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Maneuverability by the sea lion *Zalophus californianus*: turning performance of an unstable body design

Frank E. Fish[1,*], Jenifer Hurley[2] and Daniel P. Costa[3]

[1]*Department of Biology, West Chester University, West Chester, PA 19383, USA,* [2]*Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039-9647, USA* and [3]*Department of Biology and Institute of Marine Sciences, University of California, Santa Cruz, CA 95064, USA*

*Author for correspondence (e-mail: ffish@wcupa.edu)

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Summary

Maneuverability is critical to the performance of fast-swimming marine mammals that use rapid turns to catch prey. Overhead video recordings were analyzed for two sea lions (*Zalophus californianus*) turning in the horizontal plane. Unpowered turns were executed by body flexion in conjunction with use of the pectoral and pelvic flippers, which were used as control surfaces. A 90° bank angle was used in the turns to vertically orient the control surfaces. Turning radius was dependent on body mass and swimming velocity. Relative minimum radii were 9–17% of body length and were equivalent for pinnipeds and cetaceans. However, *Zalophus* had smaller turning radii at higher speeds than cetaceans. Rate of turn was inversely related to turn radius. The highest turn rate observed in *Zalophus* was 690 degrees s^{-1}. Centripetal acceleration measured up to 5.1 g for *Zalophus*. Comparison with other marine mammals indicates that *Zalophus* has a morphology that enhances instability, thus providing enhanced turning performance. Enhanced turning performance is necessary for sea lions to forage after highly elusive prey in structurally complex environments.

Key words: maneuverability, stability, turning, swimming, California sea lion, *Zalophus californianus.*

Introduction

Animals in motion must contend with the two seemingly opposing functional requirements of stability and maneuverability (Fish, 2002). Stability promotes steady movement along a predictable trajectory, whereas changes in rate of movement and trajectory characterize maneuverability, which represents a controlled instability. A maneuvering body undergoes translation or rotation, as opposed to a stable body in which the sum of all forces and all turning moments is zero (Webb, 1997). Stability reduces the energetic cost of locomotion by reducing resistive forces and minimizing distance traveled. Animals, however, rarely move continuously in straight lines. This is especially true in instances where potential prey must out-maneuver a predator or, the reverse, a predator must turn fast enough to catch its prey (Howland, 1974; Webb, 1983; Domenici, 2001). In addition, turning is important in the search patterns employed by animals, obstacle avoidance and course corrections due to external perturbations (Webb et al., 1996; Schrank et al., 1999; Davis et al., 2001; Webb, 2002).

The morphology of an animal dictates its movements and limits its locomotor performance (Webb, 1984; Weihs, 1989, 1993, 2002; Taylor, 1989). Regardless of locomotor mode (e.g. walking, swimming, flying), various morphologies that foster maneuverability have evolved within animal lineages, while others have enhanced stability. The wing geometry of flying vertebrates determines flight maneuverability (Norberg, 2002). Minimum turning radius performed by fish is affected by body and fin morphology (Webb, 1976, 1983, 2002; Blake et al., 1995; Webb et al., 1996). Boxfishes (*Ostracion*) use combinations of fins in conjunction with their rigid body design for powered and trimming control of stability (Gordon et al., 2000; Webb, 2002). Differences in the morphology of cetaceans are associated with turning performance and habits. Rapid-swimming pelagic dolphins (i.e. *Lagenorhynchus*) with compact bodies and restricted mobility of the flippers demonstrate high turning rates (up to 453 degrees s^{-1}) but have a greater length-specific minimum turning radius compared with slow-swimming cetaceans with more flexible bodies and mobile flippers (Fish, 2002). Cetaceans with more flexible body designs sacrifice speed for maneuverability to function in complex environments (i.e. pack ice, flooded forests or rivers).

Analysis was performed by Fish (2002) that indicated that certain morphological characteristics were associated with stability performance in cetaceans. These characteristics were based on an arrow model (Harris, 1936; Wegener, 1991; Fish, 2002). Stability was dependent on the location and design of control surface relative to the center of gravity and on rigidity of the body. In that maneuverability represents a controlled instability, the possession of morphological characters that deviate from a design that maintains stability is expected to enhance turning performance.

