

RESEARCH ARTICLE

Terrestrial locomotion of the northern elephant seal (*Mirounga angustirostris*): limitation of large aquatically adapted seals on land?

Kelsey A. Tennett¹, Daniel P. Costa², Anthony J. Nicastro³ and Frank E. Fish^{1,*}

ABSTRACT

The aquatic specializations of phocid seals have restricted their ability to locomote on land. The amphibious northern elephant seal, *Mirounga angustirostris*, is the second largest phocid seal in the world, with males reaching 2700 kg. Although elephant seals are proficient swimmers and deep divers, their extreme size and aquatic specializations limit terrestrial movement. The kinematics of terrestrial locomotion in northern elephant seals were analyzed from video recordings of animals observed on the beach of Año Nuevo State Reserve, CA, USA. The seals moved using a series of rhythmic undulations produced by dorsoventral spinal flexion. The traveling spinal wave moved anteriorly along the dorsal margin of the body with the chest, pelvic region and foreflippers serving as the main points of contact with the ground. The hindflippers were not used. The spinal wave and foreflippers were used to lift the chest off the ground as the body was pushed forward from the pelvis as the foreflippers were retracted to pull the body forward. Seals moved over land at 0.41–2.56 m s⁻¹ (0.12–0.71 body lengths s⁻¹). The frequency and amplitude of spinal flexions both displayed a direct increase with increasing speed. The duty factor for the pelvic region decreased with increasing velocity while the duty factor of the foreflipper remained constant. Kinematic data for elephant seals and other phocids were used in a biomechanical model to calculate the mechanical energy expended during terrestrial locomotion. The elephant seals were found to expend more energy when traveling over land for their size than smaller phocids. The unique method of terrestrial movement also exhibited greater energy expenditure on land than values for large quadrupeds. The trade-off for the northern elephant seal is that its massive size and morphology have well adapted it to an aquatic existence but limited its locomotor performance (i.e. speed, endurance) on land.

KEY WORDS: Phocid, Kinematics, Spinal flexion, Undulation, *Mirounga angustirostris*

INTRODUCTION

The suborder Pinnipedia is composed of three extant families of amphibious marine mammals: Otariidae (sea lions and fur seals), Odobenidae (walruses) and Phocidae (true seals) (Ray, 1963;

Fyler et al., 2005; Ferguson and Higdon, 2006). Pinnipeds are unique in that they are neither fully aquatic nor fully terrestrial, but they exhibit characteristics that make them more specialized for an aquatic existence (Howell, 1930; King, 1983; Riedman, 1990; Kuhn and Frey, 2012; Garrett and Fish, 2014). Such aquatic characteristics include modification of the forelimbs and hindlimbs into flippers, decreased pelage density and possession of blubber to enhance buoyancy, insulate the body and promote a streamlined body shape (Matthews, 1952; Fish et al., 1988; Fish, 1993).

Despite their aquatic specializations, pinnipeds continue to spend a large portion of their lives on land to breed, pup (birthing), molt, rest and locomote (Howell, 1930; Ray, 1963; King, 1983; Beentjes, 1990; Riedman, 1990; Stewart and DeLong, 1993; Hindell et al., 2003; Ferguson and Higdon, 2006; Kuhn and Frey, 2012; Garrett and Fish, 2014). Otariids and odobenids can locomote quadrupedally on land (Howell, 1930; English, 1976; Fay, 1981; Gordon, 1981; King, 1983; Burkhardt and Frey, 2008). The more aquatically adapted phocid seals, however, are no longer able to bring the hindlimbs forward to support the caudal portion of the body, restricting them to an undulatory pattern of movement (Murie, 1870; Allen, 1880; Howell, 1929; Matthews, 1952; Backhouse, 1961; O’Gorman, 1963; Tarasoff et al., 1972; Alejev, 1977; Beentjes, 1990; Garrett and Fish, 2014). Aristotle described phocids as misshapen quadrupeds (Peck and Foster, 1993). Terrestrial locomotion by phocids typically uses dorsoventral undulations of the spine in an ‘inchworm’ manner (Ray, 1963; Deméré and Yonas, 2009). This motion has also been described as a caterpillar-like movement (Le Boeuf and Laws, 1994; Kuhn and Frey, 2012), rocking-horse gait (Lansing, 1959) and a wriggling, serpentine motion (Allen, 1880). The foreflippers can also be used to assist in forward progression, but the seals’ inability to use the hindlimbs limits performance in speed and duration of movement (Murie, 1870; Howell, 1929; Matthews, 1952; Backhouse, 1961; O’Gorman, 1963; Tarasoff et al., 1972; Alejev, 1977; Beentjes, 1990).

The terrestrial locomotion of phocid seals provides an example of the evolutionary constraints that are associated with morphological compromises, which reduce locomotor performance in one medium while enhancing locomotor performance in another (Fish, 2000). A major trade-off of becoming more aquatically specialized is losing the ability to effectively move on land (Fish, 2000, 2001, 2018). Previous studies have qualitatively described the variation in terrestrial locomotion within the Phocidae by evaluating the anatomical, physiological, and behavioral characteristics (Murie, 1870; Howell, 1929; Matthews, 1952; Backhouse, 1961; O’Gorman, 1963; Ray, 1963; Tarasoff and Fisher, 1970; Tarasoff et al., 1972; Gordon, 1981), but quantitative data were lacking. Garrett and Fish (2014) were able to analyze phocid terrestrial locomotion by quantitatively analyzing the kinematics of terrestrial movements in harbor seals (*Phoca vitulina*) and gray seals (*Halichoerus grypus*). Their study was quantitatively limited in

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that they had no absolute scale and could only use relative measures of kinematics for wild seals.

The northern elephant seal, *Mirounga angustirostris*, is the second largest phocid seal in the world, with males reaching up to 4 m in length and 2700 kg (Le Boeuf, 1981; Deutsch et al., 1990). The large size of the elephant seals may be due to sexual selection and combat between males for mates (Le Boeuf, 1981; Le Boeuf and Laws, 1994), yet recent analysis suggests that aquatic mammals may be driven to larger body sizes because of energetic constraints due to the interplay of feeding efficiency and thermoregulation (Gearty et al., 2018). *Mirounga angustirostris* exhibits the typical undulatory pattern of movement seen in all phocids, but there are no studies detailing the kinematics of terrestrial locomotion for this particular species. Although previous studies have grossly described the unique patterns of terrestrial locomotion for phocids, it is necessary to examine the basic kinematics to quantitatively define the coordination between the body and limb movements as well as document parameters such as speed, duty factor, frequency of spinal flexions and amplitude of heave of spinal flexions.

The main objective of this study was to examine terrestrial locomotion of *M. angustirostris* through basic kinematic analysis with absolute measures of performance. The description and analysis of the motion of the elephant seal had not previously been performed. The movements of the eye, spinal flexion, foreflipper and pelvic region were analyzed to determine the coordination between the different areas of the body as well as their association with speed. The kinematics analyzed for *M. angustirostris* were compared with those found by Garrett and Fish (2014) for *P. vitulina* and *H. grypus*. It was predicted that *M. angustirostris* would exhibit kinematics different from those of smaller phocid seals based on scaling, indicating that its massive size placed additional constraints on terrestrial locomotion. To assess potential limitations due to large body size, a biomechanical model was developed to compare the energetics of phocids moving on land.

MATERIALS AND METHODS

Video data collection

The terrestrial movements of wild male northern elephant seals, *Mirounga angustirostris* (Gill 1866), were video recorded at Año Nuevo State Park, CA, USA (37.1331°N, 122.3331°W), where the terrain consisted mainly of flat bluffs extending down to gradually sloping sandy beaches (<4 deg). The substrate in both locations was sufficiently compacted so that there was no slippage of the propulsive forelimbs. Video recording of the seals was performed in mid-January 2015 and early January 2016 when the pupping season was coming to an end and the breeding season was at its peak (Reiter et al., 1981). As females were pupping and nursing, video recording of movements was confined to male elephant seals. Recordings were collected between 07:00 h and 10:00 h over 5 day periods.

