KINEMATICS AND ESTIMATED THRUST PRODUCTION OF SWIMMING HARP AND RINGED SEALS

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Summary

The propulsive motions of swimming harp seals (*Phoca groenlandica* Erxleben) and ringed seals (*Phoca hispida* Schreber) were studied by filming individuals in a flume. The seals swam at velocities ranging from 0·6 to 1·42 m s^{-1}. Locomotion was accomplished with alternate lateral sweeps of the hind flippers generated by lateral flexions of the axial body in conjuction with flexion of the flippers. The frequency of the propulsive cycle increased linearly with the swimming velocity, and the maximum angle of attack of the flipper decreased, but the amplitude remained constant. The kinematics and morphology of this hind flipper motion indicated that phocid seals do not swim in the carangiform mode as categorized by Lighthill (1969), but in a distinct mode that mimics swimming by thunniform propulsors. The hind flippers acted as hydrofoils, and the efficiency, thrust power and coefficient of thrust were calculated from unsteady wing theory. The propulsive efficiency was high at approximately 0·85. The thrust power increased curvilinearly with velocity. The drag coefficient ranged from 0·012 to 0·028 and was found to be 2·8–7·0 times higher than the theoretical minimum. The drag coefficient was high compared with that of phocid seals examined during gliding or towing experiments, indicating an increased drag encumbered by actively swimming seals. It was determined that phocid seals are capable of generating sufficient power for swimming with turbulent boundary layer conditions.

Introduction

Compared with the variety of vertebrate swimmers, pinnipeds of the families Phocidae (true seals) and Odobenidae (walrus) demonstrate a unique mode of aquatic locomotion using alternate lateral sweeps of the hind flippers in a sculling action (Tarasoff, 1972; Tarasoff, Bisaillon, Pierard & Whitt, 1972; Aleyev, 1977; Gordon, 1981). Lighthill (1969) and Tarasoff *et al.* (1972) suggested that phocid swimming motion approximates carangiform fish propulsion and efficient locomotion was possible due to narrowing of the tarsal region and the lunate outline of the hind flippers similar to the caudal fin of many fish.

Only recently have the energetics and hydrodynamic characteristics of phocid swimming been investigated. The metabolic cost of swimming (Innes, 1984; Davis, Williams & Kooyman, 1985) and drag forces from towing and gliding experiments have been measured (Innes, 1984; Williams & Kooyman, 1985). However, hydrodynamic models reveal increased drag and thrust for actively swimming animals, compared to passive drag measurements, as a result of changes in the flow regime about the animal associated with movement of the body and appendages (Lighthill, 1971; Webb, Kostecki & Stevens, 1984), so that thrust estimates may be more advantageous for actively swimming animals (Webb, 1975a).

The purpose of the present study is to describe the swimming kinematics of two species of phocid seals. Based on the detailed kinematics, an appropriate hydrodynamic model is chosen to estimate the energetic cost of swimming.

Materials and methods

Experimental animals and water flume

One juvenile male and two adult female harp seals and one adult male and one adult female ringed seal were filmed individually while swimming in a recirculating aquatic flume (Fig. 1; Flyght swimmer's treadmill, Flyght, Sweden; see Astrand & Englesson, 1972) at the University of Guelph. In this flume, the swimming seals remain stationary relative to the camera or observer. The seals were confined to the portion of the basin away from the walls and floor by a wide-mesh nylon net; seals were forced to breath from a 170-l respiratory port that was ventilated at $0.8–5 \, l \, s^{-1}$ to maintain the CO_2 concentrations at less than 1 %. The dorsum of the seals was filmed from overhead through a $1.33 \times 0.51 \times 0.76 \, m$ clear Lexan viewing box located over the portion of the flume used by submerged seals when they were swimming submerged and facing into the current. Lateral views of the swimming seals were taken through the large window in the wall of the basin.

Seals oriented into the current and swam steadily at speeds between 0.6 and $1.42 \, m \, s^{-1}$ as measured with a portable flow meter (Marsh McBirney, model 201, Gaitherburg, MD, USA). Although seals were tested at regular speed intervals, variation of current speed with depth in the flume (<7 %) prevented precise control of swimming speed when seals swam at different depths.

While not in the flume the seals were housed in 20 000-l freshwater tanks with haul-outs. Tank water was replaced with well water at 8–12 °C at $2.1 \, l \, s^{-1}$ (Ronald, Johnson, Foster & Vanderpol, 1970).

Film analysis

Rectilinear submerged swimming was filmed at 24 frames s^{-1} with a Bolex H-16, ciné camera equipped with a Kern Switar 10 mm lens (F/1.6) using Kodak 4-X reversal film no. 7277 (ASA 320) or Kodak Tri-X reversal film no. 7278 (ASA 160).

Lighting was augmented by two colour-corrected floodlamps suspended over the test basin.

Film records were analysed by sequentially tracing hindlimbs as displayed with a stop-action projector (Lafeyette Instrument Co., model 00100; Fig. 2). Data acquisition was restricted to those film records in which the posterior portion of a steadily swimming seal was in view for at least one cycle, where no net acceleration was observed. From these records, flipper planiform area (A, m^2), amplitude of the propulsive stroke for a full cycle (a, m) and one-half cycle (a', m), angle of attack (α, radians), lateral velocity (W, m s^{-1}) and stroke cycle frequency (f, Hz) were calculated.