As opposed to cetaceans, which have specialized to a fully aquatic lifestyle, all pinnipeds (sea lions, seals, walrus) possess a morphology that permits various degrees of movement in both terrestrial and aquatic environments (Fish, 1993, 1996). The amphibious habits of pinnipeds require use of the paired appendages for locomotion (Howell, 1930; Ray, 1963; English, 1976; Gordon, 1981; Fish et al., 1988). The divergent body designs and modes of propulsion of pinnipeds suggest differences in turning performance in water compared with cetaceans. California sea lions (*Zalophus californianu*) have relatively large flippers and highly flexible bodies (Ray, 1963; Aleyev, 1977). These sea lions are highly agile in water and have been considered to swim with a high degree of maneuverability (Godfrey, 1985).

We quantitatively examined turning performance of *Zalophus californianus* using videography. As data are not available for other species of sea lion or fur seals, we compared data on turning performance of *Zalophus californianus* with similar data collected from cetaceans to assess how differences in morphology influence aquatic maneuverability.

Materials and methods

One adult male and one adult female sea lion *Zalophus californianus* Lesson 1828 were examined at the Long Marine Laboratory of the University of California, Santa Cruz. Physical measurements of the sea lions are provided in Table 1. Body length (L) was measured as the distance from the tip of the nose to the tip of the tail. Projected area and length of the spread pectoral and pelvic flippers were determined from scaled photographic slides input with a Polaroid SprintScan 35 slide scanner into a Power Macintosh 7500 and analyzed using NIH-image software (Version 1.57). Aspect ratio (AR) of the flippers was calculated as flipper length^2/flipper projected area. The position of the center of gravity (CG) was determined according to the method of Domining and De Buffrénil (1991): animals laid on a wooden board resting on a cylindrical pipe; the board was rolled over the pipe until the animal was balanced; the balance point was measured from the animal's nose, and CG was expressed as a percentage of L.

The sea lions were maintained in an outdoor facility consisting of three interconnecting, saltwater pools (568 000 liter volume) with concrete decking for use as haul-out areas. Animals were tested in a 9.1 m diameter pool with a depth of 2.4 m. The sea lions were maintained on a diet of herring and capelin and were exercised daily and weighed weekly to ensure optimal body condition.

The sea lions were trained using classical and operant conditioning and positive reinforcement techniques to swim rapidly to a target that was affixed to the end of a pole. Each sea lion was directed by a trainer to swim from the concrete deck to a position on the opposite side of the pool indicated by a second trainer striking the target on the water surface. As the sea lion was arriving at the target position, the trainer on the deck recalled the animal with a second target strike. In this manner, the sea lions executed rapid 180° turns. Animals were given 5-min rests between five consecutive turns. White zinc oxide dots were placed on the dorsum and flanks of the animals at a position approximating CG.

Video recordings of sea lion turning were made using a Panasonic camcorder (DV-510) at 60 Hz. The camcorder was held by an observer 2.7 m directly above the position of the turn. Video records were analyzed frame-by-frame at 30 Hz with a video recorder (Panasonic AG-7300) and video monitor (Panasonic CTJ-2042R). Only those records in which the animal's body remained horizontal to the water surface throughout the turn were used. The sequential positions of the CG marker were recorded onto transparencies from the video monitor. As the sea lions rolled 90° during the turn (Godfrey, 1985), the position of the lateral zinc oxide dot was followed through its curved trajectory. The center of rotation of the turn was determined geometrically (Youm et al., 1978). This technique allowed for determination of the trajectory of CG, despite distortion in observing the actual position of the marker due to refraction from surface waves. Absolute and length-specific values of turning radius (r; measured in m and L, respectively) and average velocity (U; measured in m s^{-1} and L s^{-1}, respectively) were measured. Centripetal acceleration (a_c) was measured in m s^{-2} and multiples of gravitational acceleration ($\boldsymbol{g}$; 9.8 m s^{-2}), where a_c was computed according to:

$$a_c = U^2/r\boldsymbol{g}\,. \tag{1}$$

Centripetal force (F; measured in N) was computed as:

$$F = ma_c = mU^2/r\,, \tag{2}$$

where m is the animal's mass in kg. Angular displacement was used to calculate the turning rate (TR) in degrees s^{-1}.

As maximal performance was being evaluated, the highest values of turning velocity and turning rate and the smallest

Table 1. *Sea lion morphometrics*

Animal	Body length (m)	Mass (kg)	Pectoral flipper area (m^2)	Pectoral aspect ratio	Pelvic flipper area (m^2)	Pelvic aspect ratio	Total flipper area* (m^2)	CG position (% body length)
Male	1.89	137.8	0.069	4.13	0.044	1.95	0.227	48.6
Female	1.72	88.2	0.061	4.16	0.028	1.85	0.180	48.0

*Total flipper area=2×(pectoral flipper area+pelvic flipper area).

values of turn radius were reported for each sea lion. In addition, mean values for the extreme 20% of values were calculated. Means were calculated with variation expressed as ±1s.d.). Comparisons of means were made using *t*-test (Data Desk, version 3.0). Regression equations and correlation coefficients were computed using KaleidaGraph version 3.0 software.

