4-2015

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Recommended Citation

Garrett, J. N., & Fish, F. E. (2015). Kinematics of terrestrial locomotion in harbor seals and gray seals: Importance of spinal flexion by amphibious phocids. *Marine Mammal Science, 31*(2), 459-478. http://dx.doi.org/10.1111/mms.12170

Marine Mammal Science

MARINE MAMMAL SCIENCE, **(*): ***–*** (*** 2014)

DOI: 10.1111/mms.12170

Kinematics of terrestrial locomotion in harbor seals and gray seals: Importance of spinal flexion by amphibious phocids

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Abstract

Pinnipeds are amphibious mammals with flippers, which function for both aquatic and terrestrial locomotion. Evolution of the flippers has placed constraints on the terrestrial locomotion of phocid seals. The detailed kinematics of terrestrial locomotion of gray (*Halichoerus grypus*) and harbor (*Phoca vitulina*) seals was studied in captivity and in the wild using video analysis. The seals exhibited dorsoventral undulations with the chest and pelvis serving as the main contact points. An anteriorly directed wave produced by spinal flexion aided in lifting the chest off the ground as the fore flippers were retracted to pull the body forward. The highest length-specific speeds recorded were 1.02 BL/s for a gray seal in captivity and 1.38 BL/s for a harbor seal in the wild. The frequency and amplitude of spinal movement increased directly with speed, but the duty factor remained constant. Substrate did not influence the kinematics except for differences due to moving up or down slopes. The highly aquatic nature of phocids seals has restricted them to locomote on land primarily using spinal flexion, which can limit performance in speed and duration.

Key words: terrestrial locomotion, phocid, kinematics, undulation, terrain, *Phoca vitulina*, *Halichoerus grypus*.

Pinnipeds are not fully terrestrial nor are they fully aquatic mammals. The three extant families within Pinnipedia (Otariidae, Odobenidae, Phocidae) exhibit characteristics that make them more specialized for aquatic life rather than a terrestrial existence (Howell 1930, King 1983, Riedman 1990, Kuhn and Frey 2012). Aquatic specializations for the pinnipeds include modification of the forelimbs and the hind limbs into flippers for which the latter are the primary means of propulsion in water (Howell 1930, Ray 1963, Williams and Kooyman 1985, Feldkamp 1987, Fish *et al.* 1988, Kuhn and Frey 2012).

Despite their aquatic specializations, pinnipeds continue to rely on terrestrial locomotion on land for much of their life cycle (*e.g.*, pupping, reproduction, molting, and resting; King 1983, Riedman 1990, Stewart and DeLong 1993, Hindell *et al.* 2003, Ferguson and Higdon 2006). For the walrus and phocid seals, use of the hind flippers for swimming enhances propulsion in water (Ray 1963, Gordon 1981, Fish *et al.* 1988). Although the walrus (*Odobenus rosmarus*) and otariid seals can locomote quadrupedally on land (Howelll 1930, Fay 1981, Gordon 1981, King 1983, Burkhardt

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and Frey 2008), the phocids are no longer able to bring their hind limbs forward to support the caudal portion of the body when on land (Howell 1930, Matthews 1952). As a consequence, the primary means of terrestrial movement for phocids are limited to either an undulatory locomotion that relies on dorsoventral flexibility of the spine along with the use of the fore flippers for progression (Murie 1870, Matthews 1952, Backhouse 1961, Tarasoff *et al.* 1972) or a sinuous type of movement using lateral flexing of the body (O'Gorman 1963).

The terrestrial locomotion of phocid seals provides an example of the evolutionary constraints that reduce locomotor performance (*i.e.*, speed, efficiency, energy cost), which are associated with morphological compromises for operating in different habitats (Fish 2000). Although becoming more aquatically adapted, phocids as well as other pinnipeds are limited with respect to terrestrial locomotion (Fish 2000, 2001). Past studies have looked at the variation in locomotor modes among members of Pinnipedia through evaluation of the anatomical, physiological, and behavioral characteristics that exist within the three pinniped families (Backhouse 1961, O'Gorman 1963, Ray 1963, Tarasoff and Fisher 1970, Tarasoff *et al.* 1972, Gordon 1981, Kanatous *et al.* 1999, Kuhn and Frey 2012). Examinations of terrestrial locomotion particularly for phocids were limited to gross descriptions without collecting quantitative data. In addition, descriptions of terrestrial locomotion by phocids were made without consideration of terrain (*i.e.*, vertical and horizontal dimension of the land) and substrate (*i.e.*, composition of the land surface) as influencing factors on performance (Backhouse 1961, Tarasoff *et al.* 1972, Kuhn and Frey 2012) except by O'Gorman (1963).

The main objective of this study was to examine the terrestrial locomotion of phocid seals by detailing and quantifying the kinematics. This study aimed to address how the movements of the body and fore flippers are coordinated and how these movements determined the speed of terrestrial locomotion. In addition, consideration was given to variation in terrestrial movement among phocid species and the influence of substrate type on seal locomotion. Although the previous studies of terrestrial locomotion by phocids described the unique locomotor pattern of these pinnipeds, detailed kinematics are necessary to define the distinct neuromuscular coordination between body and limb movements and determine constraints on terrestrial locomotion with increasing aquatic adaptation.

Materials and Methods

The terrestrial movements of wild gray (*Halichoerus grypus*) and harbor (*Phoca vitulina*) seals were video recorded at Duck Island, Maine, which is part of the Isles of Shoals located 8 km southeast from Portsmouth, New Hampshire (43°0′19″N, 70°36′13″W). Approximately 100–200 seals were typically found on the island during low tide. To avoid disturbing dependent pups, data collection was performed after 15 July 2011 and during the month of August, the timing of which was well after the end of the pupping period for harbor seals (from mid-May to the end of June) and gray seals (from late December to mid-February) (Skinner, 2006). Harbor seal pups are typically weaned 23.9 d after birth (Skinner 2006), which ensured there would be no dependent pups present on the island.

The seals were examined along the shoreline of Duck Island, which consisted largely of rocky substrate with many areas being covered with brown algae (*Fucus* sp.), which dominates temperate rocky intertidal shores (Pearson *et al.* 2010). The terrain was comprised of varying degrees of inclines and small cliffs.

