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Observations of Dolphin Swimming Speed and Strouhal Number

J. J. Rohr
E. W. Hendricks
L. Quigley
SSC San Diego

F. E. Fish
West Chester University

J. W. Gilpatrick
National Marine Fishery Service

J. Scardina-Ludwig
SeaWorld San Diego

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Space and Naval Warfare Systems Center
San Diego, CA 92152-5001

EXECUTIVE SUMMARY

OBJECTIVES

The principal objective of this study was to record maximum dolphin swimming speeds sustainable for several seconds utilizing different motivational strategies for both captive and free-ranging dolphins. Video records were used to determine relationships between the various kinematic parameters, particularly the Strouhal number, which characterizes dolphin-swimming motion. Comparisons were made, where possible, with results from previous studies.

RESULTS

Nearly 2000 swimming-speed measurements were obtained from recordings of both captive and free-ranging dolphins. Captive dolphins studied were *Tursiops truncatus* (bottlenose dolphin), *Delphinus delphis* (short-beaked common dolphin), and *Pseudorca crassidens* (false killer whale). Free-ranging dolphins observed were *Tursiops* and *Delphinus capensis* (long-beaked common dolphin). In all cases, some form of motivation was provided for the dolphins to swim fast. The highest swimming speeds recorded were those of captive dolphins, and ranged from 8.0 to 8.2 m/s, typically lasting for a few seconds.

Several kinematic variables, and combinations thereof, were determined for dolphins swimming in large pools. The average values of the tail-beat peak-to-peak amplitude (A_{p-p}) for *Tursiops truncatus* and *Pseudorca crassidens* were respectively $22\% \pm 2\%$ ($n=51$) and $23\% \pm 2\%$ ($n=23$) of their body length. These values of A_{p-p} agree with the $20\% \pm 3\%$ ($n=56$) reported by Fish (1993) and the $19\% \pm 1\%$ ($n=30$) reported by Kayan and Pyatetskiy (1977) for trained *Tursiops*, also swimming in large pools. Corresponding tail-beat frequency (f) throughout the velocity range of present ($\approx 3-7.5$ m/s) and past (Fish, 1993; $U \approx 1-6$ m/s) *Tursiops* measurements, increase almost linearly with increasing velocity ($f \propto 0.34 U$; $R^2 = 0.79$).

Average Strouhal numbers ($A_{p-p}f/U$) calculated from present and past (Fish, 1993) swimming recordings of *Tursiops truncatus*, were 0.25 ± 0.04 ($n = 51$) and 0.27 ± 0.05 ($n = 56$), respectively. These values compare well with the average Strouhal number of 0.25 ± 0.02 ($n=17$) observed by Kayan and Pyatetskiy (1977), also for captive *Tursiops*. The average Strouhal number calculated for *Pseudorca crassidens* was 0.29 ± 0.04 . Average Strouhal values were within the 0.25 to 0.35 range predicted by theoretical models for maximum propulsive efficiency (Triantafyllou et al., 1993).

RECOMMENDATIONS

Although the fastest swimming speeds reported for trained dolphins agree, there is a large discrepancy between reported swimming speeds of trained and free-ranging dolphins. Maximum swimming speeds of free-ranging dolphins are as much as two times that reported for captive dolphins. Consequently, additional recorded observations are necessary to increase confidence in existing measurements of maximum dolphin swimming speeds in the wild. Because of the low probability of recording maximum speeds, large data sets using different motivational strategies are considered essential. A study of the relationship between jump height and underwater swimming speed (prior to the jump) of captive dolphins would be particularly helpful for determining the correction term required to infer

underwater swimming speed from jump height. It would also be desirable to compare swimming speeds and swimming motion of dolphins as a function of depth to study the effect of wave drag.

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1. INTRODUCTION

1.1 SWIMMING SPEEDS

Incredible stories are told regarding the rapidity of movement of this creature. It appears to be the fleetest of all animals, marine and terrestrial, and it can leap over the masts of large vessels.

Aristotle, on dolphin, *Historia Animalium*

The previous passage illustrates how extraordinary and incredulous accounts of the swimming abilities of dolphins can be. Since there is no evidence that the muscles of dolphins are exceptionally powerful (Pershin, 1988; Fish, 1993), reports of exceptionally high swimming speeds have served as an invitation to look for some underlying, perhaps yet to be discovered, drag-reducing mechanism. Since Sir George Cayley (Gibbs-Smith, 1962), almost two centuries ago, recognized the drag-minimizing shape of dolphins, many additional, naturally evolved, speed-enhancing attributes have been proposed (Kramer, 1960; Hertel, 1963; Webb, 1975; Fish and Hui, 1991). These include drag reduction through both passive (Kramer, 1960, 1965; Fitzgerald and Fitzgerald, 1995) and active (Lang, 1966) compliant skin dampening; dermal ridges (Purves et al. 1975); mucus secretions (Sokolov et al., 1969); boundary-layer heating (McGinnis et al., 1972); skin folds (Aleyev, 1977); forcing a turbulent boundary layer (Webb, 1978); and producing favorable pressure gradients through the oscillating movements of the animal's flukes (Gray, 1936, 1957). A detailed discussion of these hypothesized drag-reducing mechanisms can be found in Fish and Hui (1991).