Results

The pectoral flippers and pelvic flippers represented 64.8% and 35.2% of the total projected flipper area, respectively. Mean *AR* of the pectoral flippers was 4.15, whereas mean *AR* of the pelvic flippers was 1.90. The mean position of CG from the anterior end of the animal as a percentage of *L* was 48.3%. This position coincided with the posterior insertion of the pectoral flippers.

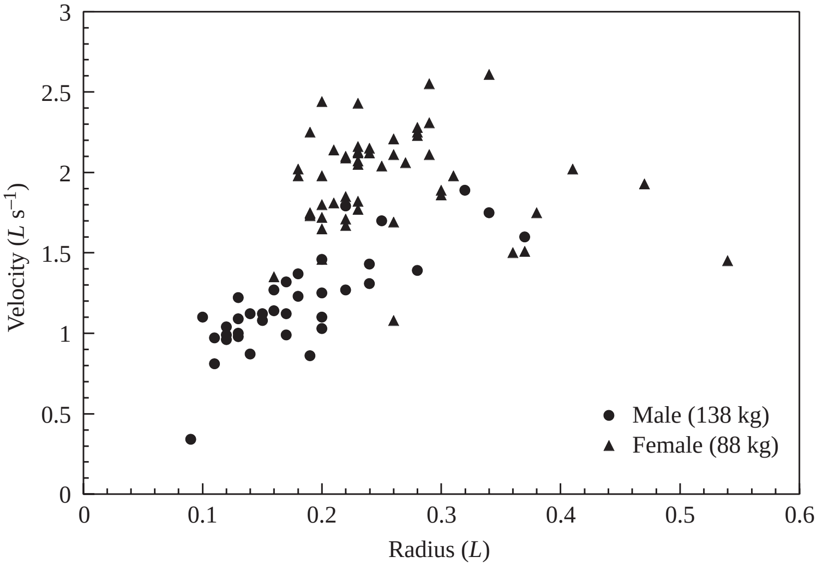

Fig. 1. Plot of relative turning radius and turning velocity for two sea lions.

A total of 88 steered turning sequences was analyzed for the male (*N*=36) and female (*N*=52) sea lions. Sea lions approached the target position at a depth of 0.5–1.0 m below the water surface. Before initiating the turn, each sea lion was oriented with its venter facing ventrally, its pectoral flippers adducted (i.e. movement towards the midline of the body) against the lateral flanks of the body, and the pelvic flippers and the digits adducted. At the start of the turn, the head was displaced into the turn and rolled slightly by twisting and flexing of the neck. The pectoral flippers then were abducted (i.e. movement away from the midline of the body) and supinated (i.e. outward rotation) as the body rolled approximately 90°. The head and body were hyperextended, assuming a U-shaped configuration through the middle of the turn. The pelvic flippers were abducted. The digits of the pelvic flippers were also abducted, which spread the interdigital webbing and increased the projected area of the flippers. As the sea lion straightened the body at the end of the turn, the head and body were rolled, restoring the orientation of the body with the venter facing downwards. The pectoral flippers were pronated (i.e. inward rotation) and adducted against the body, increasing streamlining. The digits of the pelvic flippers were adducted, decreasing the area of the interdigital webbing, and the flippers were adducted so that they were oppressed with the plantar surfaces in contact to each another.

The above locomotor sequence was executed in 1.07±0.08 s and 0.90±0.25 s for the male and female sea lions, respectively. The smaller female had faster maximum absolute and length-specific turning velocities of 4.47 m s^{-1} and 2.61 L s^{-1}, respectively, compared with the maximum velocities of 3.58 m s^{-1} and 1.89 L s^{-1} for the male sea lion (Fig. 1). For the fastest 20% of velocities (Table 2), the female sea lion swam statistically faster than the male (t=–6.56, d.f.=15, P<0.05). Turning radius was significantly different (t=–10.02, d.f.=15, P<0.05) between the two sea lions (Fig. 1; Table 2). The minimum length-specific turning radius of the male sea lion was 0.09 L, which was 43.8% smaller than the length-specific turning radius of the female.