Male seals ($N=70$) were recorded periodically in different locations when they freely moved. Movements by males occurred as individuals transited between the water and the beach, to basking spots, or toward or away from rival males. Animals were recorded with a Sony camcorder (model no. HDR-SR11; 30 frames s^{-1}) that was mounted on a tripod. The camera was positioned approximately perpendicular to the animal's rectilinear path in order to record the animal's movement from a lateral view. Videos were taken approximately 6–12 m away from the seal in order to obtain several locomotory cycles as animals moved through the field of view of the camera. Once a seal finished a locomotory cycle, a

researcher would stand in the animal's trail with a 0.5 m scale. When it was unsafe to move into the field of view, videos were scaled using the fully extended body length of the individual in the video sequence. Body length (BL) was measured to be the distance from the tip of the rostrum to the base of the tail when the body of the seal was fully extended. Elephant seal mass (M , kg) was estimated using the regression equation from Haley et al. (1991) as:

$$M = 301.337 SA^{1.319} BL^{0.539}, \quad (1)$$

where SA (m^2) is the projected lateral area determined by tracing the outline of a fully extended body.

This study was made possible through the National Marine Fisheries Service permit no. 19108 and was approved by West Chester University IACUC Protocol 201510.

Kinematic analysis

Video sequences from different individual male seals ($N=70$) were analyzed using ImageJ software (NIH version 1.45i). Kinematic variables included horizontal velocity (V), frequency of spinal flexions (f), average duty factor of the pelvic region and foreflipper (proportion of cycle) and amplitude of heave of the spinal flexion (A). Absolute (m) scales of measurement were used for all videos as well as relative scales based on body length (BL) in order to compare *M. angustirostris* data with data provided in Garrett and Fish (2014) on harbor seals (*P. vitulina*) and gray seals (*H. grypus*).

V was measured using the eye as a marker. The movement of the eye represented the speed of the seal as it progressed forward. V (in $m s^{-1}$) was calculated for each seal using the equation:

$$V = \frac{\text{Distance traveled}}{\text{No. of frames} \times 0.033}. \quad (2)$$

Distance traveled was considered to be the horizontal distance traversed by the seal (in m), accounting for the total number of frames and spinal flexions; 0.033 is the duration of each frame (in s). The length-specific V ($BL s^{-1}$) was calculated by dividing the fully extended BL of the seal (in m) by the speed in $m s^{-1}$. f (Hz) was calculated as the inverse of the period of a stride, where a stride represents a complete cycle of motion. Duty factor (proportion of the cycle) was calculated for the foreflippers and pelvic region, as the hindflippers played no role in forward progression. Duty factor was computed as the proportion of time that a body part (i.e. foreflipper, pelvic region) remained in contact with the ground for a full stride (Garrett and Fish, 2014). A (m) was measured from the lowest point on the spine at mid-body when the body was extended, to the highest point on the spine on the trunk at the peak of spinal flexion.

To provide a more detailed examination of the kinematics of the body and appendages, seven sequences were analyzed frame-by-frame for individual male elephant seals using ProAnalyst® (version 1.5.4.8, 3-D Professional ed., Xcitex Inc. 2011). The seven sequences were selected to exemplify movements over the range of speeds. This analysis was used to quantify the coordination of the body movements. Specific points on the body were analyzed using 2D feature tracking, which allowed the user to manually track pre-defined points on the body and determine speed, acceleration and displacement of the different body points (Fig. 1). The features tracked included the eye, the highest point of the spinal wave, the foreflipper tip and the pelvic region or tail base. The highest point of the spinal wave created during forward progression was tracked

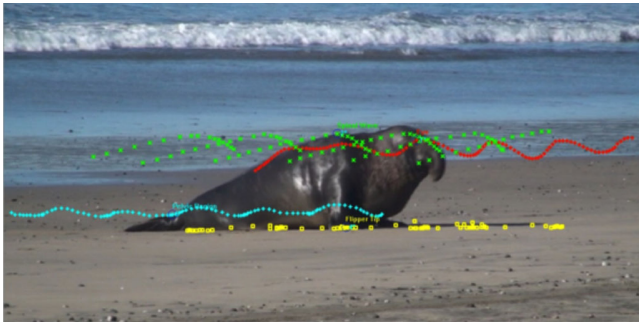


Fig. 1. Feature tracking of the eye (red), spinal wave (green), foreflipper tip (yellow) and pelvic region (blue) from ProAnalyst®. Whereas the movements of the pelvic region and eye are displayed as sinusoidal curves, the movements of the spinal wave (top curves) and foreflipper tip (bottom symbols) are discontinuous.

using the dorsal margin of the mid-body. Feature tracking was completed over multiple strides.

Data corresponding to the forward velocity (m s^{-1}) of the eye, spinal wave, pelvic region and foreflipper tip were exported from ProAnalyst® and graphed in Excel. The patterns of horizontal movements of the four points were used to determine accelerations and decelerations among the different parts of the body during forward progression. These data corresponded to the vertical displacements (m) of the eye, spinal wave, foreflipper tip and pelvic region in addition. The raw data used for the graphs were filtered in ProAnalyst® using a first-order low-pass, Butterworth filter (10 Hz cut-off).

Comparison of the phase cycles between the spinal wave and the eye served to express the relative displacement between the two waves. The spinal wave was considered to be the feature that led locomotion, with the movement of the eye following shortly after. The phase difference between the spinal and eye movements was calculated for each seal by dividing the average amount of time it took to complete one cycle of the forward movement of the eye by the average amount of time to complete one cycle of the spinal wave. The proportion of time was then multiplied by 360 deg (i.e. one full cycle) to display the phase difference in degrees (Garrett and Fish, 2014). Phase differences were similarly calculated for the pelvic region and foreflipper. The pelvic region was considered to lead and served as the reference point to determine the phase difference.

Comparative data were obtained from Garrett and Fish (2014) for speed (BL s^{-1}), frequency (f ; Hz), heave amplitude (A ; BL) and duty factor of the foreflipper (proportion of cycle) for harbor seals (*P. vitulina*) and gray seals (*H. grypus*). These data were used for comparison with data from *M. angustirostris* (Table 1).

Table 1. Mean (\pm s.d.) relative kinematic values for elephant, gray and harbor seals

	Elephant seal <i>Mirounga</i> <i>angustirostris</i> $n=70$	Gray seal <i>Halichoerus</i> <i>grypus</i> $n=15$	Harbor seal <i>Phoca</i> <i>vitulina</i> $n=37$
Mean V (BL s^{-1})	0.29 ± 0.11^a	0.81 ± 0.17^b	0.92 ± 0.22^b
Mean f (Hz)	1.45 ± 0.22^a	2.19 ± 0.38^b	2.73 ± 0.25^c
Mean A (BL)	0.07 ± 0.02^a	0.09 ± 0.03^b	0.11 ± 0.03^b
Mean foreflipper DF (proportion of cycle)	0.55 ± 0.11^a	0.54 ± 0.07^a	0.54 ± 0.08^a

V , velocity; f , frequency; A , amplitude; DF, duty factor; BL, body lengths.

Values with the same letter (a, b, c) denote seal species that were not found to be significantly different from one another.

Analysis of mechanical energy of terrestrial locomotion

To determine the mechanical power (P) expended by the elephant seals for terrestrial locomotion in comparison to smaller phocids (harbor seal, gray seal), a computational biomechanical model was developed. Variables input into the model included BL, M , absolute and relative V , f and A (Table 2). Kinematic data for harbor and gray seals were obtained from regression equations by Garrett and Fish (2014). As Garrett and Fish (2014) were unable to measure body lengths and masses of the wild seals that they studied, median values were determined from Jefferson et al. (2015). P was examined among the different species at their maximum velocities (V_{\max}) and at the velocity of 0.6 BL s^{-1} ($V_{0.6}$). The latter velocity was chosen as this was a speed common to all species studied.

The oscillatory character of the motions of specific body parts of seals, as seen in Fig. 1 and 2, and in Movie 1, permits an analysis of the locomotion that determines the power expenditure of the animals. In oscillatory motion that propagates as a wave, as depicted in Fig. 1, the vertical and horizontal motions are coupled. Fig. 1 shows that the elements of the seal marked for analysis (the eye, for example) follow a traveling wave with both vertical (transverse) and horizontal motions. Energies, both kinetic and potential, are associated with these motions. The analysis models the wave apparent in the rhythmic undulations produced by dorsoventral spinal flexion. Of course, not all elements (points) on an elephant seal move as a traveling wave (e.g. the hindflippers, which are essentially dragged), but the bulk of the animal does undulate as is apparent from Fig. 1 and also Fig. 2, so the analysis follows the energy associated with any oscillatory motion. Thus, the transverse motion (i.e. vertical direction in the initial part of the analysis) couples to the horizontal motion, and the goal of the model is to track the rate of energy usage in the animals' undulatory motions. The model assumes that the seals travel along level ground. As videos were collected on seals traversing the flat bluffs and moving on the relatively flat beaches, the assumptions of the model were valid. Only a 15% uncertainty would be introduced if the animal were to move up or down an incline of 5 deg in a run of 10 m, which would be greater than the actual grade that the seals experienced.