The flipper planiform area was the maximum area observed during abduction of the digits (Fig. 2B). Flipper span (S; Fig. 2B) was determined by manually spreading the hind flipper of the seal and measuring the distance between digits one and five. Standard body length (L_s, m) is the linear distance between the nose and tail measured during other studies on the same seals (Innes, 1984). The surface area of the body (SA) was calculated according to the prediction equations for phocids given by S. Innes, G. A. J. Worthy, D. M. Levigne & K. Ronald (in preparation). The hind flipper aspect ratio (AR) was calculated as S^2/A, and the mean chord (C) as S/AR. The sweepback angle of the hind flipper (Λ) is the angle subtended by a line at the 1/4-chord and intersecting the perpendicular at the median axis of the flipper.

The amplitude of the propulsive stroke and the angle of attack are defined relative to the direction of swimming of the seal (see Fig. 2C,D). The amplitude is the perpendicular displacement from the path of the seal of the trailing edge of the expanded flipper, from the start of dorsiflexion at the beginning of the stroke to the start of plantar flexion at the end of the stroke. This is less than the amplitude of the combined strokes of both hind flippers, measured as the maximum distance between the commencements of consecutive strokes.

The angle of attack is the angle between the tangent of the flipper's path and the axis of the hind flipper (Fierstine & Walters, 1968; Chopra, 1976; Magnuson, 1978; Fig. 2D). The angle of attack was measured by drawing a line through the central axis of the flipper and another line from the tip of the hind flipper to its position in the next frame, adjusted for the distance the seal would swim at constant velocity in the time interval between film frames (Fierstine & Walters, 1968). The angle formed by the two lines was measured with a protractor.

The lateral velocity of the hind flipper tip was calculated as the horizontal distance moved by the trailing edge between successive traced images divided by the elapsed time. Frequency was calculated from stroke cycle period. Additionally, the stroke frequency was determined with a stopwatch during observations of seals in the flume.

Reynolds numbers are based on the seal's standard length (L_s), flume or swimming speed (U) and kinematic viscosity (v) of the flume's fresh water using the equation:

$$Re = L_s U/v .$$ (1)

Statistical procedure

Statistical analyses of the data were performed using Minitab. Regression lines were computed by the least-squares regression method. Non-linear data were logarithmically transformed for statistical analyses. Variation about means was expressed with ± one standard deviation (s.d.).

Results

Morphometrics

Twenty-eight stroke sequences were filmed. Only 12 of the sequences, representing four of the seals (two harp: two ringed), were judged to be acceptable for analysis, based on the criteria stated above.

Relevant morphological dimensions of the seals that were used for film analysis are summarized in Table 1. Average body length and hind flipper span of the harp seals were 1·5 times greater than the ringed seals, but the harp seal average flipper chord was only 1·2 times larger, resulting in greater AR for the ringed seals. Surface areas expressed as total body surface area and planar hind flipper area were both 1·2 times greater for harp seals than for ringed seals. When fully abducted during swimming, the hind flippers had an aspect ratio of 3·4–4·0 and a sweepback angle of 30–35·8°.

Seals swam with their fore flippers adducted against their sides and their necks retracted, such that their silhouettes were similar to thunniform swimmers (Fig. 2A). The tibial extensions of the hind flippers and short compressed tail result in the constricted 'peduncle', that sets the hind flippers apart from the body in what is called narrow necking (Lighthill, 1969). The peduncle width was found to be 1·9 times greater than the depth when the seals were gliding and the hind flippers held together. However, the width increased with the movements of the hind flippers during swimming to a maximum of 4·2 times the depth.

Kinematics

The seals were filmed at swimming velocities ranging from 0·6 to 1·42 m s^{-1} ($Re = 0.77 \times 10^6 - 1.79 \times 10^6$). Below 0·6 m s^{-1}, neither species swam steadily. During steady rectilinear swimming, harp and ringed seals use qualitatively similar patterns of lateral flexion of the posterior half of their bodies with alternating movements of the hind flippers. No complete wavelength was observed at any instance during the stroke cycle. The details of the body and hind flipper movements as viewed dorsally are shown in Fig. 2. While both hind flippers were swept laterally, the digits of the trailing hind flipper were abducted (spread), and the digits of the leading flipper were simultaneously adducted (closed). The tips of the trailing hind flipper were slightly bent chordwise during this motion. Tarasoff et al. (1972) and Gordon (1981) described the alternating abduction–adduction of the hind flippers as power and recovery phases of the stroke cycle for each flipper, although alternate use provides roughly continuous thrust. No seal was observed