The maximum a_c of the female sea lion was 1.84 times higher than that of the male sea lion (Table 2). When expressed as a multiple of $\boldsymbol{g}$, the maximum value for a_c was 5.13! Despite the difference in extreme values of a_c between the two sea lions, the difference in body mass resulted in maximum

Table 2. *Maximum and minimum turning performance data for sea lions and means (±s.d.) of the extreme 20% of values*

Animal	Minimum *r* (m)	Minimum *r* (L)	Maximum *U* (m s^{-1})	Maximum *U* (L s^{-1})	Maximum a_c (m s^{-2})	Maximum a_c ($\boldsymbol{g}$)	Maximum *F* (N)	Maximum *TR* (degrees s^{-1})
Male	0.16	0.09	3.58	1.89	27.41	2.80	3776.7	660.0
20%*	0.21±0.03	0.11±0.01	3.14±0.30	1.66±0.16	22.18±2.47	2.26±0.25	3056.5±340.8	513.8±63.8
Female	0.28	0.16	4.47	2.61	50.31	5.13	4437.1	690.0
20%†	0.33±0.02	0.19±0.01	4.04±0.23	2.36±0.13	39.42±4.96	4.02±0.51	3476.6±437.1	599.2±48.8

Abbreviations: *r*, radius; *U*, velocity; a_c, centripetal acceleration; *F*, centripetal force; *TR*, turning rate.

*N=7.

†N=10.

centripetal forces that were not significantly different (t=2.00, d.f.=15, P>0.05) between the two animals.

Plots of a_c as a function of turning rate (Fig. 2) showed significant correlations for both male (r=0.66, P<0.001, N=36) and female (r=0.92; P<0.001, N=52) sea lions. The equations describing the relationship are a_c=0.179+0.004TR for the male and a_c=–0.696+0.008TR for the female sea lions. The slopes of these relationships were significantly different (t=21.90, d.f.=84, P<0.001) (Zar, 1984).

F was found to increase linearly with v (m s^{-1}) for both sea lions (Fig. 3). Regressions of the data were found to be significantly correlated at P<0.001 for r=0.70 for the male and r=0.81 for the female. The regressions are described for the male and female sea lion by the equations F=392.71+777.22v and F=–1741.50+1243.50v, respectively. Comparison of the slopes showed significant difference (t=11.78, d.f.=84, P<0.001) for the two lines (Zar, 1984).

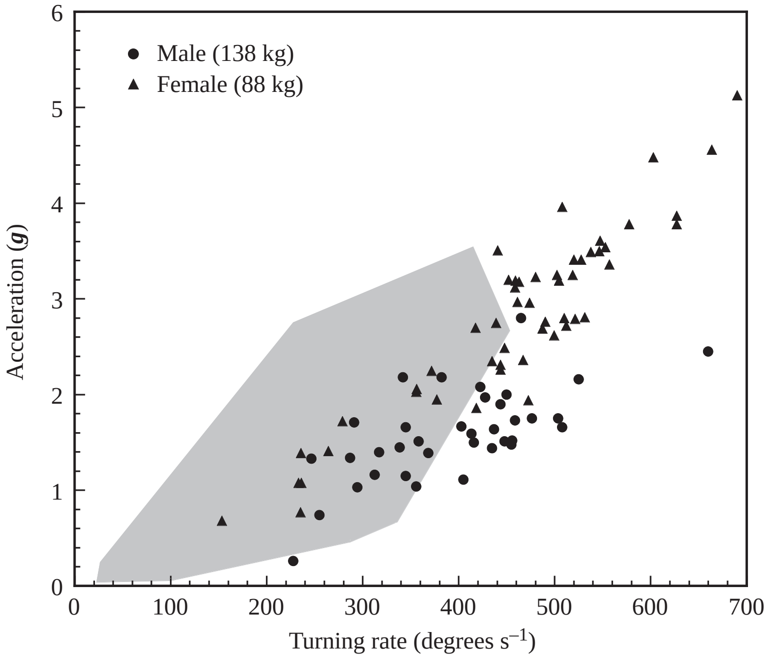

Fig. 2. Relationship between turning rate and centripetal acceleration in two sea lions. Acceleration increased directly with turning rate. The shaded area represents limits of turning performance for cetaceans from data presented by Fish (2002).