An inflatable boat was used as an observation platform. To minimize disturbance to the animals, the boat was powered toward a group of seals on the beach and then idled within 100 m from the closest seal. The boat was allowed to drift toward the seals no closer than 12.2 m. Hand-held Sony HD video cameras (model no. HDR-SR11, 30 fps) were used to record movements of the seals. The seals have experienced boats in close proximity to their haul-out sites from lobster operations and pleasure boats. The movements of the seals were recorded for no more than 15 min at any one location. The boat then moved to record another group of seals at a different location on the island. Each group of seals was recorded only once per day during the low tide period during daylight hours. This action allowed time for the seals to return to the islands and rest if disturbed. The work was conducted over a 1 wk period in the summer of 2011, and involved a total of seven visits to the study site.

Terrestrial locomotion of captive gray and harbor seals also was recorded at the Adventure Aquarium in Camden, New Jersey. Two adult female gray seals and one adult male harbor seal were recorded using a HD video camera (Sony model no. HDR-SR11, 30 fps) and a high-speed video camera (Fastec Imaging Troubleshooter model no. LE500ME, 250 fps), which were placed on tripods. The two gray seals were 113.6 kg with a length of 2.16 m (Kjya) and 146 kg with a length of 2.11 m long (Kara). The adult male harbor seal weighed 114.6 kg and was 1.22 m in length (Spanky). The gray seals appeared to be in good condition, but the harbor seal appeared overweight for its size. Video images were scaled with a meter stick recorded in the field of view prior to the start of each recording session in the region where the seals moved. Lateral views of locomotion of the seals were obtained by recording the animals as they moved across the platform of their enclosure. Under trainer control, the speed of the seal over the platform was regulated. Recordings were made on three separate days during the summer of 2011 between 0800 and 1000.

Video recordings were analyzed frame-by-frame to detail the kinematics of the movements. ProAnalyst (version 1.5.4.8, 3-D Professional edition, Xcitex Inc. 2011) was used for feature tracking of the seals over multiple strides. A stride represented a complete cycle of motion. The features tracked included the tip of the rostrum (nose), eye, highest vertical point of the dorsum created by the undulatory wave during forward progression, and tip of the distal phalanx of the first digit of the fore flippers. Absolute (meters) and relative (body lengths) scales of measurement were used for recordings from the Adventure Aquarium, whereas, only relative scale was used for video of the wild seals in the field. Body length (BL) was considered 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.

The kinematic variables measured included the speed of the rostral tip, which represented the speed of the seal as it progressed forward, the amplitude and frequency of the movement of the dorsal margin of the body, the duty factor, and the phase difference between the movements of the dorsal margin of the body and rostral tip. The amplitude represented the peak-to-peak vertical displacement averaged over successive strides. The frequency was calculated as the inverse of the period of a stride. Duty factor was measured as the fraction of the stride that the limbs of an animal are in contact with the ground. Duty factor was calculated for the fore flippers and the pelvic region, because the hind flippers played no role in forward movement.

The phasing between the dorsal margin of the body and rostral tip was an expression of the relative movements of these body components within a cycle. When considering the phase cycles for the undulatory locomotion displayed by the seals, the dorsal margin of the body of the seals was considered to be the feature that led locomotion, followed by the rostral tip. The phase difference between the vertical spinal and rostral movements was calculated by subtracting the percentage of time of the stride from the maximum vertical height of the rostral tip followed by the initiation of spinal movement for one complete cycle of spinal movement. The percentage of time was then multiplied by 360° (*i.e.*, one full cycle) to display the phase difference in degrees.

SPSS (PASW 18.0) was used for statistical analyses of the kinematic data. The mean ± one standard deviation, and maximum and minimum values were measured. Significance was considered for P-values <0.05. Linear regressions were determined for relationships between the kinematic variables. Data from seals in the wild were considered independent observations, whereas, observations for each of the captive seals from the Adventure Aquarium were not considered independent.

One-way analysis of variance (ANOVA) was used to determine whether the two wild seal species differed in mean speed and duty factor. The Scheffe test was used as the *post hoc* test to assess differences between specific groups. If skewness (|skew/standard error of skew|) and/or kurtosis (|kurtosis/standard error of kurtosis|) values exceeded ±2, the assumption of homogeneous variances was not met based on Levene's test and the kinematic variables were compared among species using the Kruskal-Wallis test. The nonparametric Tukey test served as the *post hoc* test using the formula from Zar (2010) for nonparametric multiple comparisons with unequal sample sizes.

Separate analysis of covariance tests (ANCOVA) were used to evaluate the effects of speed, the species of seal, and their interaction on other kinematic values. ANCOVA was also included to assess the effects of terrain on seal movement with substrate type and speed serving as the fixed factor and covariate, respectively.

RESULTS

Pattern of Terrestrial Locomotion

Examination of video showed that both seal species used their sternal and pelvic regions as the primary contact points with the ground, while the dorsal margin of the body flexed and extended during forward progression (Fig. 1, 2). At the beginning of the stride (0.000 s), the dorsal margin of the seal's body is extended and the entire venter of the body is in contact with the ground from chest to pelvic regions (Fig. 1). Prior to flexion of the dorsal margin of the body, the fore flippers rest on the surface and are laterally rotated at a ~45° angle to the body of the seal. The hind flippers were not in contact with the ground prior to flexion of the spine. The dorsal margin of the body then began to visibly flex dorsally in the lumbar region (0.096 s). The flexion of the dorsum traveled anteriorly in the form of a wave. As a result of the spinal flexion, the pelvic region of the seal was drawn forward along with the hind flippers (0.096–0.192 s). Simultaneously, the fore flippers began to retract posteriorly. The head of the seal was depressed as spinal flexion increased.

Spinal flexion continued to travel anteriorly until it reached the shoulders of the seal (0.192 s). At this point (0.224 s), the pelvic region was no longer drawn forward when the dorsal margin of the body maximally arched (Fig. 1). The fore flippers continued to retract by flexing the elbow and metacarpophalangeal joints and thus pulled