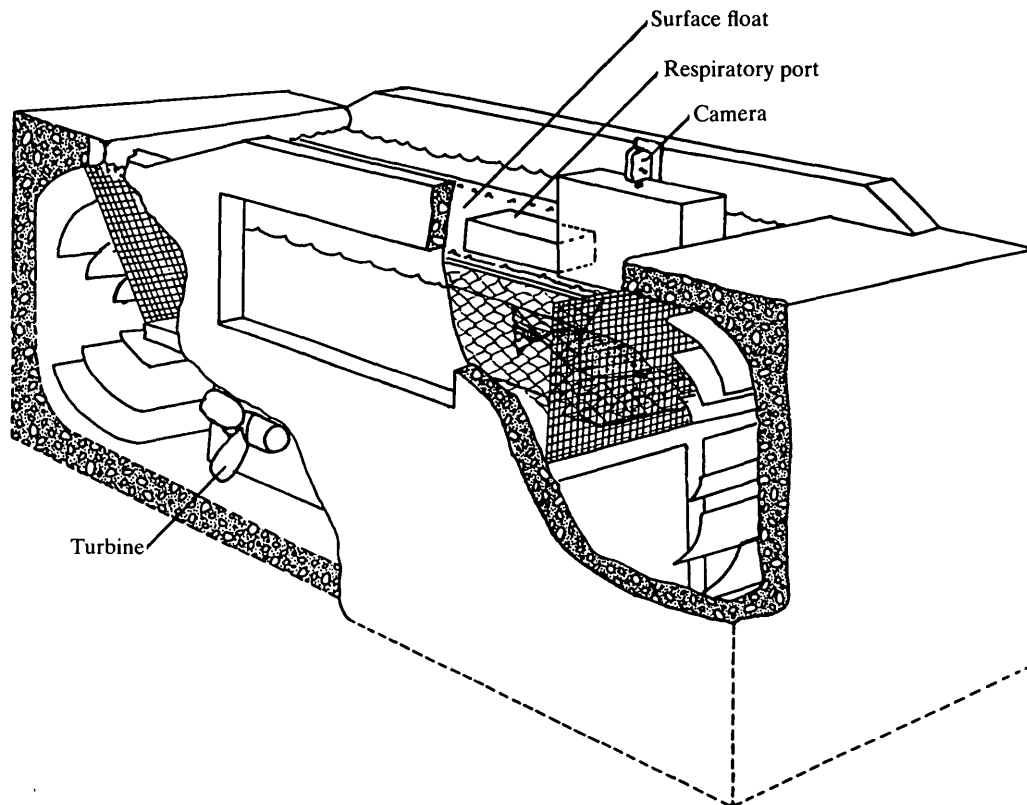Surface float

Respiratory port

Camera

Turbine

Fig. 1. An exposed schematic drawing of the aquatic flume used to film the swimming kinematics of ringed and harp seals. A water current is created by two hydraulic turbines (one of which is shown). The water circulates forward through the divided corridor, under the working section of the mill, and is redirected by the anterior wall and curved plates into the working section. The water is returned to the turbines by the posterior wall and curved plates. The seals were forced to swim away from the working section's floor and walls by a net bag attached to the anterior safety grid and the surface float. This surface float forced the seal to breath from a ventilated respiratory port. The section of the float above a swimming seal was replaced with a Lexan box to allow filming from above. The portion of the flume below the floor is outlined by the dotted lines. The flume is approximately 5·7 m long, and the seal pictured is approximately 1 m in length.

to swim with the digits of both flippers abducted simultaneously as reported by Howell (1930) and Backhouse (1961).

At the initiation of the stroke at maximum body and peduncle excursion, the chordwise axis of the trailing hind flipper was oriented parallel to the seal's direction of travel. This hind flipper was dorsiflexed and the tibia-fibula was flexed as the limb was swept laterally through an arc in the horizontal plane (Fig. 2). During the first half of the stroke the rate of hind flipper dorsiflexion increased more rapidly than during the second half. The mean angular excursions due to

Table 1. *Morphometrics of harp and ringed seals for which kinematic records were obtained*

Animal no. Dimension	Harp seals		Ringed seals	
	80-5	74-5	78-1	78-2
Sex	Male	Female	Female	Male
Body mass (kg)	69·0	97·0	59·0	58·5
Standard body length (m)	1·43	1·64	1·09	1·03
Surface area (m²)	1·16	1·37	1·07	1·07
Fineness ratio*		4·6	3·8	3·7
Flipper span (m)	0·41	0·40	0·36	0·34
Planar flipper area (m²)	0·050	0·046	0·035	0·029
Aspect ratio	3·37	3·47	3·71	3·95
Flipper chord (m)	0·12	0·12	0·10	0·09

* Fineness ratio was determined independently by Innes (1984).

dorsiflexion were 1·2 ± 0·3 rad and 1·9 ± 0·2 rad for harp and ringed seals, respectively.

The hind flipper dorsiflexion resulted in a rapid increase of the flipper's angle of attack, which remained positive through the entire stroke (Fig. 3). Maximum angles of attack of 0·58–0·31 rad for the harp seals and 0·58–0·32 rad for the ringed seals were reached from approximately the first third to the middle of the stroke. The angle of attack remained within 20 % of maximum through an average of 33 % of the stroke cycle (Fig. 3). The end of the stroke was accompanied by a drop in the angle of attack, so that the hind flipper was essentially parallel to the direction of forward motion of the seal. Departure from a symmetrical change in angle of attack over the stroke cycle was believed to result from the seal's active movements *via* flipper dorsiflexion and tibial-fibula flexion during the stroke (Innes, 1984).

At the initiation of the stroke, the digits of the leading hind flipper were adducted and plantarflexed. This action resulted in a reduction of total surface area for the flipper. Tibial-fibula extension was observed throughout the stroke as the flipper was swept laterally. At the termination of the stroke, the hind flipper was dorsiflexed, so the orientation of its chordwise axis was approximately parallel to the direction of motion for the seal (Fig. 2C).