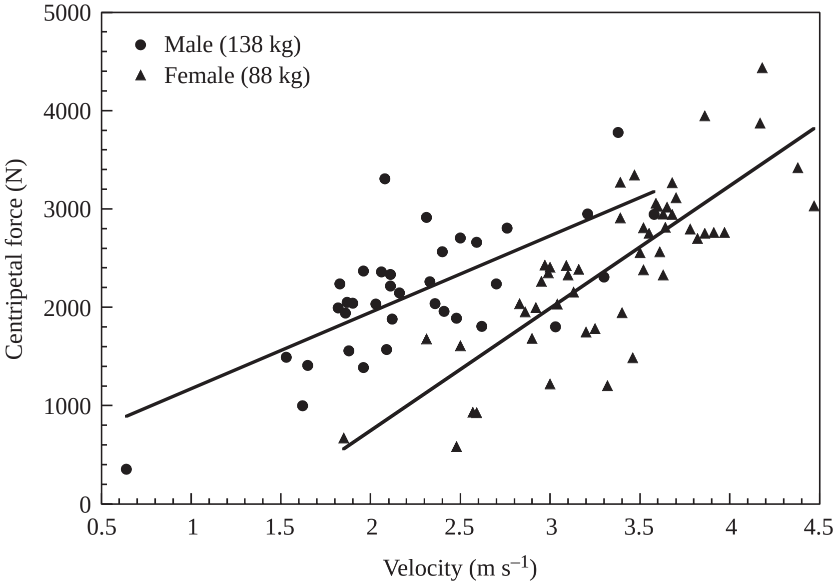

Fig. 3. Relationship between centripetal force and turning velocity for the two sea lions. Solid regression lines were computed by the least-squares method for each sea lion. Regressions were statistically significant at P<0.001. Regression equations are provided in the text.

Discussion

Morphology for maneuverability

Morphological parameters associated with stability were reported by Fish (2002) and are presented in Table 3. Stability, and thus reduced maneuverability, is encouraged when (1) the control surfaces are located distant from CG, (2) the concentration of projected area of the control surfaces is located posterior of CG, (3) the control surfaces display sweep (i.e. angle between the axis of the control surface and the longitudinal axis of the body; Bertin and Smith, 1998) and dihedral (i.e. angle between the horizontal plane of the body and the planar surface of the control surface), (4) the control surfaces have limited mobility, (5) CG is located anteriorly and (6) the body is inflexible (Breder, 1930; Harris, 1936; Hurt, 1965; Aleyev, 1977; Smith, 1992; Weihs, 1993; Fish, 2002). Marked variation between the relative design of the body and the placement of control surfaces in otariid pinnipeds and cetaceans indicates functional differences in turning performance between these marine mammals (Fig. 1; Table 3). Sea lions deviate from a stable configuration compared with the bottlenose dolphin *Tursiops truncatus*. Therefore, it is predicted that *Zalophus* will be more highly maneuverable compared with cetaceans.

The control surfaces of sea lions are represented by pectoral and pelvic flippers. The roots of the larger pectoral flippers are located near the center of gravity. This placement of the pectoral flippers is dynamically unstable. The flippers provide little rotational dampening about the yaw and pitch axes (Fig. 4), although they could retard rotational and translational motion in regard to roll and heave, respectively. The smaller pelvic flippers are in the preferred location to develop sufficient torque to act like an aeroplane

Table 3. *Comparison of morphometric parameters related to stability*

Stability parameter	*Zalophus*	*Tursiops*
Control surfaces location with respect to CG	Pectoral flippers located near CG; pelvic flippers located far from CG	Pectoral flippers anterior of CG; flukes and peduncle located far from CG; dorsal fin located near CG
Concentration of control surface area with respect to CG	64.8% of control surface area located near CG	12.5% of control surface area located near CG*
Placement of CG in body	CG located at 0.48*L*	CG located at 0.41*L*[†]
Dihedral of control surfaces	Variable	Constrained[†]
Sweep of control surfaces	Variable	Constrained[†]
Mobility of control surfaces	Highly mobile	Pectoral flippers constrained; dorsal fin fixed; flukes and peduncle laterally constrained; mobile dorso-ventrally[†]
Flexibility of body	Highly flexible	Reduced flexibility[‡,§]

*F. E. Fish (unpublished data); [†]Fish (2002); [‡]Bonner (1989); [§]Long et al. (1997).
L, body lengths; CG, center of gravity.

stabilizer or ship rudder and to resist rotational instabilities (Fig. 4).