The vertical motion as described by the coordinate y can be approximated as a function of the horizontal position, x , and time,

Table 2. Kinematics and power expenditure during terrestrial locomotion of phocids at maximum speed and 0.6 BL s^{-1}

Parameter	Elephant seal <i>Mirounga</i> <i>angustirostris</i>	Gray seal <i>Halichoerus</i> <i>grypus</i>	Harbor seal <i>Phoca</i> <i>vitulina</i>
BL (m)	3.44	2.13*	1.8*
M (kg)	821.5	250.0*	97.5*
V_{\max} (m s^{-1})	$2.56 (0.71)^{\dagger}$	$2.68 (1.26)^{\dagger}$	$2.49 (1.38)^{\dagger}$
$V_{0.6}$ (m s^{-1})	$2.16 (0.6)^{\dagger}$	$1.28 (0.6)^{\dagger}$	$1.08 (0.6)^{\dagger}$
f (Hz) (V_{\max})	2.03	3.00	2.97
f (Hz) ($V_{0.6}$)	1.88	1.84	2.58
A (m) (V_{\max})	0.33	0.11	0.14
A (m) ($V_{0.6}$)	0.31	0.09	0.08
P (W) (V_{\max})	5530	652	468
P/M (W kg^{-1}) (V_{\max})	6.7	2.7	4.8
P (W) ($V_{0.6}$)	3290	77	47
P/M (W kg^{-1}) ($V_{0.6}$)	4.00	0.31	0.48

BL, body lengths; M , mass; V_{\max} , maximum velocity; $V_{0.6}$, velocity of 0.6 BL s^{-1} ; f , frequency; A , amplitude; P , power.

*Values based on median values from Jefferson et al. (2015).

† Values in parentheses represent velocities in BL s^{-1} .

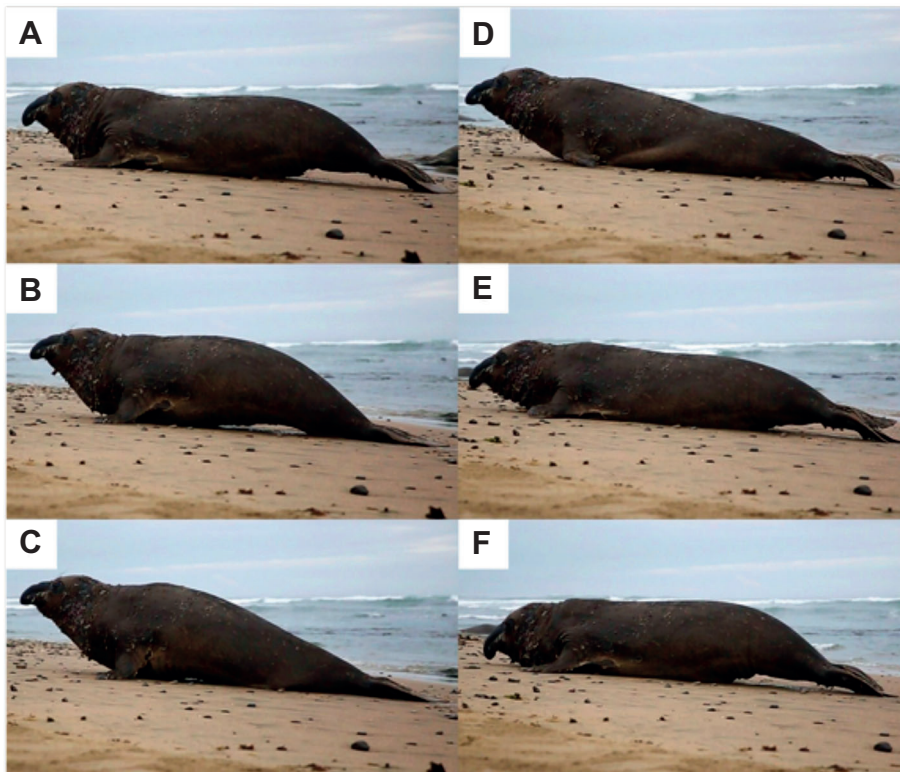


Fig. 2. Sequence (A–F) of a typical stride during a locomotor cycle for *Mirounga angustirostris*.

t , as a traveling wave given by:

$$y(x, t) = A \cos(kx - \omega t) = A \cos\left(\frac{2\pi x}{\lambda} - 2\pi f t\right), \quad (3)$$

where k is the wavenumber, λ is the wavelength, ω is the angular frequency and f is the frequency. A represents the heave amplitude of an oscillating element of the seal. In the analysis to follow, let $\mu = M/\text{BL}$, where M is the mass of the seal and BL is the length of the seal. The kinetic energy dK associated with a small element of mass dM of the seal is $dK = (1/2)dM V_{\text{trans}}^2$, where V_{trans} is the transverse speed of a body component. To determine V_{trans} , we differentiated $y(x, t)$ with respect to time, yielding:

$$V_{\text{trans}} = \frac{dy}{dt} = \omega A \sin(kx - \omega t). \quad (4)$$

Using this and putting $dM = \mu dx$, we have:

$$dK = \frac{1}{2}(\mu dx)(\omega A)^2 \sin^2(kx - \omega t). \quad (5)$$

Dividing by dt gives the rate at which kinetic energy passes through an oscillatory element of the seal, and thus the rate at which energy is carried and used by the seal. The ratio dx/dt that then appears on the right is the horizontal speed of the animal, V , thus:

$$\frac{dK}{dt} = \frac{1}{2} \mu V \omega^2 A^2 \sin^2(kx - \omega t). \quad (6)$$

The average rate at which kinetic energy is transported is:

$$\left\langle \frac{dK}{dt} \right\rangle = \frac{1}{2} \mu V \omega^2 A^2 \langle \sin^2(kx - \omega t) \rangle = \frac{1}{4} \mu V \omega^2 A^2. \quad (7)$$

Here, we have taken the average over an integer number of cycles and have used the fact that the average value of the square of the sine function over an integer number of cycles is $1/2$.

Elastic potential energy is also carried by the oscillations of the seal. In any oscillatory system, the average kinetic energy equals the average potential energy and they are in phase (Full, 1989). Thus, the average power, $\langle P \rangle$, which is the average rate at which both kinetic and potential energies are used by the seal, is then:

$$\langle P \rangle = 2 \left\langle \frac{dK}{dt} \right\rangle = \frac{1}{2} \mu V \omega^2 A^2 = 2\pi^2 \mu V f^2 A^2. \quad (8)$$

Statistical analysis

SPSS (version 20.0.0.1) was used for statistical analyses. The mean, maximum, minimum and standard deviation (s.d.) were calculated for the kinematic variables. The locomotor sequence of each seal was only recorded once to maintain independence of the samples. As males tend to be territorial, moving to new sites on multiple beaches reduced the likelihood of resampling individuals. Multiple strides were averaged for each recorded sequence. Means are expressed ± 1 s.d. Significance was considered at $P \leq 0.05$. Regressions with a confidence interval of 95% were used to determine whether V had a significant influence on f , A and duty factor.

One-way analysis of variance (ANOVA) was used to determine whether elephant seals, harbor seals and gray seals differed with respect to kinematics. A Tukey test was used as the *post hoc* test to assess differences between species if significance was found with the ANOVA. If skewness (|skew/std. error of skew|) and/or kurtosis (|kurtosis/std. error of kurtosis|) values exceeded ± 2 , the assumption of equal variances was not met based on Levene's test and the kinematic variables were compared using the non-parametric Welch's ANOVA. The non-parametric Games–Howell test served as the *post hoc* test.