The mean amplitudes of a single, trailing hind flipper during the stroke cycle for harp and ringed seals were 0·33 ± 0·03 and 0·31 ± 0·04 m, and were independent of swimming speed. This represents a length-specific amplitude of 0·26 ± 0·05 L. However, due to the arrangement of the two hind flippers with respect to the trunk, the combined amplitudes of the hind flippers were 0·45 ± 0·04 and 0·46 ± 0·05 m for harp and ringed seals, respectively. Lateral flexion of the trunk, when measured by the amplitude of the tail, accounted for the majority of the lateral displacement by the hind flippers. The tail amplitude represented 87 and
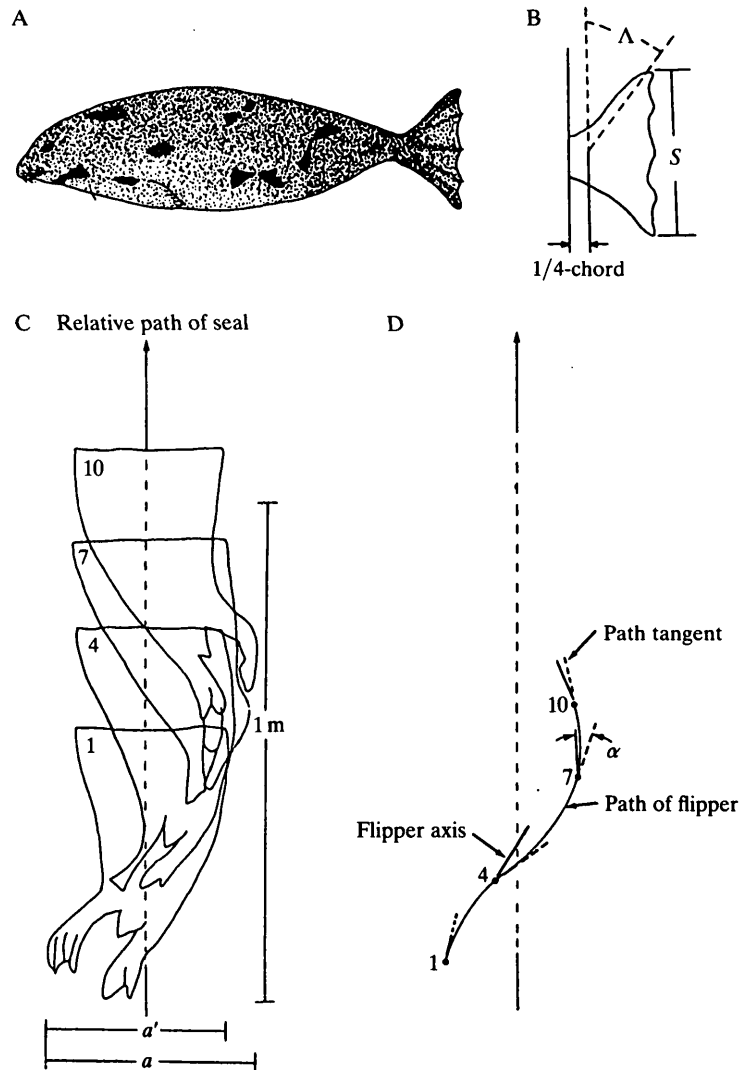
Fig. 2. Diagram of the morphometric and kinematic measurements. (A) Lateral view of a swimming seal showing the necking of the body near the hind flipper. (B) Planiform of hind flipper during power stroke showing span (S) and sweepback angle (Λ) measured from the 1/4-chord. (C) Sequential tracings from films of the dorsal view of the posterior half of a ringed seal swimming at $1 \cdot 42\,\mathrm{m\,s^{-1}}$ during half a complete stroke cycle. Numbers indicate the frame of the film and the one-half (a') and full-cycle (a) amplitudes are labelled. (D) Orientation and movement of the hind flipper with respect to swimming direction direction of the seal used for estimation of the angle of attack (adapted from Fierstine & Walters, 1968; Magnuson, 1978).

77 % of the combined hind flipper amplitude for harp and ringed seals, respectively.

The lateral velocity (W) of the tip of the hind flipper showed an asymmetrical trend over the stroke cycle (Fig. 3). Lateral velocity increased rapidly from zero to
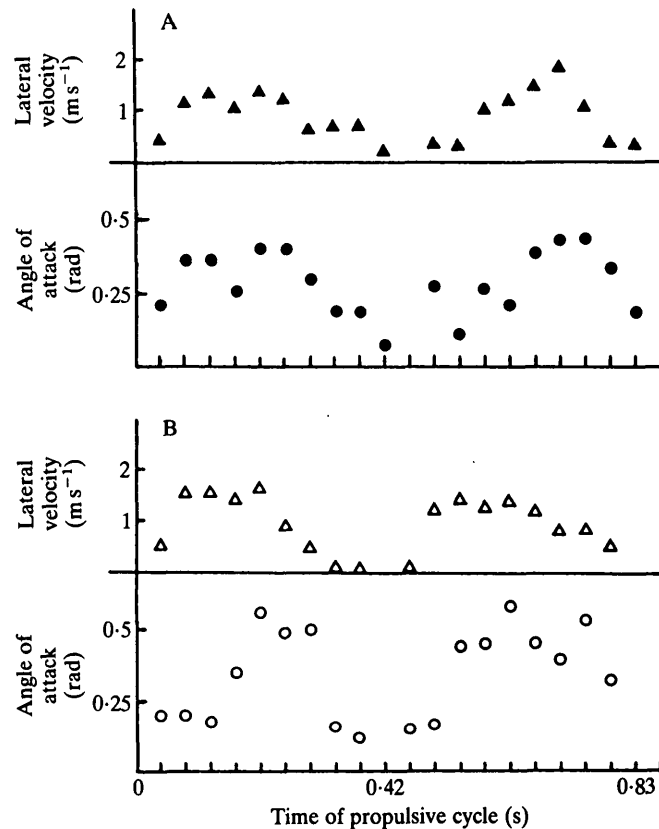
Fig. 3. Plot of the change in angle of attack (α, in radians) and lateral velocity (W, in m s^{-1}) with respect to time (in s) of the trailing hind flipper for a representative harp seal swimming at $U = 1.26$ m s^{-1} (A) and ringed seal swimming at $U = 1.28$ m s^{-1} (B) through a complete stroke cycle.