The attitude of the *Zalophus* flippers is highly variable because of the high mobility of the pectoral and pelvic flippers (English, 1976; Godfrey, 1985). Both the sweep and the dihedral can be changed. Sweep resists yawing, whereas dihedral combats roll (Breder, 1930; Hurt, 1965). The ability of the sea lion to adduct the pectoral flippers against the body and adduct the pelvic flippers can effectively produce a condition where the animal is devoid of control surfaces and potentially susceptible to all instabilities. The mobility of the pectoral and pelvic flippers also permits dynamic production of lift, which can induce torques around CG to promote instabilities. The location of the pectoral flippers close to CG would not produce large torques and would be less effective in rapidly inducing turns. The large projected area of the flippers may help compensate for the reduced torque. However, the pectoral flippers are used for propulsion (Howell, 1930; Feldkamp, 1987), and propulsors arranged around CG are postulated to promote maneuverability (Webb et al., 1996).

The body of *Z. californianus* is highly flexible (Fig. 5). Bending of the body and neck is an integral component of turning in conjunction with the flippers of pinnipeds (Aleyev, 1977; Godfrey, 1985). The extremely pliable neck and body permit a sea lion to bend over backwards, reaching their pelvic flippers (Riedman, 1990). This dorsal bending was the preferred bending direction used by sea lions during turns (Godfrey, 1985; this study). Dorsal bending of the spine allows the body to curve smoothly, maintaining a streamlined appearance throughout the turn. As the turn is unpowered, a streamlined body will minimize drag and limit deceleration as direction changes.

Humbolt penguins (*Spheniscus humboldti*) and beluga

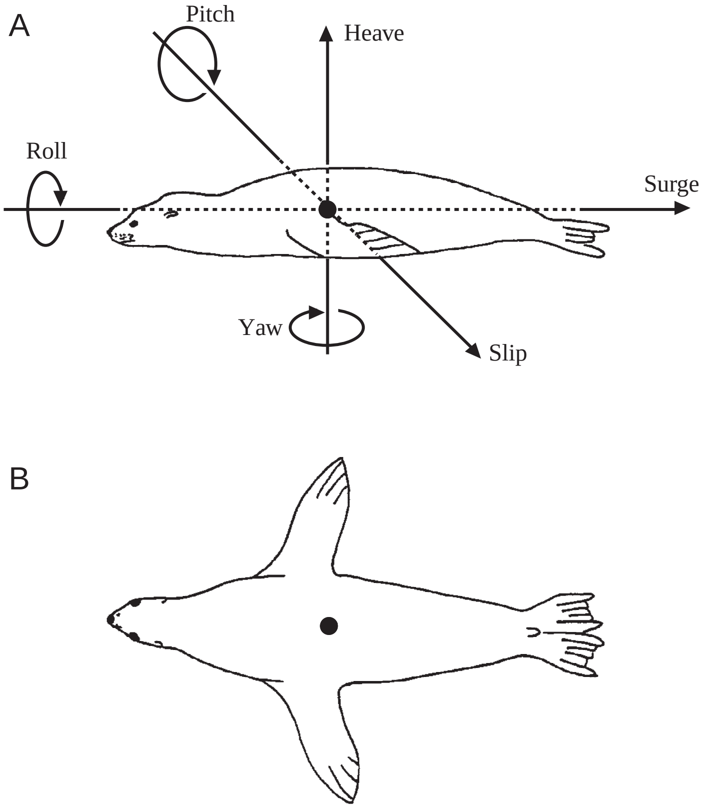

Fig. 4. Illustrations of the flipper design and location for the sea lion from lateral (A) and dorsal (B) views. The position of the center of gravity (CG) is indicated by the filled circle. Rotational and translational instabilities associated with a three-dimensional axis system are projected on the lateral view of the sea lion. Rotational instabilities include roll (rotation around the *x*-axis), pitch (rotation around the *y*-axis), and yaw (rotation around the *z*-axis). Translational instabilities include movement along the three axes as surge (*x*-axis), heave (*y*-axis) and slip (*z*-axis).

Fig. 5. Body flexibility in the sea lion demonstrated by dorsal bending.

whales (*Delphinapterus leucas*) bank during unpowered turns so that the ventral aspect of the body is directed towards the inside of the turn (Hui, 1985; Fish, 2002). Although the difference in bending direction may be due to vertebral mechanics (Long et al., 1997; Gal, 1993a,b; Pabst, 2000), the use of banking appears to be common in animals that lack a dorsal keel and use the pectoral appendages to resist slip. High bank angles provide a greater projected area facing the axis of the turn.

For the cetaceans, there are multiple control surfaces (e.g. flippers, flukes, dorsal fin and caudal peduncle) that are arranged in a configuration promoting a higher degree of stability than in sea lions (Fish, 2002). The flippers of most cetaceans have limited mobility. One notable exception is the humpback whale (*Megaptera novaeangliae*), which has long, mobile flippers and is highly acrobatic (Edel and Winn, 1978; Fish and Battle, 1995). The humpback whale flippers are for maneuvering associated with unique prey capture behaviors (Jurasz and Jurasz, 1979). However, flexibility in the body of cetaceans is generally constrained (Bonner, 1989; Long et al., 1997) by comparison to that of otariids.