RESULTS

The mean body length (BL) for the male northern elephant seals studied was 3.44 ± 0.46 m. The lateral area measured from video was

$1.37 \pm 0.40 \text{ m}^2$. Based on the equation by Haley et al. (1991), mean mass (M) for the elephant seals was $821.5 \pm 406.3 \text{ kg}$ with a maximum of 2715.3 kg .

Examination of recorded video showed that male northern elephant seals moved across the beaches using a series of rhythmic undulations produced by dorso-ventral spinal flexion with support from the foreflippers and pelvic region. The sternum, pelvis and foreflippers served as the main points of contact with the ground, while the spine flexed and extended during forward progression. The trail left by the body was smooth with no periodic depression, unlike the depression left lateral to the trail by the flippers. Spinal flexion was characterized by an anteriorly directed wave along the dorsal margin of the body, which served to move the seal's mass forward. Fig. 2 provides an example of a typical stride observed during a locomotor cycle for *M. angustirostris*. Bouts of movement in male elephant seals typically began by lifting the head and neck before letting them fall forward to initiate forward progression. The motion of the seals seemed limited as they did not maintain multiple strides for extended periods ($<30 \text{ s}$). Bouts of movement were interposed by prolonged rest periods.

The beginning of the stride (Fig. 2A) was initiated when the seal flexed the lumbar region of its spine, causing the pelvic region to lift off the ground. The manus of the foreflipper rested flat on the ground anterior to the sternum at an angle of $\sim 45^\circ$ to the body. The distal ends of the hindflippers remained in contact with the ground, but were dragged passively and provided no support for the caudal region of the body.

The wave induced by spinal flexion continued to move anteriorly, causing the thoracic and abdominal regions to lift as the pelvic region was placed back on the substrate (Fig. 2B). The seal began to rise up on its foreflippers, using them for support as the weight of the body was shifted forward. The foreflippers rotated postero-laterally as the neck began to extend forward.

The spinal wave continued to travel anteriorly until it reached its peak over the shoulders of the seal (Fig. 2C). The abdominal region was placed back on the ground and the chest was lifted slightly higher with the full support of the foreflippers. The foreflippers were fully extended with the shoulders positioned directly over the manus and acted like crutches. The neck was extended forward in preparation for the anterior region of the body to fall towards the ground.

As the seal began to fall forward, it shifted its weight from the foreflippers to the sternum (Fig. 2D). At this point, the spine was fully extended and the body was in contact with the ground from the sternal to pelvic regions. The tail base, just caudal to the pelvic region, and the foreflippers were simultaneously lifted. The foreflippers began to move antero-laterally.

The spine was flexed and the pelvic region was lifted once again (Fig. 2E). The foreflippers moved antero-laterally to prepare for the shift in the body weight resulting from the forward-moving spinal wave. The neck was truncated and positioned close to the ground as the seal moved its foreflippers anterior to the sternum.

Fig. 2F marks the beginning of a new stride, where the spinal wave continued to move anteriorly along the dorsal margin, causing the abdominal and pelvic regions to lift off the ground and the thoracic region to bear the weight of the body. The manus of the foreflipper was placed flat on the ground anterior to the sternum and shoulder girdle in preparation to pivot and support the thoracic region of the body as the spinal wave reached its peak. This sequence continued in a rhythmic, cyclical fashion until the animal tired and ceased locomotion (Fig. 1).

Some seals displayed a slight variation from the above description. Two seals did not use their foreflippers and forward progression was accomplished solely by spinal flexion. The foreflippers were held to the side for the entire locomotory cycle. One seal used its foreflippers for the beginning of its locomotory

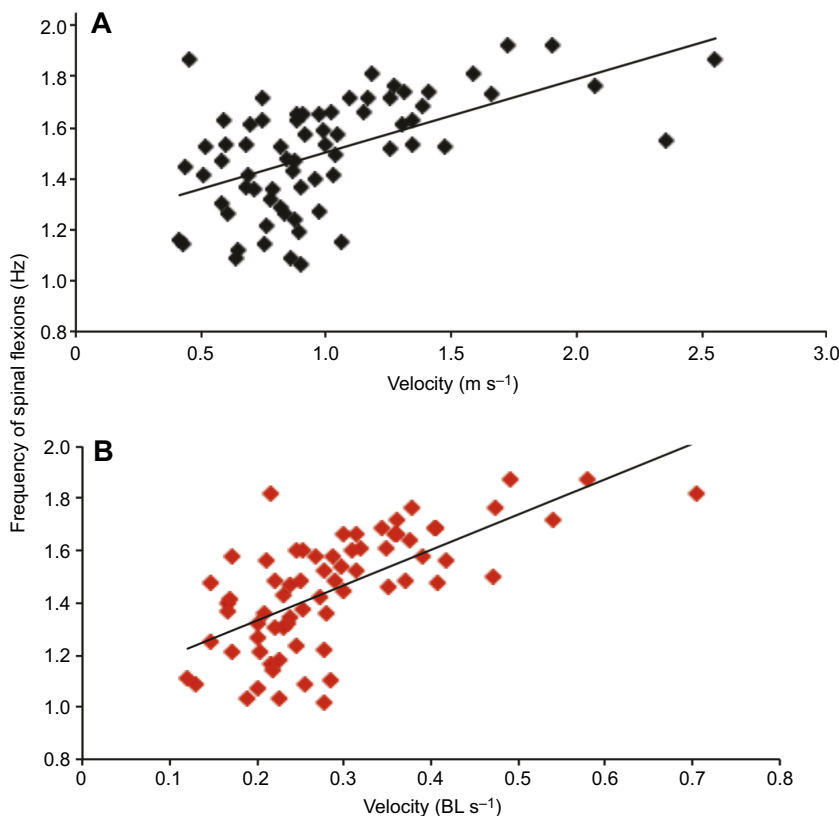


Fig. 3. Scatter plot indicating the relationship between velocity (V) and the frequency (f) of spinal flexions. Data are shown for (A) absolute velocity in m s^{-1} (linear regression; $N=70$; $f=0.29V+1.17$, $r=0.55$, $P<0.001$) and (B) relative velocity in body lengths (BL s^{-1}) (linear regression; $N=70$; $f=1.36V+1.06$, $r=0.67$, $P<0.001$).

cycle but stopped using them after experiencing a stumbling motion. The foreflippers were held to the side for the remaining strides. Another seal, which was being chased by a rival male, used its foreflippers for the initial strides of locomotion but quickly ceased the use of its foreflippers after experiencing a stumbling motion. All seals dragged their hindflippers along the ground throughout the entire locomotory cycle.

Kinematics of terrestrial locomotion

Seventy locomotor sequences were examined for male adult and subadult elephant seals. The seals exhibited mean V of $1.00 \pm 0.43 \text{ m s}^{-1}$ ($0.29 \pm 0.11 \text{ BL s}^{-1}$). V ranged from 0.41 to 2.56 m s^{-1} ($0.12\text{--}0.71 \text{ BL s}^{-1}$).

The stride frequency (f) ranged from 1.02 to 1.88 Hz. For elephant seals, f increased directly with V (Fig. 3). The relationship of f to V was statistically significant for absolute ($F_{1,68}=30.092$, $r=0.55$, $P<0.001$) and relative ($F_{1,68}=54.071$, $r=0.67$, $P<0.001$) values.

The amplitude of spinal flexions (A) of the elephant seals showed a direct increase with increasing speed ($F_{1,68}=13.688$, $r=0.41$, $P<0.001$) for absolute values (Fig. 4). A ranged from 0.12 to 0.46 m. There was no significant relationship between V and A using length-specific values ($F_{1,68}=2.159$, $r=0.12$, $P=0.146$). The mean A

for length-specific values was $0.07 \pm 0.01 \text{ BL}$ over the range 0.04–0.11 BL (Fig. 4).

The average duty factor of the foreflipper (excluding the four seals that did not use their foreflippers during locomotion) was 0.55 ± 0.11 with a range of 0.31–0.80. Fig. 5 shows that the duty factor of the foreflipper did not display any significant relationship with V in m s^{-1} ($F_{1,64}=0.903$, $r=0.19$, $P=0.345$) or in BL s^{-1} ($F_{1,64}=3.656$, $r=0.23$, $P=0.06$). Duty factor of the pelvic region ranged from 0.27 to 0.79. Duty factor of the pelvic region showed a direct decrease with increasing V in both absolute ($F_{1,68}=17.541$, $r=0.45$, $P<0.001$) and relative ($F_{1,68}=23.843$, $r=0.51$, $P<0.001$) measurements (Fig. 5).