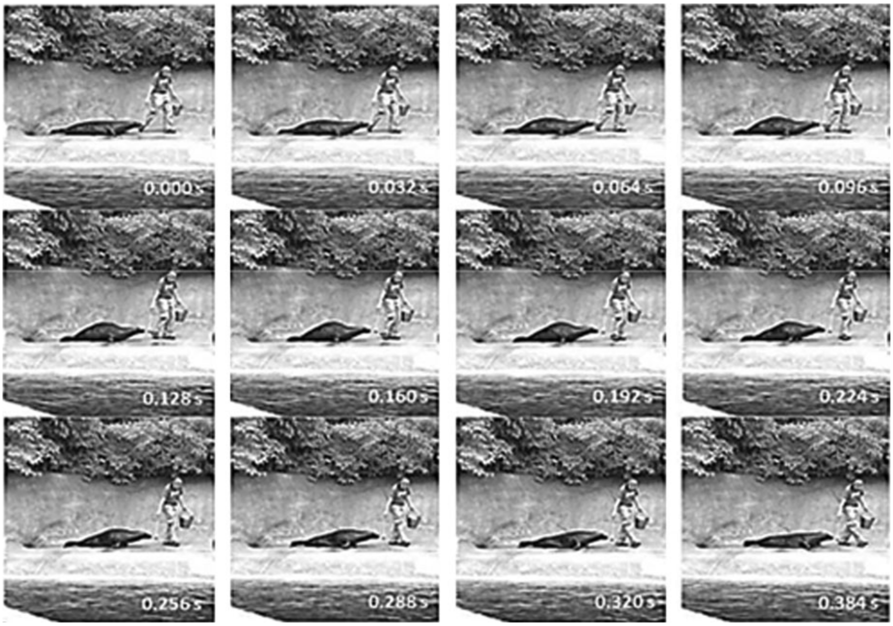

Figure 1. Undulatory sequence exhibited by a gray seal (Kjya) over a level concrete surface. The sequence was recorded at 250 fps. The time of each frame is provided in seconds.

the seal forward. The chest was lifted off the ground as the body pivots over the fore flippers. The head of the seal was elevated as spinal flexion approached the shoulders.

Subsequently, the sternal region of the seal was lifted off the ground and brought forward with a push from the pelvic region and simultaneous extension of the trunk (0.256–0.288 s; Fig. 1). The fore flippers also aided in this movement by continuing to transfer the weight of the seal forward on the metacarpophalangeal joints through extension of the elbow and rotation at the shoulders. The cervical region of the seal appeared to extend along with the lumbar region of the seal. Towards the end of the stride (0.320–0.384 s), the chest of the seal again made contact with the ground (Fig. 1). The fore flippers were lifted off the ground and moved with the anterior displacement of the chest once the weight of the seal was transferred past the shoulders. When not in contact with the ground, the fore flippers began to protract forward as the sternal region approached the ground. The fore flippers made contact with the surface shortly after the chest of the seal contacted the ground. Upon contact, the fore flippers were oriented anteriolaterally and then rotated posteriolaterally from the body. The head of the seal descended as the body came to rest on the ground. The hind flippers were lifted again from the ground. Repeated strides gave the seal an undulatory movement in an inchworm fashion.

For the one harbor seal observed in captivity, the fore flippers were not used and forward progression was accomplished solely by spinal flexion (Fig. 2). The fore flippers were held to the sides of the seal, occasionally extending laterally above the ground.

For many seals, the metatarsophalangeal region of the hind flippers appeared to be relaxed during locomotion as they were noted to swing freely with the movements of

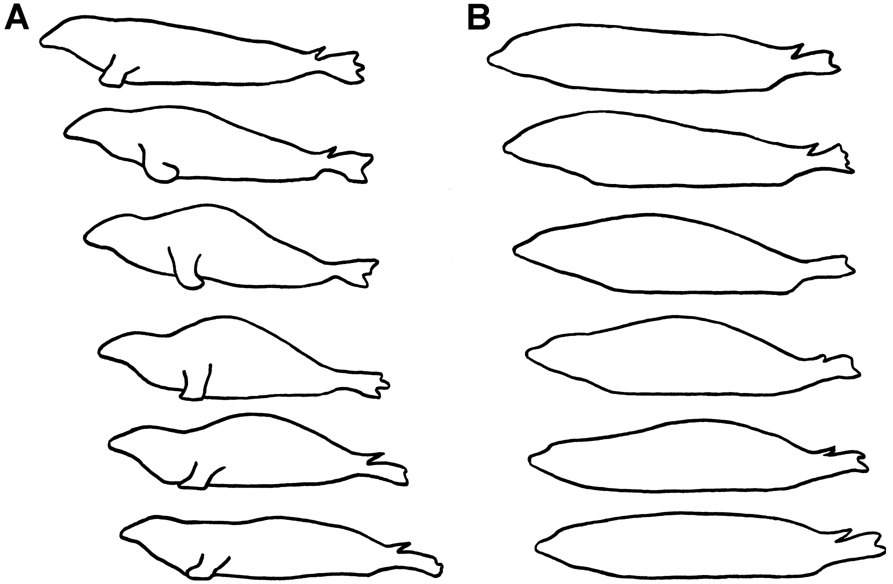

Figure 2. Lateral view of movements over one stride cycle for captive gray seal (A, Kjya) and harbor seal (B, Spanky) moving over a level concrete surface. The sequences are tracings from video recordings at intervals of 0.067 s. The sequence is initiated from the bottom of the figure.

the seal. Several individuals were also observed to completely drag the hind flippers along the ground throughout the locomotor cycle.

The seals were observed to keep their heads lifted above the ground while pointing their rostral tip anteriorly throughout the stride (Fig. 1, 2). Many seals in the field, however, were observed to lower their heads to the ground prior to entry into the water. Individuals were observed to occasionally turn their heads to the right or left side during a stride.

Kinematics of Terrestrial Locomotion

One captive harbor seal moved solely by spinal undulation (Fig. 3). Six locomotor sequences were examined for this individual. The seal had a mean speed on land of 0.53 ± 0.03 m/s (0.65 ± 0.04 BL/s) with a maximum recorded speed of 0.57 m/s (0.71 BL/s).

There was only one recorded locomotor sequence for the 146.0 kg captive gray seal, whereas, 26 locomotor sequences recorded for the 113.6 kg gray seal. The gray seals moved with a mean speed of 0.94 ± 0.21 m/s (0.84 ± 0.11 BL/s). The high variation in speed was a consequence of deliberate attempts by the trainers to elicit the seals to move over a variety of speeds. The maximum speed was 1.21 m/s (1.02 BL/s). The captive gray seals constantly used simultaneous movements of the fore flippers while locomoting (Fig. 3).