a maximum in the first third to the middle of the stroke as the trailing flipper was swept medially. Lateral velocity remained constant through the middle of the stroke and then decreased gradually to zero by the end. The mean lateral velocity ($\overline{W}$) increased with increasing swimming speed and ranged from 0.49 to 0.92 m s^{-1} for the harp seals and 0.52 to 0.94 m s^{-1} for the ringed seals. Maximum lateral velocity (W_{max}) was roughly in phase with maximum angle of attack (Fig. 3).

The frequency of the propulsive cycle (f), based on film records, was linearly related to swimming speed for both species (Table 3). The relationship was described by the equation $f = 0.71U + 0.15$ ($r = 0.93$; $P < 0.05$) for the harp seals and $f = 0.61U + 0.39$ ($r = 0.89$; $P < 0.01$) for the ringed seals. Propulsive frequencies were 8–24 % lower for the harp seal compared with the smaller ringed seal over a similar range of velocities. This trend was supported by frequency data measured by timing hind flipper strokes with a stopwatch. The positive linear relationship of frequency with swimming speed for harp and ringed seals is consistent with the results reported for swimming harbour seals, *Phoca vitulina*

Table 2. *Comparison of swimming modes*

Criteria	Carangiform mode	Thunniform mode	Phocid seals
Body			
Fineness ratio	5·6–6·2[j]	3·5–5·0[d,j]	3·7–4·6[l]
Position of maximum thickness	0·3–0·5L[h]	0·4–0·7L[b,d,h]	0·5–0·6L[l,h]
Peduncle			
Joints	One[i]	Two[e]	Two
Width/depth	0·4–1·5[h]	1·5–4·4[h]	1·9–4·2
Narrow necking	Present[i]	Present[i]	Present
Caudal fin/flipper			
Trailing edge	Scooped out or notched[i,g]	Not scooped out or notched[i,g]	Not scooped out or notched
Aspect ratio	4·3–5·7[j]	5·5–8·7[e] 3·4–5·5 for cetaceans[c,n]	3·4–4·0
Sweep-back angle (degrees)	45–50[j]	25–30[f]	30–35·8
Flexibility	Tips more rigid than centre[i]	Centre more rigid than tips[i]	Centre more rigid than tips
Kinematics			
Body undulation	Confined to posterior 1/2 to 1/3[g,i]	Confined to caudal peduncle in fish and posterior 1/3 in *Tursiops*[a,g,i]	Confined to posterior 1/2 of body in combination with movement of 'peduncle'
Length-specific amplitude	0·2–0·21[g]	0·2–0·3[c,g]	0·26
Wavelength/body length	<1·0[g,k]	1·0–2·0[i]	>1·0
α_{max} (rad)	0·4[m]	0·28–1·1[g,j]	0·31–0·58
Feathering parameter	0·57[m]	0·3–0·6[j]	0·41–0·59

[a] Parry (1949); [b] Walters (1962); [c] Lang & Daybell (1963); [d] Hertel (1966); [e] Fierstine & Walters (1968); [f] Lighthill (1969); [g] Webb (1975a); [h] Aleyev (1977); [i] Lindsey (1978); [j] Magnuson (1978); [k] Blake (1983); [l] Innes (1984); [m] Videler & Hess (1984); [n] Videler & Kamermans (1985).

(Davis *et al.* 1985), and fore flipper propulsion by sea lions, *Zalophus californianus* (Feldkamp, 1987). Also, the inverse relationship of body length to frequency is in agreement with scaling effects demonstrated for various species and locomotory modes (Pedley, 1977).

Discussion

Swimming harp and ringed seals displayed the gross axial and appendicular movements reported previously for the pinniped families Phocidae (Backhouse, 1961; Ray, 1963; Tarasoff *et al.* 1972; Ridgway & Harrison, 1981a,b) and Odobenidae (Ray, 1963; Fay, 1981; Gordon, 1981). These swimming movements

characterize a unique appendicular propulsive mode that achieves effective aquatic locomotion by alternating lateral strokes of the hind flippers in conjunction with oscillations of the body.

Lighthill (1969) and Tarasoff *et al.* (1972) originally described the swimming motion of phocids as being similar to that of carangiform swimmers, which include clupeid fish and mackerel (Lindsey, 1978). Present observations on the physical dimensions and swimming motions of harp and ringed seals indicate that, although there is overlap with the morphometrics and kinematics of carangiform swimmers, these phocid seals are different from carangiform swimmers (Table 2).