Phase difference

The mean phase difference between the spinal and eye movements for northern elephant seals was 23.93 ± 11.34 deg and ranged from 11.43 to 42.31 deg (Fig. 6). The mean phase difference between movements of the pelvic region and foreflippers was 21.55 ± 11.08 deg ranging from 0.05 to 30.86 deg (Fig. 6).

Comparison of elephant seals with other phocids

The median M for gray and harbor seals obtained from Jefferson et al. (2015) was 250.0 and 97.5 kg, respectively (Table 2). M for

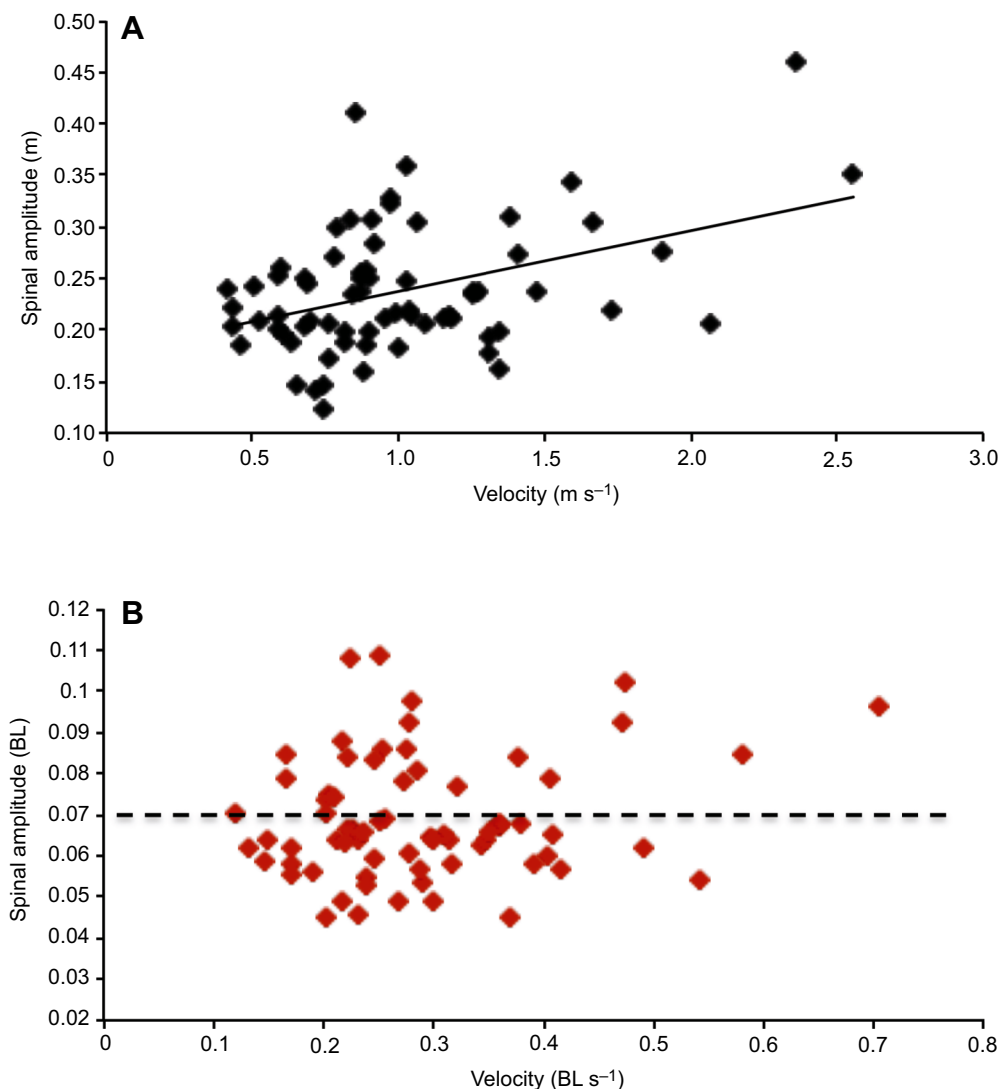


Fig. 4. Scatter plot indicating the relationship between velocity (V) and the amplitude (A) of heave of spinal flexions. Data are shown for (A) absolute velocity in m s^{-1} and amplitude in m (linear regression; $N=70$; $A=0.06V+0.18$, $r=0.41$, $P<0.001$) and (B) relative velocity in BL s^{-1} and amplitude in BL. The dashed line indicates the mean of the spinal amplitude ($N=70$).

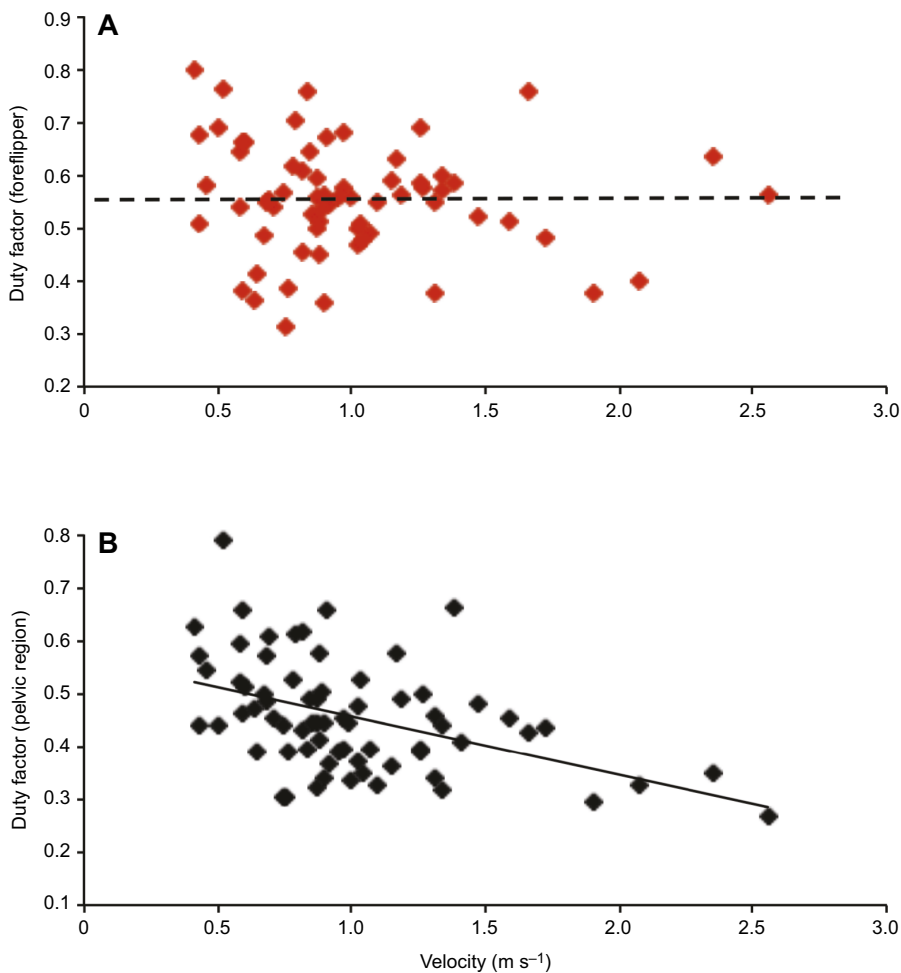


Fig. 5. Scatter plot indicating the relationship between velocity and average duty factor. Data are shown for (A) the foreflipper and (B) the pelvic region. The dashed line indicates the mean duty factor of the foreflipper ($N=70$) and the solid line indicates the linear regression for duty factor of the pelvic region ($N=70$; duty factor $= -0.11V + 0.57$, $r = 0.45$, $P < 0.001$).

the elephant seals was 3.3 and 8.4 times greater than that for gray and harbor seals, respectively.

Table 1 provides relative kinematic values for male elephant seals as well as data from Garrett and Fish (2014) for wild harbor seals and gray seals. There was an overall significant difference in speed (BL s⁻¹) amongst the three species ($F_{2,31.780} = 175.877$, $P < 0.001$). Both harbor seals and gray seals had an average relative speed that was significantly higher than that of elephant seals ($P < 0.001$) by 3.17 and 2.79 times, respectively. Maximum speed for harbor and gray seals was only 1.94 and 1.77 times higher, respectively, than the maximum speed of an elephant seal.