The frequency of spinal movement was directly related to the relative speed for the captive gray seals ($r = 0.70$), but displayed an inverse relationship ($r = -0.54$) for the captive harbor seal. This difference may have been due to the difference in body

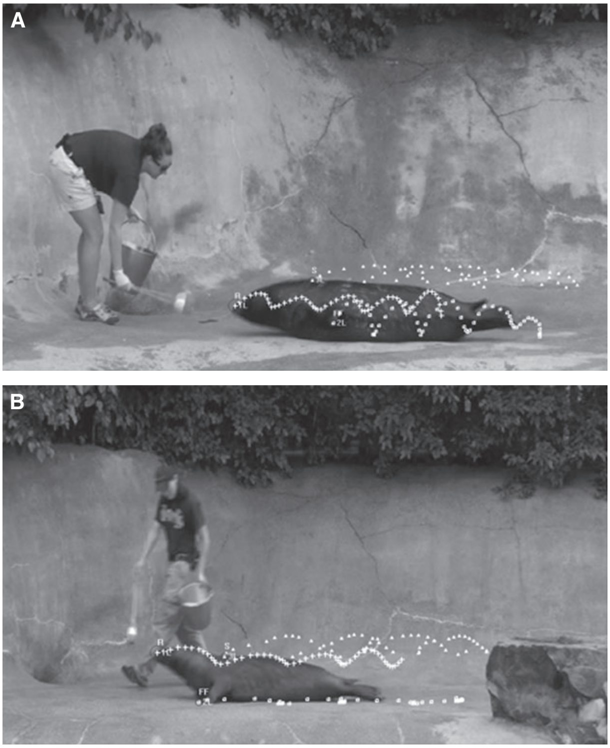

Figure 3. Feature tracking patterns of the captive harbor seal (top, Spanky) and gray seal (bottom, Kjya) moving over a level concrete surface. Specific points were tracked over multiple strides, including the maximum point of the dorsal margin of the body during progression (solid triangles), the rostrum (crosses), and the tip of the fore flippers (open squares).

condition between the individuals of the two species. The mean spinal frequency of the gray seals was 2.35 ± 0.16 Hz, over the range in speed of 0.5–1.2 m/s (0.6–1.0 BL/s). The harbor seal showed a mean spinal frequency of 2.64 ± 0.12 Hz that occurred between 0.4–0.6 m/s (0.6–0.7 BL/s) (Fig. 4).

The spinal amplitude showed a direct increase with increasing speed for the captive gray seals ($r = 0.93$) using absolute values. Spinal amplitude displayed an increasing trend with the relative speed for captive gray ($r = 0.77$) and harbor seals ($r = 0.66$). The harbor seal displayed mean spinal amplitude of 0.05 ± 0.00 m (0.07 ± 0.00 BL) that extended over a speed range of 0.5–0.6 m/s (0.6–0.7 BL/s) (Fig. 5). For both seals, the amplitude of the movements of the dorsal margin of the body was greater than for the rostral tip. The mean phase differences between the spinal and rostral waves for captive gray and harbor seals were 0.84° ± 0.11° and 0.87° ± 0.02°, respectively.

The duty factor of the fore flippers for the captive gray seals decreased with increasing relative speed ($r = -0.69$). The fore flippers were in contact with the ground for an average of 57.8% ± 4.0% of each undulatory cycle (Fig. 6) for both species of seals. The pelvic region was not observed to lift from the ground at any point during the cycle (*i.e.*, duty cycle equals 100%).

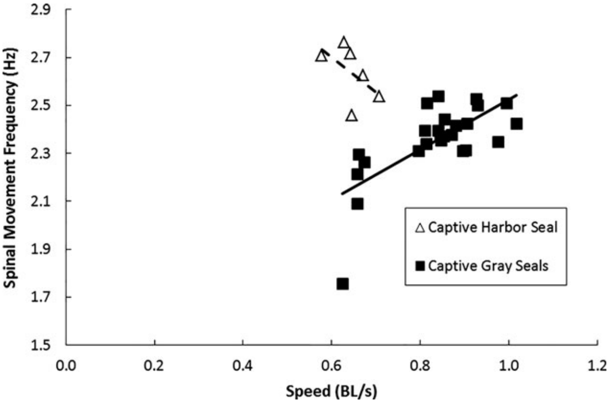

Figure 4. Scatterplot displaying the frequency (Hz) of the dorsal margin of the body against speed (BL/s) for captive harbor ($y = -1.46x + 3.57$, $r = -0.54$; dashed line) and gray seals ($y = 1.05x + 1.48$, $r = 0.70$; solid line).

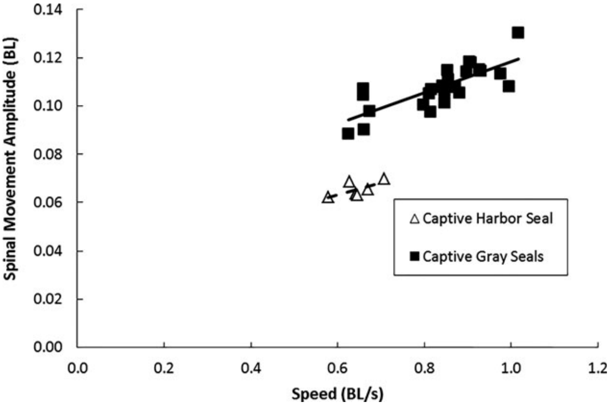

Figure 5. Scatterplot displaying the amplitude (BL) of the dorsal margin of the body against speed (BL/s) for captive harbor ($y = 0.05x + 0.03$, $r = 0.66$; dashed line) and gray seals ($y = 0.65x + 0.05$, $r = 0.77$; solid line).

Kinematics of Wild Seals on Level Ground

Wild harbor ($n = 37$) and gray seals ($n = 15$) exhibited similar undulatory movements in concert with use the fore flippers for terrestrial locomotion (Fig. 7). The mean speed of the wild harbor seals was 12.7% greater (0.92 ± 0.22 BL/s) than the gray seal species (0.81 ± 0.17 BL/s), though the speeds did not differ significantly ($P = 0.082$).

The frequency of spinal undulations was significantly influenced by speed ($P = 0.005$), species ($P < 0.001$), and the interaction of these two variables ($P = 0.007$). These findings related to both seal species, with spinal frequency increasing significantly with speed for the harbor ($P = 0.006$) and gray seals

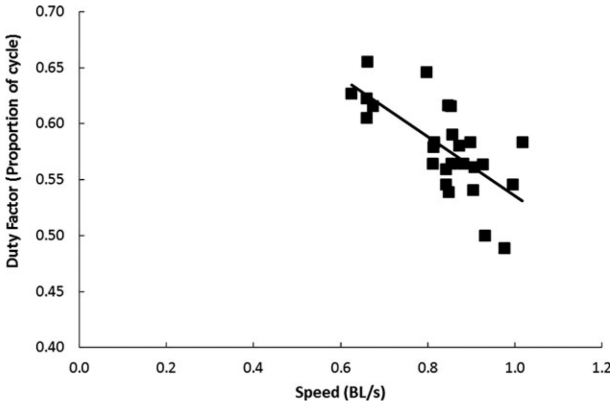

Figure 6. Scatterplot representing duty factor against speed (BL/s) for the captive gray seals ($y = -0.26x + 0.80$, $r = -0.69$).