The differences are most striking with regard to body and tail dimensions. The fineness ratio of the phocid seals was at least 18 % lower than in carangiform swimmers, indicating a stockier body form for the seals. In addition, the position of the maximum girth of the body was displaced further posteriorly for seals. Although carangiform swimmers and seals exhibit narrow necking of the caudal peduncle, the seal peduncle has a greater depth to width ratio. Whereas carangiform swimmers possess a single mobile joint for control of caudal fin pitch (Lindsey, 1978), phocid seals have two joints in the peduncle corresponding to the tibiofemoral and ankle joints. Also, the hind flipper of phocids is not notched or scooped out and has a lower sweepback angle than the carangiform caudal fin.

The kinematics of carangiform swimmers and phocid seals are similar in that undulations are confined to the posterior half of the body, and the maximum angle of attack and feathering parameter (see below) are equivalent. However, the length-specific wavelength is less than 1 for carangiform fish (Webb, 1975a; Blake, 1983), whereas it is greather than 1 in ringed and harp seals. The magnitudes of the kinematic parameters are not different from the range of values for the thunniform mode (Table 2).

The body dimensions and swimming motion of phocid seals are more similar to those of thunniform swimmers (Lindsey, 1978), which use 'lunate tail' propulsion (Chopra, 1974, 1976), than to those of carangiform swimmers (Table 2). A similar conclusion was independently derived by Aleyev (1977). Thunniform swimmers include scombrid and lamnid fish, cetaceans and extinct ichthyosaurs (Lighthill, 1969).

The thunniform mode is characterized by a body shape with a massive rounded anterior, streamlined shape and extreme narrow necking of the peduncle (Lindsey, 1978). Only one-half to one full wavelength is visible in the body whenever there is significant lateral movement at the peduncle and tail (Fierstine & Walters, 1968; Lindsey, 1978), although large lateral undulations are found within the posterior one-third of the body of the cetacean *Tursiops truncatus* (Parry, 1949). The amplitude to body length ratio is characterized as 0·2–0·21 (Webb, 1975a), but can be greater than 0·3 (Fierstine & Walters, 1968). Thrust is generated exclusively by the stiff lunate tail which acts as a hydrofoil (Magnuson, 1978). The angle of inclination of the caudal fin is changed throughout the stroke cycle by a double-jointed system which maintains continuous maximal thrust (Lindsey, 1978).

The body and flipper shape of harp and ringed seals is consistent with thunniform morphology except for the paired hind flippers. The morphological similarities are particularly striking with regard to the degree of narrow necking formed by the tibia-fibula and compressed tail anterior to the flipper. The configuration of two tibia-fibula and the interposed tail functionally mimics a streamlined caudal peduncle found in thunniform swimmers (Webb, 1975a). The trailing hind flipper, which is reinforced by bony elements, represents a stiff, lunate hydrofoil with a sweepback angle that is within the range of scombrid fish with fast sustained speeds (Tarasoff *et al.* 1972; Magnuson, 1978). In *Phoca*, aspect ratios are equivalent or higher than values for the coastal dolphins *Tursiops* and *Sotalia* ($AR = 3.5$ and 3.4, respectively; Videler & Kamermans, 1985), but low compared with values for scombrid fish ($AR = 5.5$–8.7; Fierstine & Walters, 1968; Magnuson, 1978) and the pelagic cetacean *Lagenorhynchus* ($AR = 5.5$; Lang & Daybell, 1963). In addition, the body shape of the seals, as represented by the fineness ratio, is within the range of tuna and cetaceans (Hertel, 1966), indicating a streamlined body form and the optimal value for minimum drag with maximum volume (Webb, 1975a).

Kinematic analysis of swimming phocid seals further supports the use of a thunniform-like propulsive system. The mobile joints in the hind flippers of phocid seals are equivalent to the double joint system of tuna, allowing large specific amplitudes and control of the heave and pitch of the hind flipper throughout the stroke. The range of maximum angles of attack is higher than in non-oscillating hydrofoils, but is consistent with values of the oscillating caudal fin of tuna (Fierstine & Walters, 1968). Fierstine & Walters (1968) stated that oscillating hydrofoils appear to perform more efficiently at higher angles of attack than non-oscillating hydrofoils. However, Chopra (1976) suggested that the angle of attack has an upper bound because large values of angle of attack reduce thrust and thus efficiency.

Hydromechanical analysis of lunate-tail propulsion uses unsteady wing theory to calculate the total thrust generated and the rate of working accomplished by a rigid hydrofoil (Chopra & Kambe, 1977). Thrust is obtained from an oscillating hydrofoil by the posteriorly inclined force component and leading edge suction (Chopra, 1975). In the model developed by Chopra & Kambe (1977) and simplified by Yates (1983), the relationship between the reduced frequency and the proportional feathering parameter can be used to determine the coefficient of thrust (C_T) and swimming efficiency (η). The reduced frequency (σ) is a measure of the unsteady effects of the flow about the hydrofoil, and is equal to $\omega C / U$, where ω is the radian frequency, equal to πf (Yates, 1983). The proportional feathering parameter (θ) is the ratio of the angle of attack to the feathering angle, and equals $U\alpha / \omega h$, where α represents the maximum angle of attack and h is one-half the amplitude a'.