A major obstacle towards assessing dolphin-swimming capabilities is the difficulty in accurately measuring burst speeds, i.e., maximum speeds sustainable for a few seconds. Vogel (1994) has suggested that reports of speeds of swimming organisms often include so many egregious overestimates that extreme skepticism is generally recommended when dealing with the literature. Fish (1992) has specifically questioned swimming speed measurements based on observations from ships, airplanes, and the shoreline, because these estimates were often determined without fixed reference frames, information on currents, or the use of accurate timing instruments. Consequently, the most reliable dolphin burst swimming-speed data to date have been obtained from trained animals swimming in a free-ranging environment (Lang and Norris, 1966; Lang and Pryor, 1966). However, it has been noted that trained animals may not be suitably motivated to swim at their maximum potential (Lang, 1963; Lang and Daybell, 1963; Lang, 1975). Measurements in captivity are further criticized because of the limited pool size (Lang, 1975) and the shallowness of the water depth (Purves *et al.*, 1975). In addition, since captive animals are deprived of the main stimulus for high-speed swimming provided by nature (i.e., catching food and fleeing predators), there is the question as to whether or not captive animals' athletic condition is generally as good as dolphins in the wild (Gray, 1957; Pershin, 1988).

A wide range of reported swim data for the dolphin species observed here is compiled in table 1. Swimming speeds in table 1 are grossly distinguished by the length of time which they were thought to be sustained, and are simply referred to as: 1) burst—supportable for a few seconds; 2) maximum sustained—supportable for minutes; and 3) average cruising—supportable for hours. One characterization of the flow around the dolphin is the Reynolds number (Re) a dimensionless number that reflects the ratio of the inertial and viscous forces. The Reynolds number is defined as:

$$\text{Re} = L U / \nu, \quad (1)$$

where L is the length of the dolphin, U is the average swimming speed of the dolphin, and ν is the kinematic viscosity of seawater. For the high Reynolds number flow around the dolphin, typically of the order 10^6 , mechanical power output is nearly proportional to the cube of the velocity (Shapiro, 1961; Fish, 1993). Consequently, a factor of two discrepancy in swimming speed (such as seen in table 1 for *Tursiops truncatus*) results in about a factor of eight in the animal's power requirements.

The present swimming-speed data were obtained from the following three sources: 1) video recordings of captive dolphins, which include bottlenose dolphins (*Tursiops truncatus*), a short-beaked common dolphin (*Delphinus delphis*), and a false killer whale (*Pseudorca crassidens*) trained to swim fast; 2) video recordings of the release of free-ranging dolphins (*Tursiops*); and 3) open-ocean aerial photogrammetry of a school of long-beaked, common dolphins (*Delphinus capensis*) responding to the sound of an approaching airplane. Although one or more of the previous criticisms concerning the determination of burst swimming speed equally applies to the present study, it is nevertheless believed that through: 1) utilizing different motivational strategies; 2) obtaining a large number of swimming-speed measurements of both free-ranging and trained dolphins; and 3) recording the observations on film or tape for repeated swimming-speed analysis, the present effort will contribute towards a richer data base from which dolphin swimming capabilities may be more reliably assessed.

1.2 STROUHAL NUMBER AND SWIMMING KINEMATICS

If the premises of the theory are correct, then the undulating animal, aided by its intricate sensory system, may be able to reextract a portion of the kinetic and pressure energy stored within the vortex, and regeneratively use it again for propulsion. This, rather than laminar flow, may be the explanation for the great efficiency with which it is thought fishes and dolphins swim.

Rosen, *Water Flow About a Swimming Fish* (1959)

In addition to the aforementioned drag-reducing mechanisms proposed to explain reports of extraordinary dolphin swimming speeds, a highly efficient propulsive method using vorticity control, has also been postulated. Almost 40 years ago, Rosen (1959, 1961, 1963) discovered, through a series of innovative flow visualization experiments, a system of vortices appearing along the sides of swimming fish and dolphins. Rosen (1959, 1961, 1963) hypothesized that some of the rotational energy surrounding the undulating motion of a fish or dolphin could be regained for propulsion through proper synchronization of the animal's body to the vortex flow. Rosen (1959, 1961) further deduced, based on what he referred to as his "vortex peg theory" of undulatory propulsion, an equation for dolphin and fish motion. This equation predicted swimming speed to be proportional to the product of the tail-beat amplitude (extreme position to centerline) and frequency. Rosen (1959, 1961) referred to this proportionality as the "fish" constant and hypothesized that it was nearly the same for fish and dolphins.

Table 1. Range of relevant dolphin swimming speeds reported.

Species	Speed (m/s)	Methodology	Speed Classification	Source
<i>Delphinus delphis</i>	13.2	Undocumented Estimate	Burst	Pershin (1969)
<i>Delphinus delphis</i>	10.3	Boat Observations	Burst	Gray (1936)
<i>Delphinus delphis</i>	12.5 to 13.9	Undocumented Estimate	Maximum Sustained	Tomilin (1957)
<i>Delphinus delphis</i>	9.3	Undocumented Estimate	Maximum Sustained	Kellogg (1940)
<i>Delphinus delphis</i>	9.3	Boat Observations	Maximum Sustained	Johannessen and Harder (1960)
<i>Delphinus delphis</i>	2.8	Undocumented Estimate	Average Cruising	Nowak (1991)
<i>Delphinus delphis</i>	1.6*	Undocumented Estimate	Average Cruising	Hui (1987)
<i>Tursiops truncatus</i>	15.0	Cliff Estimation	Burst	Lockyer and Morris (1987)
<i>Tursiops truncatus</i>	12.5	Undocumented Estimate	Burst	Pershin (1988)
<i>Tursiops truncatus</i>	>8.3	Theodolite Tracking	Burst	Würsig and Würsig (1979)
<i>Tursiops truncatus</i>	7.8*	Boat Observations	Burst	Ridgway and Johnston (1966)
<i>Tursiops truncatus</i>	10.3	Boat Observations	Maximum Sustained	Lockyer (1978)
<i>Tursiops truncatus</i>	6.0*	Captively Trained	Maximum Sustained	Fish (1993)
<i>Tursiops truncatus</i>	2.1	Radio Tagged	Maximum Sustained	Tanaka, S. (1987)