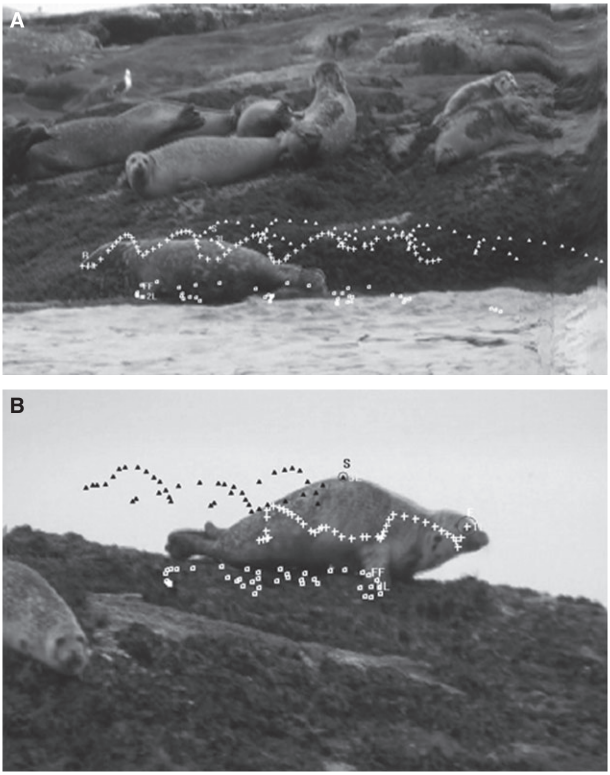

Figure 7. Feature tracking of a harbor seal (bottom) and gray seal (top) across a beach on Duck Island. Specific points were tracked over multiple strides, including the maximum point of the dorsal margin of the body during progression (solid triangles), the rostrum (crosses), and the tip of the fore flippers (open squares).

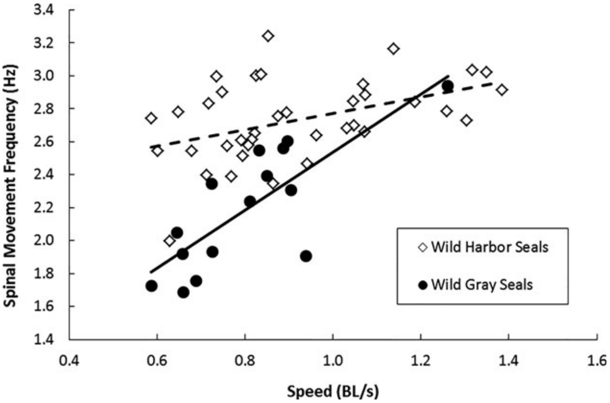

Figure 8. Plot indicating the relationship between spinal frequency (Hz) and speed (BL/s) of the wild harbor ($y = 0.50x + 2.28$, $r = 0.45$. $P = 0.006$; dashed line) and gray seals ($y = 1.76x + 0.78$, $r = 0.79$, $P < 0.001$; solid line).

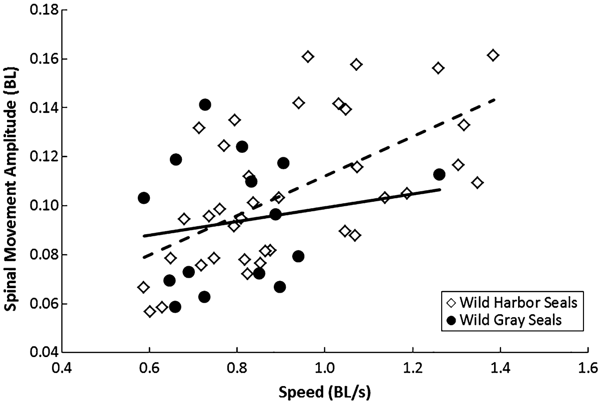

Figure 9. Plot indicating the relationship between spinal amplitude and speed (BL/s) of the wild harbor ($y = 0.08x + 0.03$, $r = 0.6$, $P < 0.001$; dashed line) and gray seals ($y = 0.03x + 0.07$, $r = 0.2$, ns; solid line).

($P < 0.001$) (Fig. 8). There was a significant relationship ($P < 0.001$) between spinal amplitude and speed for the wild harbor seals. The spinal amplitude of the gray seals extended within the 0.60–1.00 BL/s range with an average of 0.09 ± 0.03 BL (Fig. 9). The anterior speed of the spinal movement was 1.8 ± 0.5 and 1.7 ± 0.4 times faster than the anterior speed of the harbor and gray seals, respectively.

Duty factor was not dependent on speed for either wild harbor ($P = 0.693$) or gray seals ($P = 0.255$). The mean duty factor of the fore flippers for the wild harbor and gray seals was 54.1% ± 8.20% and 53.8% ± 7.10% of the cycle, respectively (Fig. 10).

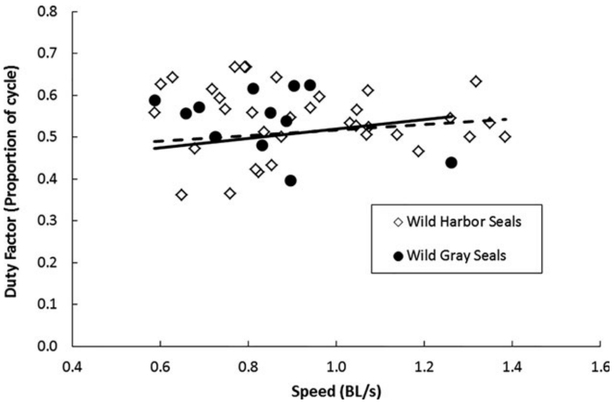

Figure 10. Plot representing duty factor against speed (BL/s) for the wild harbor and gray seals. The duty factor was independent of length-specific speed for both wild harbor seals ($y = -0.03x + 0.56$, $r = 0.1$, ns; dashed line) and gray seals ($y = -0.14x + 0.66$, $r = 0.3$, ns; solid line).