The kinematic parameters and results of the analysis of the lunate-tail propulsion of the seals are summarized in Table 3. Estimates of the coefficient of

Table 3. *Kinematic measurements used in the calculation of* C_T *(coefficient of thrust) and* η *(swimming efficiency) according to the hydrodynamic model used by Chopra & Kambe (1977)*

Species	Animal no.	U (m s^{-1})	Re	f (Hz)	h (m)	α (rad)	σ	θ	C_T	η
Ringed seal	78-2	0·75	0·77 × 10⁶	0·77	0·15	0·57	0·58	0·59	0·26	0·88
	78-1	1·00	1·08 × 10⁶	1·09	0·12	0·46	0·68	0·57	0·33	0·80
	78-2	1·10	1·13 × 10⁶	1·14	0·18	0·48	0·59	0·42	0·31	0·84
	78-1	1·10	1·19 × 10⁶	1·00	0·16	0·38	0·57	0·41	0·33	0·83
	78-1	1·28	1·39 × 10⁶	1·20	0·18	0·58	0·59	0·56	0·25	0·87
	78-2	1·38	1·41 × 10⁶	1·14	0·15	0·32	0·47	0·41	0·24	0·85
	78-2	1·42	1·45 × 10⁶	1·26	0·15	0·37	0·50	0·43	0·24	0·85
Harp seal	74-5	0·60	0·98 × 10⁶	0·55	0·19	0·58	0·69	0·54	0·36	0·86
	74-5	0·70	1·14 × 10⁶	0·71	0·15	0·51	0·76	0·52	0·35	0·85
	80-5	1·04	1·48 × 10⁶	0·80	0·17	0·44	0·58	0·54	0·26	0·87
	80-5	1·18	1·68 × 10⁶	0·92	0·15	0·31	0·59	0·41	0·32	0·85
	80-5	1·26	1·79 × 10⁶	1·14	0·17	0·42	0·68	0·43	0·38	0·84

U, swimming speed; Re, Reynolds number; f, stroke cycle frequency; h, one-half stroke amplitude; α, angle of attack; σ, reduced frequency; θ, ratio of the angle of attack to the feathering angle.

thrust and efficiency were considered to represent maxima owing to the unique kinematics of the phocids and hind flipper aspect ratios, which are slightly lower than the aspect ratio assumed by the model ($\geqslant 4$). A low aspect ratio influences the performance of a hydrofoil by increasing its drag (Magnuson, 1978). The propulsive efficiency (η) was approximately 0·85 for both species. A general trend of increasing efficiency with increasing velocity was not found, as had been reported for other swimmers (Webb, 1975a; Fish, 1984), perhaps because of the small sample and restricted range of velocities.

Generally, the efficiencies of undulatory swimmers are high, because they generate thrust throughout most of the stroke cycle (Lighthill, 1969). Webb (1975b) reported efficiencies of 0·7 and 0·9 for rainbow trout and sockeye salmon, respectively. Yates (1983) calculated an efficiency of 0·92 for the dolphin *Lagenorhynchus obliquidens* swimming at 5·18 m s^{-1}. Wu (1971) has suggested that, under optimal conditions, the propulsive efficiency for lunate-tail propulsion may be as high as 99 %. However, lower efficiencies should be realized by the seals because of the low value of the proportional feathering parameter.

The mean thrust power output (P_T) required for swimming is given by:

$$P_T = \tfrac{1}{2}\eta\rho C_T U^3 S(h/C)^2 . \tag{2}$$

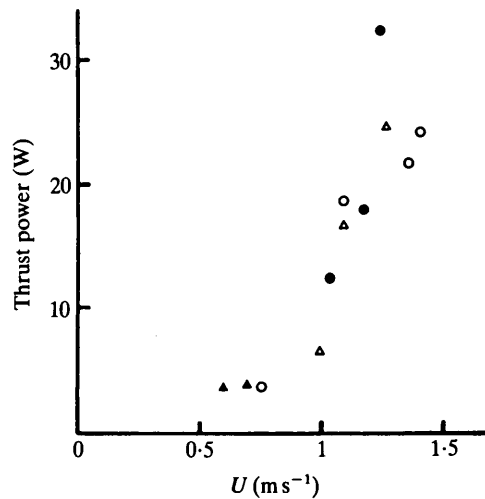The calculated thrust power of harp and ringed seals shows a curvilinear increase

Fig. 4. The thrust power, P_T, as a function of the swimming velocity, U. Individual values for harp seals 74-5 (▲) and 80-5 (●), and ringed seals 78-1 (△) and 78-2 (○) were calculated from the hydromechanical model by Chopra & Kambe (1977). Log-transformed data were used to compute least-square regression equations for the seals as presented in the text.

with increasing swimming velocity (Fig. 4). Least-square regression equations computed from log-transformed data are given for the harp seals as:

$$P_T = 12\cdot95U^{2\cdot85}, r = 0\cdot97, P < 0\cdot01, \tag{3}$$

and ringed seals as:

$$P_T = 9\cdot84U^{3\cdot05}, r = 0\cdot93, P < 0\cdot01. \tag{4}$$

The larger harp seals have a slightly higher P_T than the ringed seals over their range of swimming speeds. Over a two-fold range of velocity the ringed seals had a 6·3-fold increase in thrust power and the harp seals had an 8·9-fold increase. Such differences exhibited by the two seals were due to size effects. The flipper chord of the harp seal is larger than that of the ringed seal, and this leads to increased values of η and C_T. The large flipper planar area of the harp seal along with C_T gives estimated values of thrust power greater than values calculated for the ringed seals at similar velocities. Also, the greater surface area of the harp seal, compared with the ringed seal, would incur a larger drag force and thus, ultimately, a greater thrust power requirement.