Table 1. Range of relevant dolphin swimming speeds reported. (Continued)

Species	Speed (m/s)	Methodology	Speed Classification	Source
<i>Tursiops truncatus</i>	1.7	Theodolite Tracking	Average Cruising	Würsig & Würsig (1979)
<i>Tursiops truncatus</i>	1.8 to 3.2	Captively Trained	Average Cruising	Videler & Kamermans (1985)
<i>Tursiops truncatus</i>	4.2	Cliff Estimation	Average Cruising	Lockyer & Morris (1987)
<i>Tursiops truncatus</i> [†]	7.01 to 8.3*	Captively Trained	Burst (7.5-10 s)	Lang & Norris (1966); Lang (1975)
<i>Tursiops truncatus</i> [†]	6.09*	Captively Trained	Maximum Sustained	Lang & Norris (1966); Lang (1975)
<i>Tursiops truncatus</i> [†]	3.08*	Captively Trained	Average Cruising	Lang & Norris (1966); Lang (1975)
<i>Tursiops aduncus</i>	2.7	Movement Plots	Average Cruising	Saayman, Bower & Taylor (1972)
<i>Pseudorca crassidens</i>	7.5*	Captively Trained	Burst	Fish (submitted)

Note: Burst refers to fastest speed supportable for a few seconds; maximum sustained refers to the fastest speed maintainable for the order of minutes; and average cruising refers to the speed at which the animal routinely swims. An asterisk (*) denotes captive animal(s); A dagger (†) indicates that *Tursiops truncatus* was listed in source as *Tursiops gilli*.

A similar conclusion was further developed by Triantafyllou et al. (1993). Through theoretical and experimental studies of the dynamics of the wake of an oscillating foil, Triantafyllou et al. (1993) concluded that optimal propulsive efficiency is achieved when the principal wake parameter, the Strouhal number (St), is between 0.25 and 0.35. The Strouhal number is a dimensionless number, representing the ratio of unsteady and steady motion. Applying these results to the swimming characteristics of fish and dolphins, Triantafyllou et al. (1993) defined the corresponding Strouhal number for swimming as:

$$St = A_{p-p} f / U , \quad (2)$$

where A_{p-p} is the tail-beat peak-to-peak amplitude (the distance from the peak of the tail fluke upstroke to the peak of the tail fluke downstroke), f is the tail-beat frequency, and U is the average swimming speed. Similar combinations of these kinematic swimming parameters have been previously made to characterize the swimming motion of fish (Rosen, 1959, 1963; Pyatetskiy, 1970; Webb, 1975), dolphins (Semonov et al. 1974; Kayan and Pyatetskiy, 1977), and athletes (Pershin, 1988), but not within a rigorous theoretical context for swimming efficiency.

Through analysis of swimming observations of the fish and dolphins reported throughout the literature (Reynolds numbers between 10^4 and 10^6), Triantafyllou et al. (1993) calculated corresponding Strouhal values. Generally, they found Strouhal numbers between 0.25 and 0.35, as predicted by their theory. For fish and dolphin swimming in various carangiform modes, additional corroboration can be found in the table of swimming speeds, tail-beat frequencies, and tail-beat amplitudes compiled by Webb (1975), and the Strouhal versus Reynolds figures presented by Pershin (1973, 1988). Although most of the Strouhal numbers comprising these data sets are between 0.25 to 0.35, a substantial fraction lies within the ranges 0.20 to 0.25 and 0.35 to 0.40.

The dolphin Strouhal data of Triantafyllou et al. (1993) consist of two values obtained from analysis of traces (Lang and Daybell, 1963; figures 16, 21) taken from motion picture frames of a 2.03-meter Pacific whitesided dolphin (*Lagenorhynchus obliquidens*) swimming within a pool. One Strouhal number value, 0.32, corresponded to dolphin swimming while wearing a 1.91-cm diameter drag collar. The remaining Strouhal number value, 0.30, corresponded to swimming without the drag collar.

The Strouhal numbers presented here were calculated from recordings of bottlenose dolphins (*Tursiops truncatus*) and false killer whales (*Pseudorca crassidens*) swimming in large pools (courtesy SeaWorld at San Diego, SeaWorld of Florida, and the National Aquarium). These data significantly expand the dolphin Strouhal data set of Triantafyllou et al. (1993), increasing the number of observations (100-fold), species (3-fold), and range of Reynolds number (10-fold). Functional relationships between the kinematic parameters comprising the Strouhal number are also examined. Specifically, tail-beat amplitude and tail-beat frequency are plotted as a function of swimming speed. For comparative reasons, the dolphin Strouhal number and swimming kinematic data of Lang and Daybell (1963; figure 21) and Kayan and Pyatetskiy (1977; figures 2 and 3) are included.