Comparison of Wild and Captive Seals

Table 1 provides comparisons of the kinematic values between wild and captive seals. Unlike the captive harbor seal, the wild harbor seals were observed using the fore flippers for locomotion. The body of wild species appeared leaner than the captive harbor seal. The movements of the rostral tip and dorsal margin of the body as well as the positioning of the fore flippers during locomotion of the wild individuals were more variable with regard to flexion height and length than that of the captive harbor seal. However, the wild harbor seals displayed similar undulatory patterns to that observed in the captive specimen (Fig. 11).

The mean speed of wild harbor seals was 34.4% greater than that of the captive seal. The maximum speed of wild seals was 94.3% higher than the maximum speed of the captive harbor seal.

The wild gray seals exhibited similar undulatory movements with use of the fore flippers for locomotion as observed for the captive gray seals (Fig. 11). The rostral tip, dorsal margin of the body, and fore flipper movements resembled those of the captive species but displayed more variation in the heights and lengths of the patterns. The mean speed of the captive gray seals was 3.6% greater than the speed of wild gray seals, but the maximum speed was 23.5% higher for wild gray seals (Table 1).

The average phase difference for pooled data between movements of the rostral tip and body wave on wild and captive seals was 0.89 ± 0.08 (321° ± 29°). The movements of the rostrum occurred at lower displacement values than that of the spinal movements. The mean differences between the maximum and minimum vertical heights of the rostral tip and spine were 0.11 ± 0.07 and 0.10 ± 0.07, respectively.

Influence of Terrain on Seal Movement

Tests for effects of substrate type on locomotion were carried out for the wild harbor seals, as they were the only species observed undulating on different types of level

Table 1. Means ± one standard deviation of kinematic values for captive harbor (n = 6) and gray seals (n = 26) and wild harbor (n = 37) and gray (n = 15) seals moving across level substrate. Length-specific values are provided for both captive and wild seals, but absolute values are provided only for the seals held in captivity.

	Captive harbor seal	Captive gray seal	Wild harbor seal	Wild gray seal
Mean speed (BL/s)	0.65 ± 0.04	0.84 ± 0.11	0.92 ± 0.22	0.81 ± 0.17
Mean speed (m/s)	0.53 ± 0.03	0.94 ± 0.21	–	–
Maximum speed (BL/s)	0.71	1.02	1.38	1.26
Maximum speed (m/s)	0.57	1.21	–	–
Spinal amplitude (BL)	0.07 ± 0.00	0.11 ± 0.01	0.11 + 0.03	0.09 ± 0.03
Spinal amplitude (m)	0.05 ± 0.00	0.12 ± 0.03	–	–
Spinal frequency (Hz)	2.64 ± 0.12	2.35 ± 0.16	2.73 ± 0.25	2.19 ± 0.38
Duty factor (% cycle)	–	57.8 ± 4.0	54.1 ± 8.2	53.8 ± 7.1

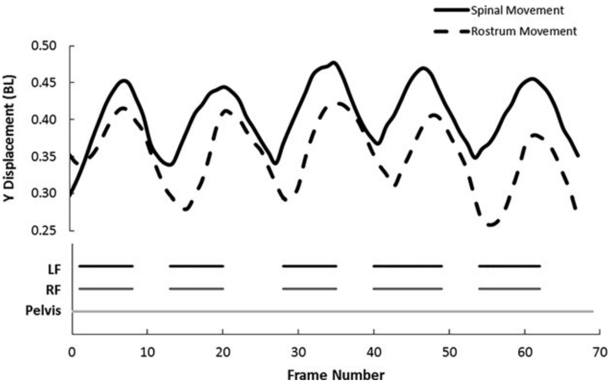

Figure 11. Sinusoidal patterns of the rostral tip and spine that were created by the undulatory movement along with the footfall pattern of the fore flippers (right fore flipper = RF; left fore flipper = LF) and pelvis with the frame number. With the exception of the one captive harbor seal, all seals included in this study displayed relatively similar patterns and footfall sequences.

substrates. Substrate, including rocky ground (n = 5) and algae (n = 32), served as the fixed effects factor and speed as the covariate. There was a significant ($P = 0.018$) positive relationship between the spinal amplitude and speed, specifically for the animals locomoting on substrate covered by algae ($P < 0.001$) (Fig. 12). The other kinematic variables were not significantly affected ($P > 0.05$) by the type of substrate or speed. The mean frequency of the locomotor cycle on algae-covered rocks was 2.5 ± 0.4 Hz and 2.1 ± 0.4 Hz for the harbor and gray seals, respectively. The frequency for harbor seals traveling over bare rocks was 2.6 ± 0.6 Hz. The mean duty factor of the fore limbs was 0.5 ± 0.1 for harbor and gray seals, regardless of substrate.

Wild harbor and gray seals were observed sliding from their haul-out sites to the water with a total of eight sliding events video recorded. Sliding was described as the seals keeping their dorsal margin of the body completely or almost completely extended, while progressing down an incline toward the water. Sliding occurred when the seal moved down substrate covered by algae with an angle of ≥15°. The fore flippers were often used during this sliding movement but appeared to act more as stabilizers because the seals extended them cranially or laterally.

Wild harbor and gray seals were observed climbing both from the water and across the ground on ledges that were covered by algae. The seals were constantly observed using their fore flippers to aid in lifting the anterior region of the body, while slight flexion and extension of the trunk aided in pushing the sternal region up and over the ledge. The claws of the fore flippers were important for climbing as they were used to grip the substrate for the seal to pull and lift itself up and over small ledges.

DISCUSSION

The observed locomotion of the harbor and gray seals showed that these seals used vertical undulations of the trunk either solely or in concert with the simultaneous movements of the fore flippers on land. Although mainly responsible for movement through water (Ray 1963, Tarasoff *et al.* 1972, Fish *et al.* 1988), the hind flippers played no part in movement on land when the seal was undulating (Tarasoff *et al.* 1972).