Efficiency and thrust are greatly influenced by the shape and structure of the hind flipper acting as a hydrofoil. The curved leading edge of the hind flipper reduces the contribution to the thrust generated by the leading edge suction without reducing the total thrust (Chopra & Kambe, 1977). If this leading edge suction is too great, premature separation of the boundary layer will occur and significantly reduce the total thrust. Efficiency also will decrease if the sweepback

angle of a hydrofoil is greater than approximately 30° (Chopra & Kambe, 1977). The average sweepback angle for the hind flippers of *Phoca* ($\Lambda = 32°$) are consistent with the above value of sweepback angle for high efficiency. In addition, flexibility of the hind flipper may be associated with an increase in efficiency at the expense of total thrust owing to a reduction in the magnitude of the instantaneous lift force (Katz & Weihs, 1978).

Little is known about the hydrodynamic effect of the alternating hind flippers in relation to swimming performance. Mordvinov (1968) reported that the adducted leading flipper may produce some thrust, but this has not been confirmed.

It is helpful to compare the drag experienced by the animal using the non-dimensional drag coefficient (C_D), since the thrust power generated varies with the size and speed of the animal. In addition, C_D can be compared to a reference drag coefficient based on a flat plate with an equivalent surface area and Reynolds number. The C_D for a flat plate represents the theoretical minimum, because no form drag is involved. C_D can be calculated as:

$$C_D = P_T / \tfrac{1}{2}\rho A U^3 . \tag{5}$$

C_D varied from 0·016 to 0·028 for the harp seals and 0·012 to 0·026 for the ringed seals. Assuming turbulent boundary conditions, based on the flow visualization experiments of Williams & Kooyman (1985), the C_D for the ringed and harp seals is 2·8–7·0 times greater than the theoretical minimum at equivalent Reynolds numbers.

In the calculation of C_D for *Lagenorhynchus* by Chopra & Kambe (1977), they assumed that C_D was overestimated because of a thrust reduction influenced by the peduncle and the small aspect ratio, and reduced C_D by 20%. Similar adjustments to the data in this study, although reducing the thrust power and C_D, still yield drag coefficients 2·2–5·6 times greater than the theoretical minimum.

Estimates of C_D for actively swimming harp and ringed seals are greater than values measured from towing and gliding experiments performed on phocid seals. Drag coefficients determined from towed or gliding phocid seals (Innes, 1984; Williams & Kooyman, 1985) were lower than C_D at similar Reynolds numbers reported in this study. Such differences are to be expected because the oscillating body and hind flippers of the seals increase the total drag. Similarly, Chopra & Kambe (1977) calculated a 167% increase in C_D for swimming *Lagenorhynchus* compared with a rigid streamlined body. Webb (1975a) found the thrust power for three cetaceans, calculated from hydromechanical models, to be 6·3–16·0 times greater the theoretical frictional drag power assuming turbulent boundary conditions. The hydrodynamic basis for increased drag due to swimming motions has been discussed by Lighthill (1971) and Webb et al. (1984). The drag increases because large-amplitude lateral body movements modify the water flow in the boundary layer and around the body, resulting in increased frictional and form drag coefficients (Webb et al. 1984). Although the thunniform swimmers should not be affected, since lateral movements are confined to the narrow peduncle, the lateral movements of the posterior half of the phocid seals may induce an increase

in the total drag. In addition, the seals can experience increased drag due to wall and surface effects, and turbulence in the flume.

The drag coefficients, determined in this study for seals swimming in turbulent water, along with the bioluminescent flow visualization experiments by Williams & Kooyman (1985), indicate that phocid seals are capable of generating sufficient power for swimming without invoking laminar flow as has been suggested as the solution to Gray's paradox for the swimming of cetaceans (Gray, 1936; Parry, 1949). If seals swam with a laminar boundary layer, the required thrust power would represent between 3·5 and 10·3 % of the thrust powers estimated above.

Metabolic power measurements provide additional support for the contention that phocids generate sufficient power to swim with a turbulent boundary layer. Measurements of gross metabolic rates by Innes (1984) of the two ringed seals used in this study swimming at $1·1 \mathrm{m s}^{-1}$ were approximately eight times the estimated thrust power. These results represent an aerobic efficiency of 12·4 % for the ringed seals. This is below a typical maximum aerobic efficiency of approximately 20 %, so that phocids have adequate power input and output to swim under turbulent boundary conditions.

Use of the pelvic appendages as the main effector for aquatic propulsion by lateral undulation in the vertebrates has only been observed in the families Phocidae (Backhouse, 1961; Ray, 1963; Tarasoff *et al.* 1972; Ridgway & Harrison, 1981*a*) and Odobenidae (Ray, 1963; Fay, 1981; Gordon, 1981). The evolution of the swimming modes of phocids and odobenids may in part be associated with their highly aquatic nature. These pinnipeds migrate considerable distances in the ocean and dive deeply (Ridgway & Harrison, 1981*a,b*). The great independence of these animals from the terrestrial habitat and their sustained activities in the water necessitate an efficient swimming mode. Whereas cetaceans have developed swimming modes and morphologies based on dorsoventral undulations with a modified tail, phocid seals swim by lateral flexion of the body combined with the pelvic appendages. Although different in orientation, both swimming modes represent highly efficient propulsive mechanisms. It may be that phocid seals utilize the hind flippers in an undulatory mode because of historical constraints associated with their early evolution from Tertiary carnivores.

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