2. MATERIAL AND METHODS

2.1 TRAINED DOLPHINS'SWIMMING PERFORMANCE TESTS

2.1.1 Dolphins

Eight trained dolphins consisting of six bottlenose dolphins (*Tursiops truncatus*), one short-beaked, common dolphin (*Delphinus delphis*) and one false killer whale (*Pseudorca crassidens*) were filmed at the San Diego SeaWorld facility to investigate burst swimming capabilities. In addition to performing in shows, the dolphins in this study participated in training, play, relationship, husbandry, and exercise sessions on a regular basis. Approximately 18 to 20 hours of their day consisted of nonstructural play, free and rest time. The dolphins subsisted on a diet of herring, smelt, mackerel, and squid supplemented with vitamins dispersed at irregular intervals throughout the day. Morphological measurements for each animal, designated by ID number, are summarized in table 2. Body length (L) is defined as the linear distance from the rostral tip to the fluke notch.

To maintain physical fitness, the dolphins perform "fast swims" around the circumference of the main performance pool in their daily exercise routine and in shows. Initial training involved instructing the animals to accelerate quickly and touch their rostrum to a target attached to the end of a pole held several meters out in front of them. Through successive approximations of positioning the target farther and farther away, the dolphins were trained to swim fast upon command. The dolphins normally swam about 0.5 m below the surface of the water and a meter from the pool walls. When the dolphins were not swimming at what the trainers judged to be at or above criteria, the trainers would slap the pole on the surface of the water to induce the dolphins to swim more rapidly. Trainers frequently sent the dolphins (*Tursiops truncatus*) in pairs to provide additional incentive to swim fast. A wide variety of rewards including tactile stimulation, environmental enrichment devices, and food were given for appropriate behaviors on a variable-ratio reinforcement schedule.

For performance in the daily shows, some of the *Tursiops truncatus* were also trained to jump vertically out of the water and touch their rostrum to a flag suspended at a known height over the center of the performance pool. During the early stages of training, the pole was held close to the surface of the water and then gradually elevated to higher levels as the animals reached the flag. After approximately 3 months of training, a flag height was attained in which the dolphins were incapable of reliably jumping. For the shows, the flag was positioned at about 90% of the maximum height reached during the practice sessions. At this height the dolphins would be challenged, yet still achieve their goal fairly consistently.

The dolphins were housed in a 1.2-million-gallon, four-pool complex with water temperatures ranging between 12° and 21° C. Video sequences were recorded in the semicircular main performance pool measuring 38 m long and 15 m wide, with a maximum depth of 8.5 m at the center of the pool. Along the borders of the pool where the dolphins swam, the depth was about 7.8 m. The curved portion of the pool was constructed of plexi-glass panels, 1.7 m wide, separated by 0.2 m wide posts allowing for an essentially unobstructed view of the animals as they swam.

Table 2. Vital statistics of SeaWorld dolphins.

Dolphin ID #	Species	Sex	Age (years)	Length (cm)	Weight (kg)
9026	<i>Tursiops truncatus</i>	M	3.5	205.7	149.2
8926	<i>Tursiops truncatus</i>	F	4	248.9	146.9
8003	<i>Tursiops truncatus</i>	F	17	256.5	187.8
8527	<i>Tursiops truncatus</i>	F	8.5	258.6	212.3
8738	<i>Tursiops truncatus</i>	F	16	269.2	219.1
8128	<i>Tursiops truncatus</i>	F	13	294.6	256.3
8736B	<i>Delphinus delphis</i>	M	15	182.8	104.8
8826	<i>Pseudorca crassidens</i>	F	10	365.8	461.8

2.1.2 Swimming Speed Measurements

Dolphin swimming speeds were recorded on videotape with a Panasonic AG-180 camcorder at a rate of 30 frames per second and analyzed using a Panasonic AG-7300 VCR. The camcorder was positioned in the upper stands, 23 m from the performance pool, allowing for a clear view of the entire area. Dolphin speeds were calculated along two different sections of the pool, either a straight 8.0-m portion along the back stone wall or a curved 5.5-m stretch behind the front plexi-glass wall. The animals were allowed several seconds to accelerate; only video sequences in which the dolphins appeared to maintain a constant speed and horizontal trajectory were used.

Swimming speed was determined by dividing the length of the marked section through which the dolphin swam by the time that it took the dolphin to swim across it. Time was determined from the frame rate. Dolphin swimming-speed measurements taken from the video could be accurately repeated to within a few percent. To assess how the plexi-glass panels and the recording position affected the swimming-speed calculations, video recordings of a cast model of a dolphin dorsal fin were made as it was moved along the normal swimming trajectory of the dolphin. The difference in distance between the actual position where the cast fin crossed the reference marks and that determined from the video recordings was insignificant.

