influence on total body drag encountered by a swimmer. For seals, increases in body size (table 1), were concurrent with an increase in total body drag during towing (fig. 4*A*). A mass-specific comparison of drag permits the relative effects of drag forces on these differently sized animals to be assessed. On a mass-specific basis drag over the range of 0.9 to 3.5 m·s⁻¹ was lower for the larger seal. The results were not as conclusive for S2 at 27 and 33 kg and may have been affected by slight modifications in towing technique by the seal. These modifications add more profile to the body and are reflected in the comparatively high drag. Consequently, at towing speeds greater than 2.0 m·s⁻¹ the mass-specific drag of S2 was found to be higher at 33 kg than when its mass was 27 kg (fig. 4*B*).

The large difference between the body drag of humans and seals (fig. 3) demonstrates the value of a streamlined shape. Clearly, limb internalization and reduc-

tion, an overall absence of surface projections, and an approximation of an elongate, tapered hull configuration contribute to the streamlined character of phocid seals (King 1962; Ray 1963). The fineness ratio (Fr) and the drag coefficient (Cd) are representative of the quality of body streamlining and, therefore, of the efficiency of streamlining in reducing drag among solid bodies. Values for the fineness ratio were 4.6 and 3.8 for adult and immature seals, respectively. The fineness ratio for seals approximates the optimum range of 3.0 to 5.0 for streamlined shapes and, in the case of the adult seal, indicates a body shape which affords the minimum drag for a maximum body volume (Fr = 4.5) (Webb 1975). In comparison, Fr ranges from 3.8 to 5.5 for a variety of cetaceans and large fishes (Hertel 1966) and from 5.5 to 7.0 for fishes swimming in the subcarangiform mode (Webb 1975).

A second way of expressing the effectiveness of body streamlining is in terms of the drag coefficient, Cd. For a given surface area and profile, a small Cd means less power is needed to keep a body in steady motion (Nachtigall 1981). This is a consequence of drag reduction brought about by the absence of flow disturbances around the body. For example, Cd based on frontal area (Cdf) for the gliding adult seal, 0.09 at $Re = 1.6 \times 10^6$ (table 3), was less than found for a number of technical bodies such as cars (0.20 at $Re = 10^7$–10^8), submarines (0.15 at $Re = 3 \times 10^8$), and torpedo shapes (0.17 at $Re = 4 \times 10^6$), although not less than the gentoo penguin (0.07 at $Re = 10^6$) (Nachtigall 1981) or porpoises (0.06 at $Re = 14 \times 10^6$, calculated from Lang, [1974]). Such a low coefficient of drag suggests that water flow around the body of seals is relatively smooth and that vortex formation is small. This is the impression one obtains in observing seals swimming through bioluminescent plankton (fig. 6). In contrast, the estimated Cd for man is three times greater than for a streamlined body such as seals' during towing at similar Re (table 3). The large coefficient of drag implies that water does not flow smoothly along the human swimmer's body (Gadd 1963) thereby resulting in high total body drag (fig. 3).

Slight alterations in this streamlined design can have a large effect on body drag. The difference in drag between the towed and gliding animals is attributed primarily to differences in body configuration. The gliding animals, particularly S2, which had the lowest Cdf under these conditions, were ideally trimmed for least resistance by symmetrical tucking of the forelimbs next to the body and partial closure of both hind limbs. During the tows the limbs were asymmetrically spread to hold the body in the turn, resulting in added body drag. S2 had the highest Cdf when towing and, therefore, presumably had to use a greater amount of trim relative to its body size to maintain its position in the turn. Although this is considered a major source of added drag during the tows, we were not able in this experiment to quantify the alterations in body configuration. Nor could we account for any added drag caused by the wake of the towing strut or proximity of the walls. These factors make it difficult to estimate by extrapolation from the towing drag/velocity curves the magnitude of drag for a gliding or swimming animal under natural circumstances. Nevertheless, it demonstrates that the drag coefficient when the swimming animal is gliding between strokes is not likely to be very different from the best trimmed glide value obtained in these tests. Furthermore, because the flippers of an actively swimming seal are likely to extend out of the streamline to a greater degree during stroking than for balance trim in a circular tow, the Cd during propulsive swimming is likely to be somewhat higher than the towed drag coefficients. The result is a range of drag coefficients, previously unavailable for estimates of power requirements and metabolic rates, that apply to the swimming seal.

As implied from the drag coefficient, the drag experienced by an active swimmer is greater than the drag of a gliding or passive body. The augmentation in drag while swimming is attributed to resistances associated with moving parts and with boundary layer separation ascribed to swimming movements (Lighthill 1971; Webb 1971; Blake 1983a). Oscillations of the body such as occur during swimming

in the subcarangiform mode result in a body drag three to four times greater than that of an equivalent rigid body (Lighthill 1971; Webb 1971). Similarly, human swimmers performing the front crawl experience body drag in excess of two times passive drag values (di Prampero et al. 1974). For Humboldt penguins, drag caused by the wings may approach 20% of total body drag (Hui 1983). In view of these findings, body drag of the passively towed seal (fig. 3) most likely underestimates the total drag of the swimming animal.