Maneuvering performance

Turns by *Zalophus* were executed in a manner as previously described (Ray, 1963; Peterson and Bartholomew, 1967; English, 1976; Godfrey, 1985). Horizontal turns were executed by extending the pectoral flippers, spreading the pelvic flippers and flexing the body.

Similarities have been made between the turning maneuvers of sea lions and the banking turns displayed by birds and aeroplanes (Ray, 1963). In the latter banking turns, the wings generate lift that is resolved into vertical and horizontal vector components. The vertical component counters the gravitational force and keeps the aircraft from losing altitude. The horizontal vector is directed towards the center of rotation and provides the centripetal force necessary for the turn.

As sea lions swim in an environment with a density similar to the body composition, these animals can be near neutrally buoyant, negating the necessity of a vertical component during turns in the horizontal plane. Thus, the sea lion can bank 90° without changing depth. The horizontally directed lift from the flippers would produce centripetal force necessary for the turning maneuver. While the pectoral flippers can be rotated to produce an angle of attack (i.e. angle between the flipper chord and the incident flow), bending of the spine would aid in orientation of the flippers for lift generation. However, there is no direct evidence that the flippers are canted at an angle of attack to effect a turn. Indeed, the location of the flippers close to CG reduces the torque to produce the turn. The pectoral flippers are particularly important in generating lift necessary to roll the body. Other surfaces used to control the turn are the head and pelvic flippers. The head leads the turn and determines direction. The pelvic flippers act as stabilizers to prevent the posterior portion of the body from deviating from the curved trajectory of the turn (Godfrey, 1985).

Minimum unpowered turn radii for the two sea lions were 0.16 m and 0.28 m, representing $0.09L$ and $0.16L$, respectively. While the length-specific radii were small, they were not substantially different from similar values for cetaceans. Minimum radii for unpowered turns by cetaceans were reported to range from $0.10L$ to $0.15L$ (Fish, 2002). The smallest radius turn was displayed by the river dolphin *Inia geoffrensis*, which had an extremely flexible body and mobile flippers (Fish, 2002). Fish display smaller turning radii than the cetaceans. Domenici and Blake (1997) reported that the knifefish *Xenomystus nigri*, angelfish *Pterophylum eimekei* and pike *Esox lucius* had minimum turning radii of $0.055L$, $0.065L$ and $0.09L$, respectively. Four species of coral-reef fishes demonstrated minimum turn radii of approximately $0–0.06L$ (Gerstner, 1999). Similarly, the boxfish *Ostracion meleagris* was capable of a $0.0005L$ turn (Walker, 2000). Such tight turns in fish are due primarily to the use of multiple propulsors to rotate about the yawing axis without translation.

Webb (1994) cautioned that comparisons of turning radius between species should be made at mechanically equivalent speeds. Despite their comparatively ordinary turning performance with respect to radius, turning ability of *Zalophus* is shown to be better than other marine mammals when turning velocity is considered as a covariant (Fig. 6). *Zalophus* generally can turn in smaller radii than cetaceans at the same swimming speeds.

Agility is defined as the rapidity in which direction can be changed and is measured as the rate of turn (Norberg, 1990; Webb, 1994). The maximum turning rate of *Zalophus* was 690 degrees s^{-1}, and maximum centripetal acceleration was $5.13\boldsymbol{g}$. Even though these are singular values, sea lions were still able to turn at high rates of 513.8–599.2 degrees s^{-1} and 2.26–4.02 $\boldsymbol{g}$ for the means of the maximum 20% of the data. Such performance is superior to turning rates for cetaceans (Fig. 2). Most turning maneuvers by cetaceans are performed at <200 degrees s^{-1} and <1.5 $\boldsymbol{g}$, although turns of 453.3 degrees s^{-1} and 3.56 $\boldsymbol{g}$ have been measured in fast-swimming *Lagenorhynchus obliquidens* (Fish, 2002). Penguins have a turn rate equivalent to sea lions at 575.8 degrees s^{-1} (Hui, 1985). Fish are capable of higher levels of agility compared with marine mammals. Data from Webb (1976, 1983), Blake et al. (1995) and Gerstner (1999) indicate that fish ranging in size from 0.04 m to 0.39 m could turn at rates of 425.6–7300.6 degrees s^{-1}. Such performance is extraordinary when it is considered that species such as *Salmo gairdneri* and *Micropterus dolomieu* are able to accelerate to 8.2 $\boldsymbol{g}$ and 11.2 $\boldsymbol{g}$, respectively (Webb, 1983).