2.1.3 Swimming Speed Inferred From Jump Height

Lang and Daybell (1963) have proposed, for the vertical jumps of dolphins, the following relationship between underwater swimming speed and jump height:

$$\frac{1}{2}mU^2 + \frac{1}{3}DL = mgh, \quad (3)$$

where g is gravity and m , L , U , D , and h are respectively the dolphin's mass, length, underwater swimming speed, underwater drag, and maximum height of its center of mass from the water surface. The correction term $\frac{1}{3}DL$ is included in an attempt to account for the excess of thrust (flukes are still beating in the water) over drag (the kinematic viscosity of air is about 70 times less than seawater) that occurs as the dolphin breaks the water surface. Without the correction term, U is more representative of the speed of the dolphin at water emergence than its swimming speed beneath the surface (Lang, 1966). To estimate the underwater drag (D), the following empirical relationship (Fish, 1993) between thrust power (P_T , watts) and swimming velocity (U , $m\ s^{-1}$) was used:

$$P_T = 28.87U^{2.91}. \quad (4)$$

At constant swimming velocity, the thrust power equals the product of the drag and the velocity; consequently, equation (4) can be rewritten as:

$$D = P_T/U = 28.87 U^{1.91} \quad (5)$$

To calculate maximum swimming speed (U) from maximum center of mass jump height (h) equation (5) was substituted into equation (3) and solved iteratively. Center of mass jump heights were obtained from the following equation:

$$h = H - 0.45L, \quad (6)$$

where H is the maximum flag height that the dolphin could touch with the tip of its rostrum, L is the dolphin length, and $0.45L$ is the estimated distance between the rostrum tip and the center of mass of the dolphin (Fish, unpublished data). Note, the underwater swimming speed calculation is sensitive to the value of the correction factor in equation (3), which is an educated guess, as well as how the jump height is defined.

2.1.4 Strouhal Number

A Sony CCD-TR81 camcorder was used to record swimming sequences of *Tursiops truncatus* and *Pseudorca crassidens* at a rate of 30 frames per second for Strouhal calculations. The camera was positioned about 5 m from the plexi-glass wall of the pool, allowing for a clear view of three panels. Strouhal number calculations required measurements of the animal's speed, tail-beat frequency (f) and peak-to-peak, tail-beat amplitude (A_p). Again, only video sequences in which the animals appeared to be swimming horizontally at a constant speed were used.

Strouhal numbers were calculated from the kinematics obtained from video recordings using a Panasonic AG-7300 VCR. Swimming speed was determined as described previously. Tail-beat frequency was calculated by dividing the frame rate by the number of frames comprising a single complete oscillation of the tail. Tail-beat peak-to-peak amplitude, along with a previously measured reference length marked on the pool wall, were measured directly on the television monitor screen. The

reference length was recorded inside and outside the pool to account for refraction effects. The reference length provided a means for converting lengths measured on the monitor screen to actual distances in meters. When Strouhal number calculations were repeated, swimming speed and tail-beat frequencies showed excellent agreement, but for tail-beat amplitudes, differences of 10 to 20% were not uncommon. This uncertainty resulted from insufficient screen resolution, framing rate, and the proximity of the tail to the water surface.

2.2 FREE-RANGING DOLPHINS—CAPTURE AND RELEASE

Since 1970, subsets of the resident population of bottlenose dolphins (*Tursiops truncatus*) inhabiting the near-shore waters of Sarasota Bay, Florida, have been captured for physiological measurements (Wells, Scott, and Irvine, 1987; Scott, Wells, and Irvine, 1990). Motivation to record the animals upon release derived from past accounts of what appeared to be extraordinarily fast swimming speeds. Table 3 lists morphological characteristics of the released animals (designated by number) typically released 1 to 2 hours after capture.

Table 3. Vital statistics of Sarasota Bay bottlenose dolphins (*Tursiops truncatus*).

Date of Capture	Dolphin ID #	Sex	Age (years)	Length (cm)	Weight (kg)
3 Jun 93	14	M	ND	263.5	209.0
3 Jun 93	94	M	ND	257.5	192.0
3 Feb 94	55	F	8	239.0	179.0
4 Feb 94	66	M	10	243.0	195.0
5 Feb 94	92	M	6	215.0	127.0
8 Feb 94	66	M	10	243.0	191.0
8 Feb 94	33	F	12	250.0	186.0
8 Feb 94	32	M	4	240.0	190.0
6 Jun 94	131	F	6	226.0	141.0
6 Jun 94	24	M	5	228.5	136.0
14 Jun 94	38	M	20	283.0	264.0
14 Jun 94	17	F	33	262.0	208.0

Table 3. Vital statistics of Sarasota Bay bottlenose dolphins (*Tursiops truncatus*). (Continued)

Date of Capture	Dolphin ID #	Sex	Age (years)	Length (cm)	Weight (kg)
17 Jun 94	3	F	5	207.0	112.5
17 Jun 94	60	M	34	ND	ND
17 Jun 94	63	F	40	ND	191
17 Jun 94	138	M	2	201.0	86

Note: ND = Not determined at capture date.

The dolphin's release was recorded with a Sony CCD-TR81 camcorder suspended from an aerostat between 45 to 60 m above the release point. The camcorder rate was 30 frames per second. The aerostat was ellipsoidal in shape, about 6 m long, 3 m wide, and was tethered to a 7.5-m long boat anchored near the release point. When inflated with 1000 m³ of helium gas, the balloon was capable of supporting the video camera, mechanisms for tilt and pan maneuvering, cable, and tether (approximately 10 kg total). A television monitor attached by a coaxial cable to the camcorder enabled adjustment of the camera orientation so that at release time, the dolphin was centered within the field-of-view of the camera. A 2.2-m pole was positioned near the dolphin release point to serve as a reference length. One end of the pole also served as the origin from which all x-y pixel locations were referenced during analysis.