There was an overall significant difference for f amongst the three species ($F_{2,119} = 317.874$, $P < 0.001$). Harbor seals flexed their spines more rapidly than both gray seals ($P < 0.001$) and elephant seals ($P < 0.001$). All three species showed an increase in frequency with increasing speed (Fig. 7). The f for the three phocids shows a negative relationship with increasing mass (Table 1).

A (BL) showed an overall significant difference amongst the three species ($F_{2,31.014} = 27.865$, $P < 0.001$). Harbor seals and gray seals both had significantly higher relative A than elephant seals ($P < 0.001$; $P = 0.009$), respectively. Table 1 shows the mean relative $A \pm 1$ s.d. for the three species of seals.

Duty factor of the foreflipper showed no significant difference ($F_{2,109} = 0.355$, $P = 0.702$) among the three species (Table 1, Fig. 8), indicating that duty factor was not dependent on body size. The combined average duty factor for the three species was 0.54. Duty factor of the pelvis was not compared statistically, because Garrett

and Fish (2014) found that harbor seals and gray seals never lifted their pelvises off the ground during terrestrial locomotion (i.e. duty factor = 1.0). Elephant seals, however, showed a distinct elevation in the pelvic region during terrestrial locomotion (duty factor = 0.46 ± 0.10).

Energetics of terrestrial locomotion

The results of the analysis of the power expended during terrestrial locomotion by elephant, gray and harbor seals are displayed in Table 2. The elephant seals had a mechanical power output (P) of 5530 W at V_{\max} . P was reduced by 40.5% when the seals were moving at a 15.5% lower speed at 0.6 BL s⁻¹. At V_{\max} , the mass-specific power (P/M) was 6.7 W kg⁻¹, which was 40.3% higher than when the elephant seal was moving at 0.6 BL s⁻¹.

DISCUSSION

Unlike other semi-aquatic mammals that have maintained the use of their hindlimbs on land, phocids have become highly aquatically specialized and evolved an osteology and myology that has restricted the use of the hindflippers for aquatic propulsion and rendered them incapable of being rotated underneath the body to assist in terrestrial locomotion (Howell, 1930; Tarasoff, 1974; Williams, 1983; Garrett and Fish, 2014). Phocids must therefore use spinal undulations assisted by the forelimbs to accomplish forward progression on land (Howell, 1929; Matthews, 1952; Backhouse, 1961; O'Gorman, 1963; Douxchamps, 1969; Tarasoff et al., 1972; Garrett and Fish, 2014). The lumbar region of phocids is highly

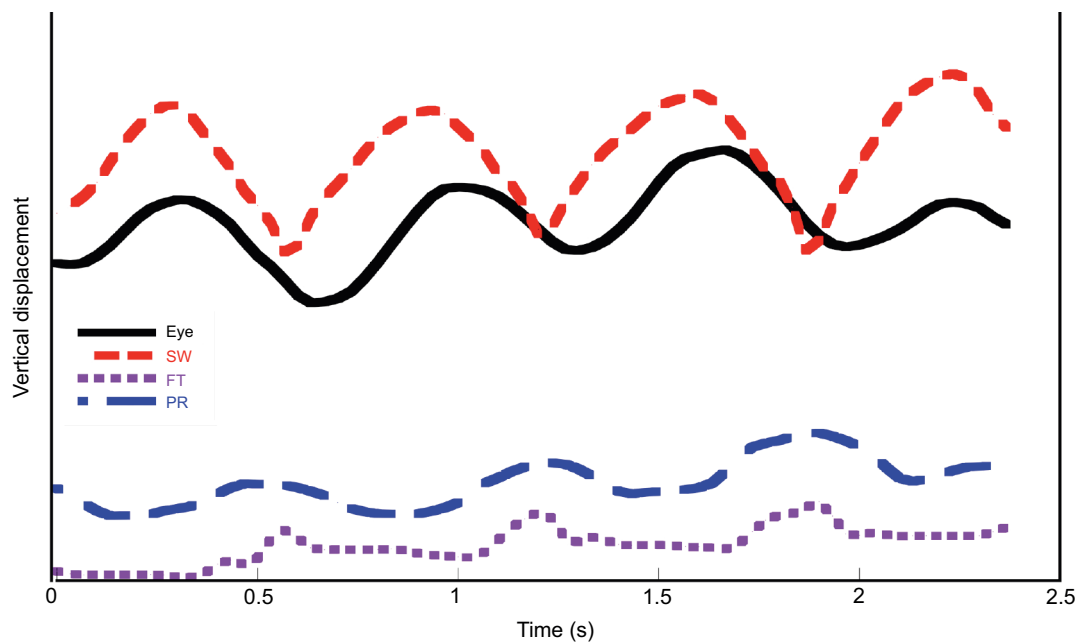


Fig. 6. Relative vertical displacements of tracked maximum spinal wave height (SW), eye, foreflipper tip (FT) and pelvic region (PR), showing phase differences for a northern elephant seal moving up the beach.

flexible with long muscular lever arms that are necessary to permit the spinal undulations (Pierce et al., 2011).

The locomotor motion of seals was described by Aristotle to be clumsy, with the seal as an imperfect or crippled quadruped (Thompson, 1907). Murie (1870) stated that seals had the oddest kind of movement that was almost sadly ridiculous with a belly-progressive gait. Despite these derogatory comments on the terrestrial locomotion of phocids, seals on land can move with surprising speed, especially on ice (Allen, 1880; Lansing, 1959; O’Gorman, 1963; Ray, 1963; Dickenson, 2016).

Elephant seal kinematics

The observed locomotion of northern elephant seals showed that these massive seals were capable of moving across sandy beaches using dorso-ventral spinal undulations with support from the foreflippers and pelvic region. In some cases, the foreflippers were not used directly to aid in forward progression. Despite being the sole means by which these seals propel themselves through

water (Ray, 1963; Tarasoff et al., 1972; Fish et al., 1988), the hindflippers were dragged passively throughout the locomotory cycle (Murie, 1870; Howell, 1929; Matthews, 1952; Backhouse, 1961; O’Gorman, 1963; Tarasoff et al., 1972; Beentjes, 1990; Garrett and Fish, 2014).

The combined undulatory and footfall pattern exhibited by phocids represents a modification of the bounding gait used on land by limbed mammals (Matthews, 1952; Backhouse, 1961; O’Gorman, 1963; Tarasoff et al., 1972; Garrett and Fish, 2014). Bounding is considered an asymmetrical gait whereby a pair of feet functions in tandem, striking the ground together in couplets or simultaneously (Hildebrand, 1989). In a true bounding gait, there is a large portion of the stride where the limbs are in an unsupported phase and display no contact with the ground (Hildebrand, 1980, 1989). This unsupported phase allows time for the hindlimbs to move into position for another bound (Howell, 1965).

While there is no true unsupported phase in phocid terrestrial locomotion, many phocids (including northern elephant seals)

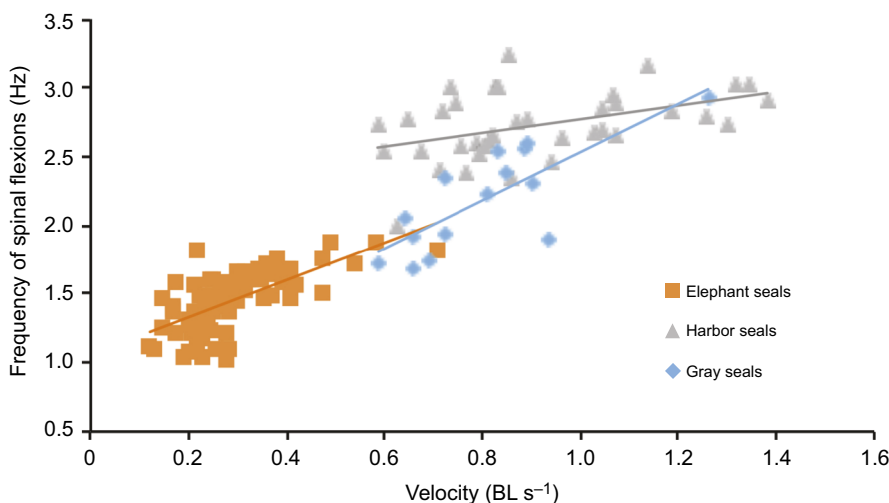


Fig. 7. Scatter plot indicating the relationship between velocity and frequency of spinal flexions of phocids. Wild elephant seals: $f=1.36V+1.06$ ($r=0.67$, $P<0.001$); harbor seals: $f=0.50V+2.28$ ($r=0.45$, $P=0.006$); and gray seals: $f=1.76V+0.78$ ($r=0.79$, $P<0.001$).