Terrestrial locomotion was previously described for phocid seals (Murie 1870, Lindsey 1938, Matthews 1952, Backhouse 1961, O'Gorman, 1963, Ray 1963, Tarasoff *et al.* 1972, Kuhn and Frey 2012). Ray (1963) described the movement on land by phocid seals as a rapid hunching, inchworm forward movement. Movement used

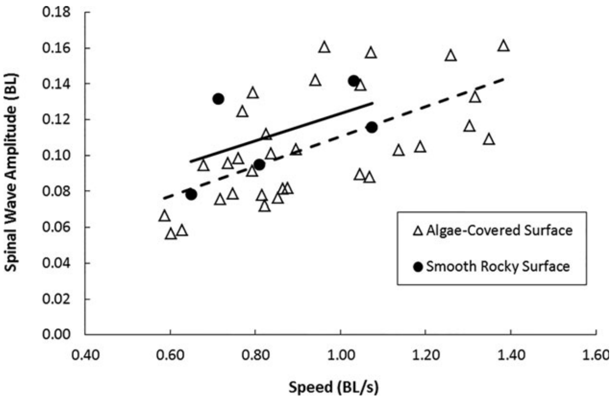

Figure 12. Relationship between spinal amplitude (BL) and speed (BL/s) for harbor seals moving across algae covered surfaces (open triangles; solid trend line; $y = 0.08x + 0.03$, $r = 0.63$, $P < 0.001$) and bare rocky substrate (closed circles; dashed trend line; $y = 0.08x + 0.05$, $r = 0.56$, ns) in the wild.

the chest and pelvis as the main weight-bearing points and progression levers (Backhouse 1961, O'Gorman 1963). The trunk flexed caudal to the chest, bringing the pelvis forward. Subsequent to this action, the trunk extended forward pushing the anterior body region ahead. Concurrently, the fore flippers were laterally rotated supporting the anterior body region above the ground (Backhouse 1961). Support by the flippers occurred by ground contact of the metacarpal ends through metacarpophalangeal hyperextension with the claws contacting the ground by interphalangeal flexion. Once the chest was lowered to the ground, the fore flippers were raised and rotated forward (Matthew 1952, Backhouse 1961, O'Gorman 1963, Tarasoff *et al.* 1972).

Tarasoff *et al.* (1972) noted three basic patterns of terrestrial locomotion for the harp seal (*Pagophilus groenlandicus*). These patterns included forward hitching of the trunk without use of the fore flippers, use of the fore flippers to drag the body with some hitching, and sinuous horizontal movements of the body. This latter motion was used for movement on ice and snow by crabeater (*Lobodon carcinophagus*) and leopard seals (*Hydrurga leptonyx*). The harp seal was observed to use horizontal sinuous movement when hurriedly retreating to an ice hole or on uneven ground (Murie 1870, Lindsey 1938, O'Gorman 1963). The horizontal sinuous gait is commonly used on snow and ice, whereas movement by vertical undulations of the body is on land. During sinuous movement, the head and shoulders are swung laterally to the same side simultaneously with the posterior end of the body reminiscent of a standing wave (O'Gorman 1963). These alternating side-to-side motions utilize both sets of flippers to aid in pushing the body forward. Although O'Gorman (1963) characterized the sinuous gait as similar to the swimming motions of the seals, large, lateral oscillations are confined to the posterior body and hind flippers during swimming by phocids (Fish *et al.* 1988).

Unlike the aquatic mammals that maintain obligatory use of the limbs for movement on land, the osteology and myology of the hind flippers render phocids incapable of rotating the limbs cranially to assist in terrestrial locomotion (Howell 1930, Tarasoff 1974). Therefore, phocids rely primarily on terrestrial gaits employing spinal flexion (Matthews 1952, Backhouse 1961, O'Gorman 1963, Tarasoff *et al.* 1972). This undulatory gait is considered to represent a modification of the bounding gait used on land by limbed mammals (Matthews 1952, Backhouse 1961, O'Gorman 1963, Tarasoff *et al.* 1972). However, in a true bounding gait, there is a large portion of the stride that is an unsupported interval (*i.e.*, period in which there is no contact with the ground; Hildebrand 1980, 1989). This gait has the advantage of allowing time for the hind limbs to move into a position for another bound (Howell 1965). Bounding is used in terrestrial gaits by various aquatic mammals, such as mink (*Mustela vison*), river otter (*Lontra canadensis*) and sea otter (*Enhydra lutris*) (Tarasoff *et al.* 1972, Williams 1983). In addition, these otters employ spinal flexion during rectilinear swimming underwater to increase speed (Williams 1989, Fish 1994). Otariids (*e.g.*, *Arctocephalus forsteri*, *Zalophus californianus*) use both fore and hind flippers to move with terrestrial gaits (*e.g.*, walk, gallop) in conjunction with spinal flexion and extension (Peterson and Bartholomew 1967, English 1976, Beentjes 1990). In otariids, spinal flexion aids in advancing the hind flippers, where protraction is hampered by the hip and knee joints being enclosed in the body.

The relative importance of spinal undulation over limbed-supported locomotion on land is indicated by the independence of duty factor from speed, specifically for the wild phocid seals. The duty factor was on average slightly greater than 50% of the cycle indicating that the fore flippers were in contact with the substrate for less than half the cycle. Typically, the duty factor of terrestrial mammals decreases with increasing speed because the limbs spend less time in contact with the ground per stride (Biewener 1983, Gatesy and Biewener 1991). This was observed for captive gray seals moving over a level even surface. However for phocids in the wild with uneven surfaces and reduced friction due to algae covering the rocks, the fore flippers did not show this trend. As a result, the amount of time that the fore flippers stay in contact with the ground does not decrease with increasing speed because the limbs are not effectively carrying the body over the surface during progression. The forelimbs may have been acting to stabilize the body during forward progression. The observations of phocids employing undulatory locomotion without the use of the fore flippers (this study, O'Gorman 1963, Ray 1963, Tarasoff *et al.* 1972) further suggests that it is the increased flexion and extension of the spine, rather than the action of the limbs, that allows the seals to obtain higher speeds. Indeed, the frequency and amplitude of the spinal undulations increased directly with the speed of the animals.

The maximum speeds of seals in this study were lower than previously reported for other phocids (O'Gorman 1963). The captive harbor seal exhibited a low performance that was probably a reflection of the condition of the animal, which was bulkier than wild seals. The condition of the captive individual most likely restricted its use of the fore flippers in terrestrial locomotion, which would further limit speed as reflected in the restricted range of speeds that the trainers could elicit. Captive gray seals had a maximum speed of 1.21 m/s, which was equivalent to a length-specific speed of 1.02 BL/s. Even though an absolute speed for gray seals in the wild could not be determined, these seals displayed a 24% increase over captive seals with respect to the length-specific speed. This would approximate a maximum absolute speed of only 1.49 m/s. Backhouse (1961) reported that gray seals could travel using spinal undulation and gripping with the fore flippers at 2.7–3.6 m/s over short distances. In these instances unlike the seals observed in the present study, the pelvis was lifted totally off the ground. Higher speeds (5.3 m/s) have been reported for other phocid species (*e.g.*, crabeater seal, harp seal), but these species used a sinuous method of locomotion while being chased over snow and ice (Lindsey 1938, O'Gorman 1963).