Using a Panasonic AG-7300 video recorder and Video Blaster card (Creative Inc.) on a 486 IBM computer, individual frames of the dolphin release sequence were digitized for analysis. Swimming-speed sequences were analyzed only when the dolphin was clearly identifiable, appeared to be moving at constant speed along a straight path, and where the motion of the balloon was not detectable. The x-y pixel coordinates of one end of the reference pole and the rostrum of the dolphin were digitized in each video frame of interest. This allowed calculation of the pixel distance that the dolphin traveled between frames. The corresponding physical distances swam by the dolphin were achieved through digitizing the ends of the 2.2-m reference pole. Velocities were calculated by converting pixel distance to meters and dividing by the elapsed time between corresponding video frames. When an independent researcher using a different digitizing program reanalyzed the fastest dolphin video sequences, swimming speeds were within 5%.

2.3 FREE-RANGING DOLPHINS—RESPONDING TO AIRPLANE

Aerial photographs of a school of long-beaked, common dolphins (*Delphinus capensis*) were taken offshore of Morro Bay, California, on 23 April 1995. The school was estimated to comprise of about 700 animals, including mothers and calves. Photographs were taken with a high-resolution, 126-mm (5-inch) format Chicago Aerial Industries KA-76 military reconnaissance camera. The camera was mounted vertically above the floor port of a twin-engine Partanavia "Observer" airplane. Dolphin school photographs were taken between the altitudes of 120 to 145 m and at a ground speed of 213 km/hr. The camera had a fixed 152-mm lens. During flights, photographers adjusted the camera f-stop (to 4.0 or 5.6) and shutter-speed (range: 1/1500th to 1/2000th) based on ambient light con-

ditions. The camera also featured forward-motion compensation that eliminates photograph image “blur” resulting from the forward movement of the aircraft (Smith, 1968; Cox 1992).

The camera cycle rate was programmed to expose for approximately 80% film image overlap, (i.e., 80% of the area photographed in one frame was photographed again in the next successive frame and so on). Successive exposed frames over the dolphin school were recorded as a complete “photo-pass.” A photo-pass typically contained 21 to 35 exposed frames of the school. For this report, five photo-passes were completed. To facilitate the simultaneous recording of time and altitude data with each camera exposure (or photo-frame) of the dolphin school, an electronic “Tattletale” analog to digital signal converter was interfaced with a Honeywell radar altimeter, the aerial camera and a laptop computer. Targets of known length were photographed at various altitudes and used to make small corrections to the radar altimeter data (Ghosh, 1988; Gilpatrick, 1996). For a 200-cm target placed at the sea surface and photographed from an altitude of 211 m, the variance in the recorded altitude data translated to an error of ± 0.9 cm (or $\pm 0.45\%$) of the estimated length.

Dolphin swimming speed was determined by calculating the time it took a dolphin to swim a measured straight-line distance. To accomplish this, the film reader would start at the beginning of a photo-pass, identify a dolphin and make a pen-mark on an acetate overlay at the tip of the dolphin’s rostrum, and note the time of the photograph (recorded to 1/100 s on the laptop computer). The reader would then track and mark the location of the dolphin in successive frames of the photo-pass. On the last frame of the photo-pass, the reader would again note the time that the photograph was taken. The distance between the initial and the last photographed locations of the dolphin in the photo-pass was then measured using a video-image analysis system.

The video-image analysis system consisted of a Cohu Inc. CCD video camera linked by an adapter to a Bausch and Lomb dissection microscope having a 2.54-cm to 17.78-cm objective. The acetate transparency containing the pen marks mapping the trajectory of the dolphin was placed on a light table under the microscope and a digital video image was captured on a Data Translation Quick Capture frame grabber board installed in a Macintosh Power PC computer. The image was then displayed on a high-resolution 40.6-cm video monitor. Measurements were made using the image processing software, NIH Image. A computer mouse was used to set the measurement point locations. The software then computed the distance in microns between measurement points in the photograph. This distance was then converted from microns to meters. The true distance traveled by the dolphin was then estimated using the following photogrammetric scale factor:

$$TD = (A_c / F) D, \quad (6)$$

where A_c is the corrected altitude (in meters) from which the photograph was taken, F is the focal length of the camera lens ($F = 0.1524$ m), D is the distance traveled by the dolphin as measured on the acetate (converted to meters), and TD is the estimated “true” distance (in meters) traveled by the dolphin along the sea surface.

To evaluate the variance associated with the measurement techniques applied in the photogrammetric study, swimming speeds were calculated from four replicate independent distance measurements, taken for 30 individual dolphins in the photographs. The precision of the replicate swimming-speed calculations were then compared using the standard deviation which averaged 0.12 m/s (range 0.03 to 0.22 m/s). These values indicated relatively little variability and suggested the measuring technique was very precise.

3. RESULTS

3.1 TRAINED DOLPHINS^{3/4} SWIMMING PERFORMANCE TESTS

3.1.1 Swimming Speed Measurements

Over 12 months, 48 research sessions at SeaWorld of San Diego provided a total number (n) of 927 recordings of *Tursiops truncatus*, *Delphinus delphis*, and *Pseudorca crassidens* that were acceptable for swimming-speed determination. Gross swimming motions were by dorsoventral bending of the body in conjunction with the flukes, which followed a sinusoidal trajectory, as has been reported previously for *Tursiops* (Fish, 1993). The propulsive motion of all three species is characterized as carangiform with lunate-tail (thunniform) swimming (Lighthill, 1969, 1970; Fish et al., 1993), and is typical of some of the fastest marine vertebrates, including scombrid fishes, laminid sharks, and cetaceans (Lighthill, 1969). None of these swim data reflect leap-swim or “porpoising” behavior, which, in general, was seldom observed during the SeaWorld recordings.