In order to determine the contribution of propulsive movements to total drag of the swimming seal, body drag of the active versus passive or gliding animals must be compared. While it is difficult to measure body drag during swimming, it may be estimated by assuming that the power generated metabolically by an actively swimming animal (*Pm*) is equivalent to the power necessary to overcome total active drag (*Pd*). The difference between body drag calculated from *Pd* and the drag of a gliding or passively towed animal is the drag associated with activity. A convenient speed for this calculation, and one for which we have both hydrodynamic and metabolic data, is the routine swimming speed. For S1 this was $1.4 \text{ m} \cdot \text{s}^{-1}$. Power output of a 63-kg seal swimming at $1.4 \text{ m} \cdot \text{s}^{-1}$ was 206 W (Davis, Williams, and Kooyman 1985). Assuming a 10% aerobic efficiency (a value intermediate to the range of efficiencies reported for fish (Bone 1974; Webb 1975), the metabolic power available to overcome drag, *Pm*, is equal to 20.6 W. Because it is assumed that *Pd* is equivalent to *Pm* and is also equivalent to the product of active drag and swimming speed, the active drag for S1 swimming at $1.4 \text{ m} \cdot \text{s}^{-1}$ is 14.7 *N*. This compares to 11.9 *N* for towed drag at this speed and 6.6 *N* for glide drag at the slightly lower speed of $1.2 \text{ m} \cdot \text{s}^{-1}$ (table 3). While the effects of intermittent surface swimming bouts as well as submerged gliding periods could not be accounted for in the estimation of total active drag, the results demonstrate the magnitude of fluctuations in drag that may occur during swimming at a routine speed. Body drag and, therefore, power requirements are

minimum during gliding phases and increase with changes in body conformation as occur during stroking movements and breathing. For the adult seal swimming at $1.4 \text{ m} \cdot \text{s}^{-1}$, these different phases resulted in more than a twofold change in total body drag.

On initial observations, it appears that seals are capable of producing levels of thrust which overcompensate for the body drag encountered during swimming (fig. 5). For example, from figure 3, submerged swimming at the top recorded speed of $4.9 \text{ m} \cdot \text{s}^{-1}$ entails a glide drag of approximately 112 *N*. However, the average thrust produced by the same animal was 392 *N*. A discrepancy between measured levels of drag and thrust has also been noted for sea turtles (Prange 1976), man (present study, figs. 3, 4), dace (Lighthill 1971), and trout, which exhibit levels of thrust exceeding 2.78 times drag on an equivalent rigid, streamlined body (Webb 1971). Three factors wholly or partially unaccounted for in these studies that could lead to the apparent discrepancy are (1) increases in drag associated with periodic surface swimming during breathing, (2) drag augmentation resulting from propulsive movements and burst activities, and (3) variations in the magnitude of thrust related to the duration of the effort. High-speed surface swimming in particular would subject seals to prohibitive levels of body drag which are greater than routine thrust capabilities. Thus, natural swimming conditions probably entail greater thrust requirements than indicated by drag data obtained from the steady-state tow situation.

Another important consideration concerning the body drag of swimmers, especially marine mammals, is the position of the body relative to the water surface. Because of respiratory demands, marine mammals are subject to interfering effects of wave action when surfacing to breathe. Wave drag will increase the relative forces on a body moving on or near the water surface by as much as four to five times submerged values (Hertel 1966). The comparatively high body drag of harbor seals (fig. 3) and humans (fig. 3; Miyashita and Tsunoda 1977) towing on the water surface attests to the additive effect of

wave drag on total resistance. Differences in towing resistance between the two conditions were particularly apparent at high speeds (>1.5 m·s^{-1}) where surface drag becomes nearly asymptotic with velocity, but drag at a 1-m towing depth remains nearly linear (fig. 3).

For some swimmers, the augmented body drag of surface swimming, at least, may be circumvented by leaping clear of the water. This maneuver, termed porpoising, theoretically aids in conserving energy during high-speed swimming in some marine mammals (Au and Weihs 1980; Blake 1983b). Seals are not considered high-speed swimmers and normally do not porpoise. However, even in this species the magnitude of drag forces at the water surface encourages avoidance of the air/water interface. According to calculations based on dolphins from Au and Weihs (1980), an 85-kg harbor seal should begin to porpoise at 5.3 m·s^{-1}. This is considerably higher than Blake's (1983b) porpoising speed prediction of 2.4 m·s^{-1}. The difference in these two values arises from increased drag associated with propulsive movements of the animal, which

is accounted for in the latter estimation. Our studies indicate that this is an important variable to be considered in predicting porpoising speeds of harbor seals. The swimming speed at which S1 began to porpoise as the animal followed the variable-speed ring tank cart was approximately 2.5–3.0 m·s^{-1}. Considering the anomalies created by wall wave refraction and turning, this range agrees reasonably well with the porpoising hypothesis and the influence of drag created by swimming movements.