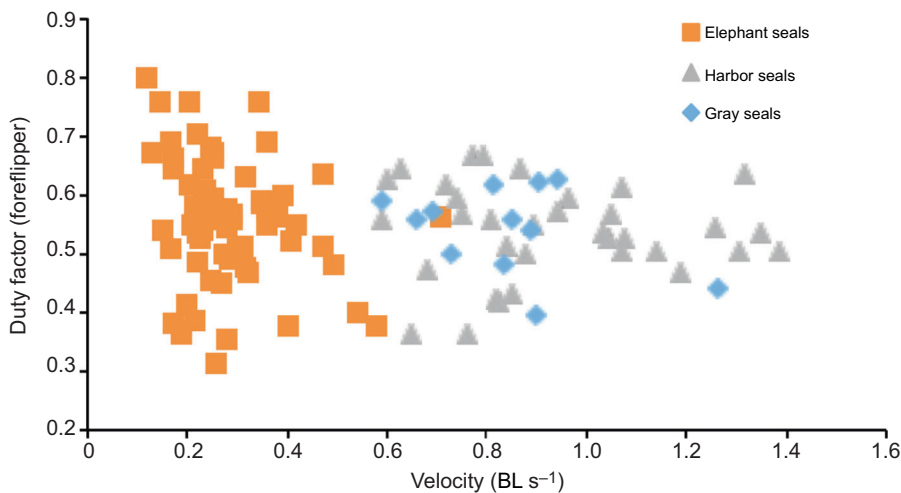


Fig. 8. Scatter plot showing the relationship between velocity and duty factor of the foreflipper (proportion of cycle) of phocids.

display a distinct gap between the body and the ground when the spine is flexed and the pelvis is lifted (Lockley, 1966). According to Biewener (2003), terrestrial animals show a decrease in the relative fraction of limb support (duty factor) and an increase in the swing phase (i.e. period where a body part is not in contact with the ground) as speed increases. Northern elephant seals showed a distinct vertical displacement in the pelvic region during forward progression and a significant decrease in the duty factor of the pelvic region with increasing speed (Fig. 5). The swing phase seen in the pelvic region of northern elephant seals during terrestrial locomotion separates them from the smaller harbor and gray seals. Garrett and Fish (2014) found that harbor and gray seals exhibited a duty factor of 100%, meaning that their pelvises never left the ground during terrestrial locomotion. Lifting the pelvic region could play a role in mitigating the friction associated with dragging the hindlimbs throughout the locomotor cycle (Garrett and Fish, 2014), therefore reducing the amount of energy required for forward progression. Because elephant seals exhibited a distinct aerial phase in the pelvic region during terrestrial locomotion, they more closely resembled the bounding gaits of terrestrial mammals (Hildebrand, 1980, 1989).

The foreflippers displayed a distinct vertical displacement during terrestrial locomotion, but the duty factor remained constant with increasing speed. Usually, terrestrial mammals will move their limbs more rapidly in order to move faster (Biewener, 2003). Over a range of Froude numbers representing a dimensionless speed, walking gaits of quadrupedal mammals have a duty factor greater than 0.5 which decreases with increasing speed, so that the duty factor for running gaits is less than 0.5 (Alexander, 1983, 1991). The limbs spend less time in contact with the ground as they move more rapidly, thereby causing the duty factor to decrease (Biewener, 1983; Gatesy and Biewener, 1991; Garrett and Fish, 2014). Garrett and Fish (2014) hypothesized that the duty factor of phocid foreflippers does not decrease with increasing speed because the foreflippers do not effectively carry the body over the substrate, but instead support and stabilize the body during forward progression. Furthermore, the longer duty factor for the seals compared with that of terrestrial mammals reduces the forces for locomotion, but limits the speed of movement (Biewener, 1983, 2003).

The anteriorly directed wave of spinal flexion traveled along the dorsal margin of the body of the seals, ending at its highest point above the shoulders (present study; Garrett and Fish, 2014). The peak of the spinal undulation, in concert with the extension and

support of the foreflippers, allowed the sternum to be lifted off the ground. The spine was then extended, causing the animal to shift its weight from the foreflippers to the sternum. The forward movement of the seal and support of the anterior trunk by the forelimbs was similar to crutching observed in the locomotion of some mudskippers, early tetrapods and primates (Harris, 1960; Kimura, 1987; Vereecke et al., 2006; Pierce et al., 2012; Kawano and Blob, 2013).

In crutching, the body rotates over a rigid vertically oriented limb that pivots on a fixed point on the ground. To move the body up over the pivot point, a force must be applied by the animal that moves the body up and forward. From the body's highest point over the pivot point, the body moves forward and down assisted by gravity in the latter half of the crutching movement. Crutching could be used as an inverted pendulum to recycle energy and reduces the cost of locomotion in elephant seals (Alexander, 1984). However, like the amphibious mudskipper (Pace and Gibb, 2005), the idea of recycling energy for the elephant seal is not warranted. Much of the seal's body remains in contact with the ground and the duty factor of the forelimbs is equivalent to that of the mudskipper. The crutching by the seal raises the anterior body off the substrate to advance by pushing from the pelvic region. In addition, the seals can take advantage of the increased elevation of the body to utilize potential energy to fall forward and advance across the ground.

Spinal flexion and extension were the primary means by which phocids advanced forward progression (this study; O'Gorman, 1963; Ray, 1963; Tarasoff et al., 1972; Garrett and Fish, 2014). Quadrupeds can move faster by increasing either their stride frequency or stride length, or both (Biewener, 2003). The relative importance of increasing the stride frequency versus the stride length depends on the type of gait employed by an animal. Because phocid seals employ an undulatory mode of locomotion and are unable to bring the hindlimbs forward to assist in increasing their stride length, they are heavily reliant on increasing their stride frequency (i.e. frequency of spinal flexions).

As with other mammals, stride frequency of the elephant seal increased with increasing speed (Heglund et al., 1974; Heglund and Taylor, 1988). Heglund and Taylor (1988) provided a set of equations relating the stride frequency relative to body mass for a variety of quadrupedal mammals. The predicted frequency was 1.55 Hz for the preferred gallop speed of a mammal of the same average mass of an elephant seal. What is remarkable is that despite the differences in gaits used by quadrupedal mammals, the predicted stride frequencies

were within the range of frequencies displayed by elephant seals. Although galloping can involve flexion and extension of the spine to increase speed (Hildebrand, 1974), the predicted preferred galloping speed (Heglund and Taylor, 1988) of 9.06 m s^{-1} is well above the locomotor performance of the elephant seal.

The limitation of using body undulations in concert with crutching with the short supporting foreflippers is expressed as the relatively low maximum speed of elephant seals (2.56 m s^{-1}). The otariids (sea lions, fur seals) can locomote quadrupedally on land with terrestrial gaits (e.g. walk, gallop). Walking speeds are low (0.72 m s^{-1}) for fur seals and sea lions (Beentjes, 1990), which must coordinate movements of the enlarged flippers. For faster terrestrial speeds up to 3.61 m s^{-1} , a gallop or a bounding gait with spinal flexion can be used (Beentjes, 1990). These quadrupedal gaits used by otariids are faster than the speeds measured for the elephant seal. Extreme running speeds by cheetahs (30.6 m s^{-1}) and pronghorns (27.8 m s^{-1}) are well known (Garland, 1983) and 12 and 10.9 times greater than the maximum speed of the elephant seal; the difference in running speed is exacerbated by both the use of long supportive limbs and the size of these high-performance terrestrial mammals. However, spinal flexion can add to the length of stride and increase running speed. Hildebrand (1974) estimated that a cheetah could use spinal flexion to theoretically run at 2.8 m s^{-1} without any legs. Maximum running speeds are highest at an optimal body mass of 119 kg and fall off at both higher and lower body masses (Garland, 1983). Even for large quadrupedal mammals (1400–6000 kg), including elephants, hippopotamus and rhinoceros, the maximum terrestrial speeds were 2.7–4.9 times higher than the maximum speed of the elephant seal (Garland, 1983; Hutchinson et al., 2003).