The maximum swimming speed for the six *Tursiops truncatus* was 8.2 m/s (n = 633). Three of the remaining five *Tursiops* observed obtained maximum swimming speeds within 8% of 8.2 m/s (see table 4). The maximum swimming speeds of the *Delphinus delphis* (n = 103) and *Pseudorca crassidens* (n = 191) were the same (8.0 m/s). The time interval during which the swimming speeds were determined varied between 0.7 to 2.8 s. Average swim speeds were 6.2 ± 0.7^1 m/s for *Tursiops*, 6.7 ± 0.5 m/s for *Delphinus*, and 6.4 ± 0.5 m/s for *Pseudorca*. When comparing swimming abilities of different-size dolphins, it is often useful to express speed in relation to length (Bainbridge, 1958; Webb 1975). In terms of body length (L), the relative maximum swimming speeds for *Tursiops*, *Delphinus*, and *Pseudorca* were 3.8 L/s, 4.4 L/s, and 2.2 L/s, respectively. The corresponding relative average swimming speeds were 2.4 L/s for *Tursiops*, 3.7 L/s for *Delphinus*, and 1.7 L/s for *Pseudorca*.

Figures 1a (*Tursiops truncatus*), 1b (*Pseudorca crassidens*), and 1c (*Delphinus delphis*) show the distribution of “fast” swimming speeds, expressed as m/s, for each of the three dolphin species. The adjective “fast” is included to denote that for all these data the trainers had tried to motivate the dolphins to swim as swift as possible. Swimming-speed distributions comprise measurements obtained along the back brick wall and behind the front plexi-glass wall, and are indicated separately. Generally, maximum swimming speeds recorded along the back wall were a few per cent higher (5% for *Tursiops*, 8% for *Delphinus*, and 12% for *Pseudorca*; see table 4a) than those recorded behind the front wall, as was, for the most part, average swimming speed (-1% for *Tursiops*, 6% for *Delphinus*, 4% for *Pseudorca*, see table 4a).

¹ The uncertainty listed here and throughout the report is equal to one standard deviation.