Although the conditions for these drag and thrust measurements were artificial, they provide a basis for quantifying some of the resistive forces and coefficients involved in the energetics and mechanics of propulsion. Since these values can be strongly influenced by the properties of the experimental apparatus, comparisons made under other conditions should be treated cautiously. Finally, as we have been able to obtain both surface and submerged drag estimates, a clearer appreciation of the high cost of swimming and breathing near the water surface is obtained.

LITERATURE CITED

ALEYEV, Y. G. 1977. Nekton. Junk, The Hague. 435 pp.

AU, D., and D. WEIHS. 1980. At high speeds dolphins save energy by leaping. Nature 284:548–550.

BILO, D., and W. NACHTIGALL. 1980. A simple method to determine drag coefficients in aquatic animals. J. Exp. Biol. 87:357–359.

BLAKE, R. W. 1983a. Fish locomotion. Cambridge University Press, London. 208 pp.

———. 1983b. Energetics of leaping in dolphins and other aquatic animals. J. Mar. Biol. Assoc. U.K. 63:61–70.

BONE, Q. 1974. Muscular and energetic aspects of fish swimming. Pages 493–528 in T. WU, C. J. BROKAW, and C. BRENNEN, eds. Swimming and flying in nature. Vol. 2. Plenum, New York.

CLARK, B. D., and W. BEMIS. 1979. Kinematics of swimming of penguins at the Detroit Zoo. J. Zool. Lond. 188:411–428.

DAVIS, R. W., T. WILLIAMS, and G. KOOYMAN. 1985. Swimming metabolism of yearling and adult harbor seals Phoca vitulina. Physiol. Zool. 58:590–596.

DI PRAMPERO, P. E., D. R. PENDERGAST, D. W. WILSON, and D. W. RENNIE. 1974. Energetics of swimming in man. J. Appl. Physiol. 37:1–5.

GADD, G. E. 1963. The hydrodynamics of swimming. New Sci. 19:483–485.

GRAY, J. 1968. Animal locomotion. Clowes, London. 479 pp.

HERTEL, H. 1966. Structure-form-movement. Reinhold, New York. 251 pp.

HUI, C. A. 1983. Swimming in penguins. Ph.D. diss. University of California, Los Angeles.

KING, J. E. 1962. Some of the aquatic modifications of seals. Nor. Hvalfangst-Tid. 3:104–120.

LANG, T. G. 1963. Porpoises, whales, and fish: comparison of predicted and observed speeds. Nav. Eng. J. 75:437–441.

———. 1966. Hydrodynamic analysis of cetacean performance. Pages 410–432 in K. S. NORRIS, ed. Whales, dolphins, and porpoises. University of California Press, Berkeley.

———. 1974. Speed, power, and drag measurements of dolphins and porpoises. Pages 553–572 in T. Y. WU, C. J. BROKAW, and C. BRENNEN, eds. Swimming and flying in nature. Vol. 2. Plenum, New York.

LIGHTHILL, J. 1971. Large-amplitude elongated-body theory of fish locomotion. Proc. R. Soc. (B) 179:125–138.

MATHEWS, D. K., and E. L. FOX. 1976. The physiological basis of physical education and athletics. Saunders, Philadelphia. 577 pp.

MIYASHITA, M., and T. TSUNODA. 1977. Water

resistance in relation to body size. Pages 395–401 in B. ERICKSSON, and B. FURBERG, eds. Swimming medicine 4: international series on sports medicine. Vol. 6. University Park Press, Baltimore.

MORDVINOV, Y. E. 1968. A study of locomotion in some pinnipedia. Zool. Zh. **47**:1394–1402.

———. 1972. Some hydrodynamic parameters of body shape in pinnipedia. Hydrobiology J. **8**:81–84.

MORDVINOV, Y. E., and B. V. KURBATOV. 1972. Influence of hair cover in some species of Phocidae upon the value of general hydrodynamic resistance. Zool. Zh. **51**:242–247.

NACHTIGALL, W. 1981. Hydromechanics and biology. Biophys. Struct. Mech. **8**:1–22.

NACHTIGALL, W., and D. BILO. 1980. Stromungsan-

passung des pinguins beim Schwimmen unter Wasser. J. Comp. Physiol. **137**:17–26.

PRANGE, H. D. 1976. Energetics of swimming of a sea turtle. J. Exp. Biol. **64**:1–12.

RAY, C. 1963. Locomotion in pinnipeds. Natural Hist. **72**:11–21.

VAN SCIVER, W. J. 1972. Scale determination of unrecognized undersea objects by stereographic photography. Mar. Tech. Soc. J. **6**:14–16.

VOGEL, S. 1981. Life in moving fluids. Willard Grant, Boston. 352 pp.

WEBB, P. W. 1971. The swimming energetics of trout. I. Thrust and power output at cruising speeds. J. Exp. Biol. **55**:489–520.

———. 1975. Hydrodynamics and energetics of fish propulsion. Bull. Fisheries Res. Board Can. **190**:1–158.