Ecological relationships

The increased levels of maneuverability, which are displayed by *Zalophus*, are associated with complexity of habitat. California sea lions forage in waters near the mainland coast, being found no further than 16 km from the coast (King, 1983). They hunt in structurally complex environments, including rocky inshore/kelp forest communities, along the continental shelf, around seamounts and in the mouths of freshwater rivers (Riedman, 1990; Reeves et al., 2002). Similarly, the river dolphin *Inia*, with its flexible neck and trunk and mobile flippers, has a small minimum turning radius and occupies complicated environments, including flooded forests and river systems. Faster swimming, but less maneuverable, dolphins are found in oceanic, open water systems (Fish, 2002). Coral-reef fishes were shown to have high maneuverability with turning radii of <0.06 L (Gerstner, 1999; Walker, 2000). These fish must operate in a habitat that is confining due to three-dimensional complexity of the corals.

Predatory behavior also necessitates high maneuverability and agility due to the scaling effects between the predator and its prey (Howland, 1974; Domenici, 2001). The turning radius of a large aquatic predator will generally be larger than that of smaller prey because turn radius is directly related to body mass. Although a large predator can swim at higher absolute speeds, the prey has superior turning performance for escape.

Zalophus feed on octopus, squid and fish, including herring, anchovies, hake, whiting and salmon (King, 1983; Riedman, 1990). These are fast-swimming prey that require high speed and maneuverability for capture. Feeding is performed alone unless large schools of prey are present, when the sea lions can feed cooperatively (Riedman, 1990). Prey size for sea lions typically falls within the 10–30 cm range (Bowen and Siniff, 1999). Fish within this size range can turn with a radius that is one order of magnitude smaller than that of the sea lion and at rates of 0.7–11.1 times the maximum rate of the sea lion (see above). Although elusive prey would appear to have an advantage in terms of turning, the sea lion's pliable neck in conjunction with its maneuverability could contribute to an advantage for the predator. In the turning gambit envisioned by Howland (1974), closure distance (i.e. straight line distance between predator and prey) is important in the outcome of predator prey chases. The mobility of the neck along with its ability to telescope can reduce closure distance and effectively decrease turn radius and increase turn rate.

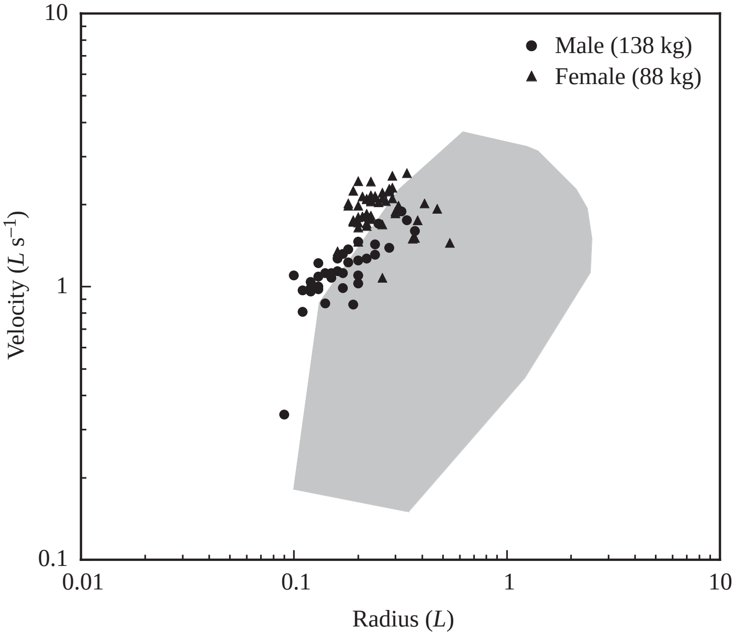

Fig. 6. Comparison of the relationship between turning radius and turning velocity for two sea lions and cetaceans. Data for the sea lion are indicated by solid circles for the male and solid triangles for the female. The shaded area represents limits of turning performance for cetaceans from data presented by Fish (2002).

List of symbols

a_C	centripetal acceleration
AR	aspect ratio
CG	center of gravity
$\boldsymbol{g}$	gravitational acceleration, 9.8 m s^{-2}
m	mass
F	centripetal force
L	body length
TR	turning rate
U	velocity

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