The form of terrestrial locomotion used by phocids appears inefficient when compared to terrestrial or semiaquatic mammals. The method of locomotion exhibited by the seals requires use of the axial musculature, which would be of greater mass than if just the limbs were employed. Furthermore, the undulatory gait of the seals required substantial vertical oscillations of the trunk of the body (Fig. 3, 7, 11). Having the bulk of the seal oscillating through a large vertical displacement would be energetically costly. Similarly, the walrus initiates its terrestrial gait with a forward lunge in which the chest is raised off the ground (Gordon 1981). The forward lunge results in a vertical displacement of center of mass through the stride, which results in an increase in the energetic cost of locomotion (Gordon 1981).

Positive and negative accelerations of the body and center of mass would be high when locomoting (Howell 1965). The vertical oscillations of the body result in potential energy and kinetic energy fluctuating in phase (Cavagna *et al.* 1977, Full 1989, Biewener 2003). Losses in potential and kinetic energy require additional muscular work to maintain forward speed of the animal with little energy recovery (Biewener 2003). Elastic recoil from tendons and footpads in the legs of terrestrial mammals can store some energy as elastic potential energy, which can be recovered and converted to kinetic energy, but the gait of phocids precludes this manner of energy recycling. Kuhn and Frey (2012) did propose that the ventral blubber could be used as a shock absorber, but there are no data to support the compliance of the blubber as a mechanism of elastic recoil to reduce energy losses. Additional energy is lost as the large vertical oscillations produce high ground reaction forces (Full 1989, Biewener 2003). High ground reaction forces would add to more energy required to overcome the friction of the hindquarters of the body that is dragged along throughout the locomotor cycle.

Terrestrial locomotion by seals may have become energetically expensive as a trade-off for becoming more aquatically adapted (Fish 2000). Williams (1999) suggested that the transition from a terrestrial to aquatic specialist required overcoming an energetic hurdle. This hurdle is viewed as the intermediate or semiaquatic state in which the transitioning species is faced with higher transport costs due to its amphibious nature without specializing to either environment. Acquiring the adaptations necessary to become an aquatic specialist, however, means that movement on land now requires a higher cost of transport as the energetic cost of locomotion is reversed (Williams 1999, Fish 2000). Because pinnipeds remain linked to the land for rest and reproduction (Riedman 1990), they are required to lead an amphibious lifestyle and therefore must cope with the higher energy costs (Fish 1993, 1996, 2000; Williams 1999).

The close proximity of pinnipeds to coastal margins (Dunbar 1949, Davies 1958, de Muizon 1982, Berta 2002, Arnason *et al.* 2006) may partially be the result of their limited mobility on land. The haul-out sites of pinnipeds remain within a short distance to the water, providing them with ready access into the aquatic environment where food is available and transport costs will be much lower (Fish 2000). Although the phocid crabeater seal has been reported to move over snow for 0.8 km when chased (Lindsey 1938) and otariid fur seals (*Callorhinus ursinus*) have been forcibly herded 1.2 km (Bartholomew and Wilke 1956), terrestrial locomotion by pinnipeds is characterized by low speeds and low stamina (Bartholomew 1952, Bartholomew and Wilke 1956, Backhouse 1961).

The properties of substrates (*i.e.*, friction, slope) affect the locomotor performance of animals (Parker *et al.* 1984, Herreid and Full 1986, Lejeune *et al.* 1998, Claussen *et al.* 2002). Phocids have been observed on an array of substrates including snow, ice, sand, pebbles, boulders, and algae (Lindsey 1938, Backhouse 1961, O'Gorman 1963, Mansfield 1967, Sullivan 1981, Schneider and Payne 1983, Stewart 1984, Calambokidis *et al.* 1987, Reeves *et al.* 1992, Le Boeuf and Laws 1994, Hall 2002). Because each substrate has different properties (*i.e.*, texture, friction), it was expected that there would be slight alterations in phocid movement associated with the types of terrain. Locomotion across algae covered rocks would incur less friction than movement across a bare, rocky beach. Alternatively obtaining a firm grip with the claws of the forelimb would be easier when moving over a rocky substrate. Gray seals have been reported to climb slopes of over 60° (Backhouse 1961). The ability to firmly grip the substrate surface would influence how quickly the seal is able to move by undulation over uneven terrain.

There appeared to be no difference in the kinematics of movement of the seals over the different substrates with the exception of sliding. Harbor seals used the sliding behavior to quickly enter the water and move over the rocky beach covered by algae when there was a sufficient downward slope. The slippery surface of the algae allowed easier movement of the pelvis compared to the generally uneven surface of the rocky terrain. Sliding was accomplished with an extended body as the seals entered the water. Movement over rocky substrate, however, appeared to use spinal mobility in concert with the forelimbs. Gripping rocks with the claws was important in the seal's ability to draw the pelvic region forward.

In conclusion, evolution toward a more aquatically adapted morphology and habits has made movement on land limited for pinnipeds. The inability to move the hind limbs under the body of the seal, transformation of the limbs into flippers, use of the hind flippers as the primary aquatic propulsor, and the development of a more streamlined body are just a few of the features that have enabled phocids to become highly aquatically derived (Howell 1930, Ray 1963, Fish *et al.* 1988). The walrus and otariid seals maintain the ability to locomote on land using all four flippers, which allows them to perform quadrupedal terrestrial gaits with the ability to locomote rapidly on land (Peterson and Bartholomew 1967, English 1976, Gordon 1981, King 1983, Beentjes 1990). However, phocid seals have become more constrained for terrestrial locomotion due to their greater aquatic specialization. For phocids, the aquatically specialized morphology has forced these pinnipeds to rely on body undulation to move on land. Morphological constraint due to the high degree of aquatic specialization of phocids to use their limbs to locomote on land resulted in a limitation of the seals for rapid and sustained terrestrial locomotion.

ACKNOWLEDGMENTS

We are indebted to Dr. William Bemis and other staff from Shoals Marine Laboratory, the National Marine Fisheries Service, and the Adventure Aquarium with particular regard to Michele Pagel and Jennifer Duffy. We are also grateful to the reviewers and the associate editor, Thomas Deméré, for their helpful suggestions to the manuscript. Video recordings of the seals around Duck Island were made possible through the NMFS permit 16223. The study was approved by the West Chester University Institutional Animal Care and Use Committee.

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Received: 21 May 2013
Accepted: 19 July 2014