Comparison kinematics with other phocids

The maximum speed observed in northern elephant seals during this study (2.56 m s^{-1}) was similar to speeds found previously. Bartholomew (1952) found that northern elephant seals could move over sandy beaches at speeds ranging from 2.22 to 2.64 m s^{-1} . Higher speeds (5.30 m s^{-1}) have been reported for other phocid species (e.g. crabeater seal, harp seal), but the methods by which these measurements were obtained were questionable because the animals were being chased across snow and ice (Lindsey, 1938; O’Gorman, 1963; Tarasoff et al., 1972). Movements for northern elephant seals were recorded for animals that moved freely, ensuring that no outside factors influenced the speed of locomotion. The relative speeds found for elephant seals were compared to the relative speeds found by Garrett and Fish (2014) for harbor and gray seals. Elephant seals moved at length-specific speeds that were slower than those of harbor and gray seals. However, with respect to absolute speed, stride length increases more rapidly than the decrease in stride frequency with increasing size, so larger animals are generally able to attain greater top speeds (Biewener, 2003).

A comparison of elephant seal kinematics with data presented previously by Garrett and Fish (2014) showed that the large elephant seals exhibited kinematic trends similar to those seen in the smaller harbor and gray seals. All species showed an increase in the frequency of spinal flexions with increasing speed (Fig. 7). Elephant seals, however, displayed a lower mean frequency of spinal flexions: 33.8% and 46.9% lower than that of gray seals and harbor seals, respectively. As phocid seals increase in size, the frequency of spinal flexions decreases during terrestrial locomotion (Table 1).

Elephant, harbor and gray seals showed an increase in the relative amplitude of spinal flexions with increasing speed. All three species required substantial vertical oscillations of the trunk of the body in

order to maintain forward progression. The vertical displacement these animals experience can result in potential and kinetic energy fluctuating in phase (Alexander et al., 1980; Cavagna et al., 1977; Full, 1989; Garrett and Fish, 2014). These energy fluctuations could store elastic energy and reduce the energetic cost of locomotion (Biewener, 2003). However, the dragging of the body would require additional muscular work to maintain forward progression with little energy recovery. Kuhn and Frey (2012) proposed that the ventral blubber could be used as a shock absorber that could store kinetic energy, but there were no data to support this claim. Therefore, without an effective mechanism to store elastic energy, the undulatory locomotion seen in phocid seals was considered energetically costly (Garrett and Fish, 2014). Elephant seals, however, displayed a relative amplitude of heave that was 22.2% and 36.4% lower than that of gray and harbor seals, respectively (Table 1), despite the distinct lift in the pelvic region exhibited by the elephant seals.

Comparative energetics of terrestrial locomotion

The large size of the elephant seal appears to present energetic consequences to its locomotion. While its mass can reduce the cost of transport when swimming and allow for more efficient diving by buoyancy regulation in water (Webb et al., 1998; Fish, 2000; Williams et al., 2000), the energetic cost on land is exorbitantly high when compared with that of smaller phocids. The power output (P) for the elephant seal was 8.5 and 11.8 times greater than P for the gray and harbor seals, respectively, at V_{\max} . At $V_{0.6}$, P for the elephant seal was 42.7 and 70.0 times greater than that for gray and harbor seals, respectively. Even when scaled for size, P/M for the elephant seal compared with the gray and harbor seals was 1.4–2.5 times greater at V_{\max} and 8.3–12.9 times greater at $V_{0.6}$.

Although the elephant seal expends a disproportionate amount of energy compared with other phocids that move with a similar locomotor pattern on land, is the energy expenditure of the elephant seal equivalent to that of massive legged, terrestrial mammals? The energy consumption as measured metabolically by oxygen consumption has been obtained for walking elephants (Langman et al., 1995, 2012). As the metabolic power input can be equated to the mechanical power output through an efficiency (Fish, 1993), the energy measurements for elephant seals and elephants can be compared using a muscle efficiency of 0.25 (Cavagna and Kaneko, 1977).

For an Asian elephant (*Elephas maximus*) of an average mass of 3133.5 kg walking at 2.2 m s^{-1} , the net metabolic power was measured as 8167.3 W (Langman et al., 2012). Similarly, an African elephant (*Loxodonta* sp.) of an average 1542 kg has a metabolic power of 7710 W while walking at 2.5 m s^{-1} (Langman et al., 1995). Using the muscular efficiency, the computed mechanical power output is 2042 and 1928 W for the Asian and African elephants, respectively. Despite equivalent speeds, the power output of northern elephant seals was 1.6–2.9 times greater than that of elephants. This difference in power output reflects that the locomotor pattern used by elephant seals is limited compared with legged locomotion. Furthermore, the particular use of spinal undulations by the elephant seals to move over land appears to be limited in terms of speed. This speed limit is evident as elephants can move up to 6.8 – 9.7 m s^{-1} (Garland, 1983; Hutchinson et al., 2003) and the maximum speed of large dinosaurs has been estimated at 3.3 – 10.5 m s^{-1} (Thulborn, 1982; Sellers and Manning, 2007). The transition from terrestrial to aquatic lifestyles with its associated morphological changes, therefore, culminates in greater locomotor costs on land (Williams, 1999; Fish, 2000).

Conclusions

Overall, the evolution of phocid seals toward a more specialized, aquatically adapted lifestyle can restrict their locomotion on land. Characteristics that make these animals more aquatically adapted are the modification of the forelimbs and hindlimbs into flippers, the use of the hindflippers as the primary propulsors through water, the inability to bring the hindlimbs under the body for terrestrial locomotion, and the possession of blubber to enhance buoyancy, insulate the body and promote a streamlined body shape (Howell, 1930; Matthews, 1952; Ray, 1963; Fish et al., 1988; Fish, 1993; Garrett and Fish, 2014). In addition to these features, male northern elephant seals are especially massive. The large size helps to make swimming more efficient (i.e. low cost of transport) and to increase submerged foraging and dive time (Fish, 2000; Hindell et al., 2000; Irvine et al., 2000). Large size in males is also associated with fighting and competition for mates, in which the larger males are usually the victors (Bartholomew, 1970; Le Boeuf et al., 1974; McClain et al., 2015). The type of terrestrial locomotion seen in northern elephant seals is similar to that of other phocids, but they exhibit distinct differences that could be a consequence of their massive size and the need to allocate more energy into forward progression. Nonetheless, these seals exhibit morphological constraints that have resulted from a high degree of aquatic specialization, therefore limiting the performance of their movement on land.

The question remains whether elephant seals have reached a limit in the size that a more aquatically adapted animal can effectively move on land. Increasing size will become prohibitively energetically expensive as supportive limbs are transformed to flippers or lost. Killer whales (*Orcinus orca*; $\leq 10,000$ kg) beach themselves along the shoreline to catch pinnipeds, but must be near the waterline to use waves in conjunction with body flexion to return to the sea (Lopez and Lopez, 1985; Jefferson et al., 2015). The average size of the elephant seals in this study is only 30% of the mass of the largest adult male elephant seals estimated. Like the northern species, southern elephant seals (*Mirounga leonine*) can move on land and can attain a maximum size of 3700 kg (Le Boeuf and Laws, 1994; Jefferson et al., 2015). Despite, the seals' ability to move on level or slightly sloping terrain, the northern elephant seals observed in the present study appeared to lack endurance and speed. The size, kinematics, morphology and energy expenditure appear to limit motion on land, particularly in comparison to large terrestrial animals.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: K.A.T., F.E.F.; Methodology: K.A.T., A.J.N., F.E.F.; Validation: F.E.F.; Formal analysis: K.A.T., A.J.N., F.E.F.; Investigation: K.A.T., F.E.F.; Resources: D.P.C.; Data curation: K.A.T.; Writing - original draft: K.A.T.; Writing - review & editing: K.A.T., A.J.N., F.E.F.; Supervision: F.E.F.; Funding acquisition: F.E.F.

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Data availability

Data are available from the West Chester University data repository: http://digitalcommons.wcupa.edu/bio_data/

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