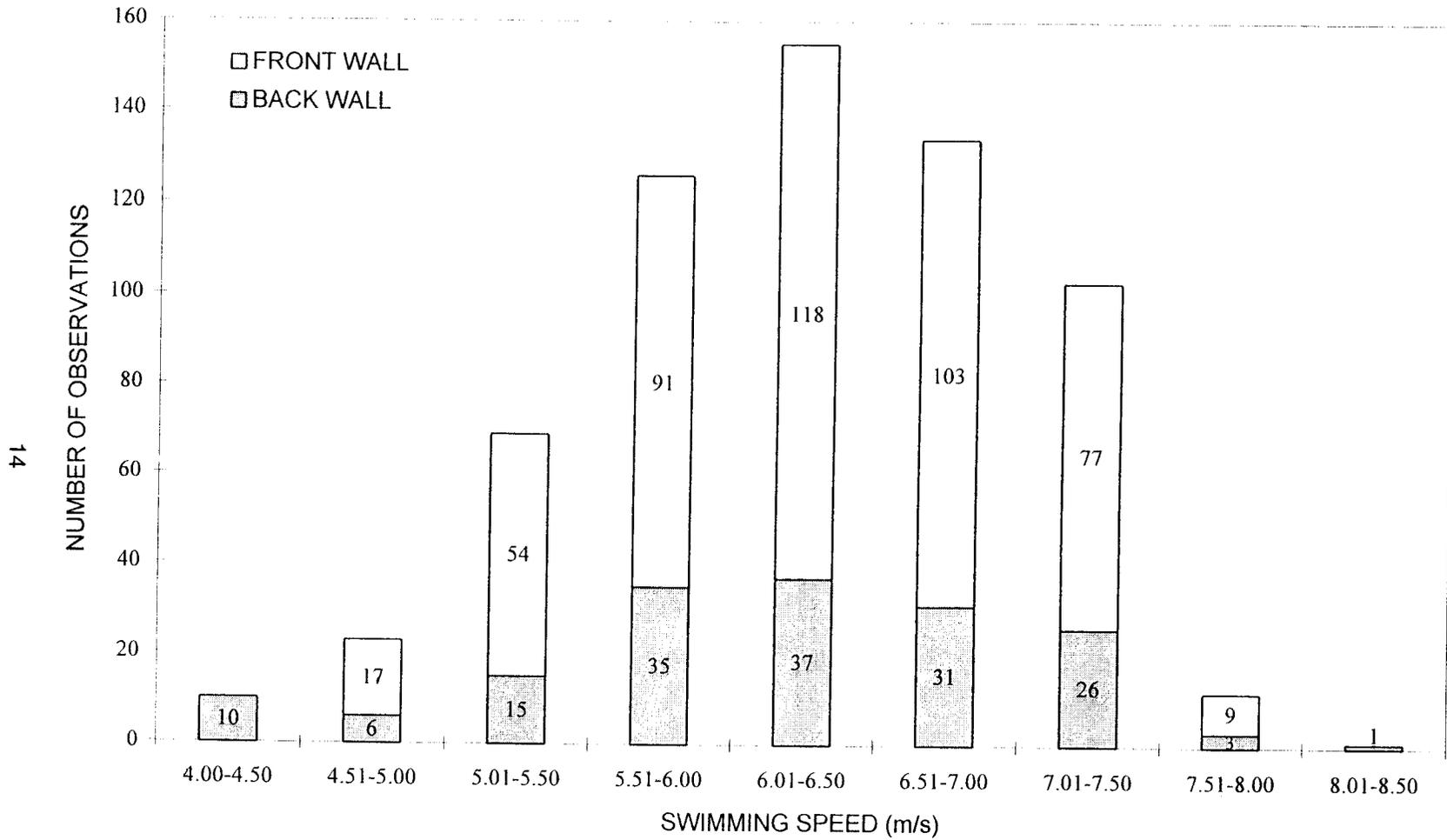


Figure 1a. Distribution of "fast" swimming speeds of six captive bottlenose dolphins (*Tursiops truncatus*) indicating front and back wall measurement locations; total number of observations equals 633.

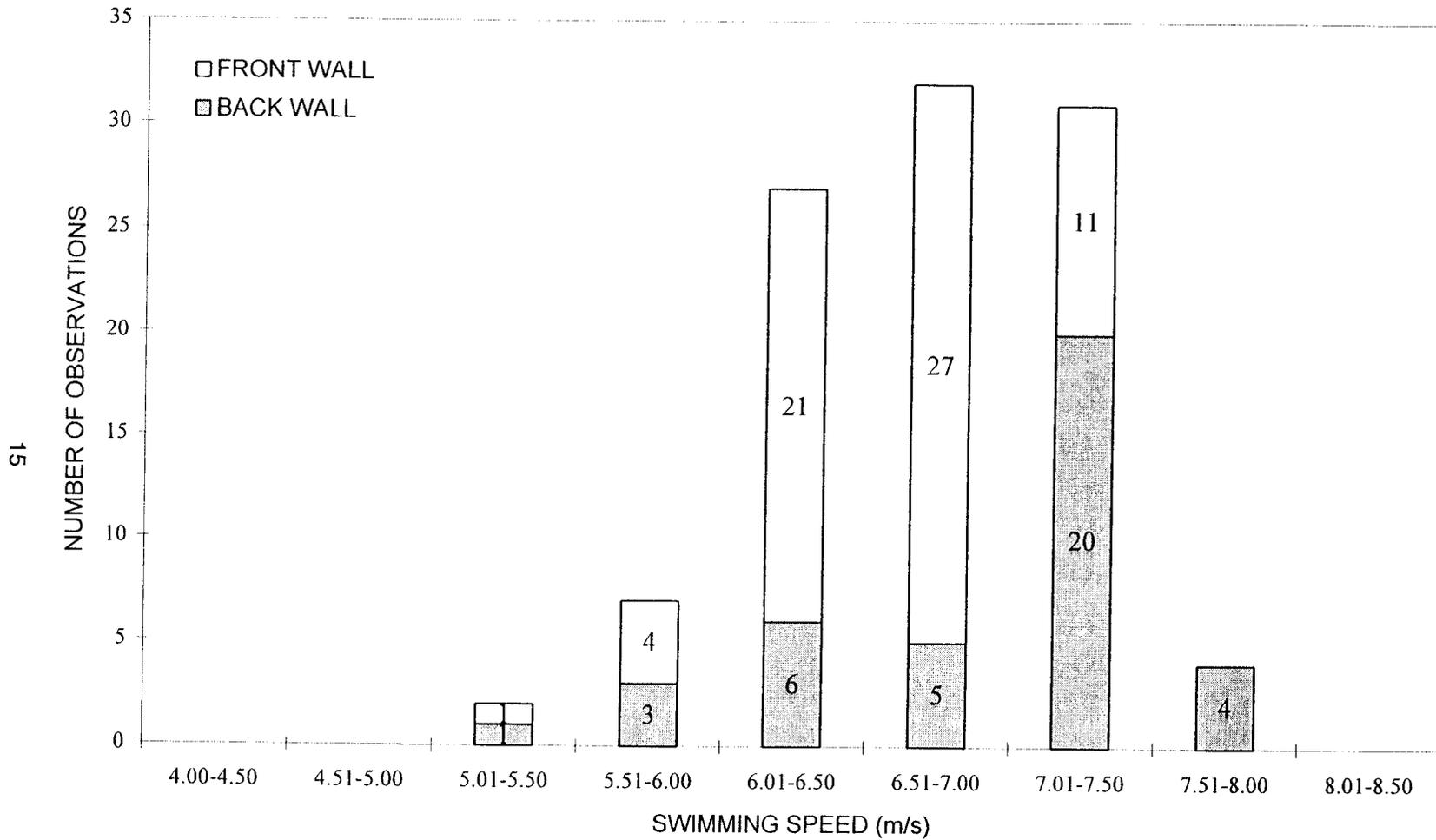


Figure 1b. Distribution of "fast" swimming speeds of a captive, short-beaked, common dolphin (*Delphinus delphis*) indicating front and back wall measurement locations; total number of observations equals 103.

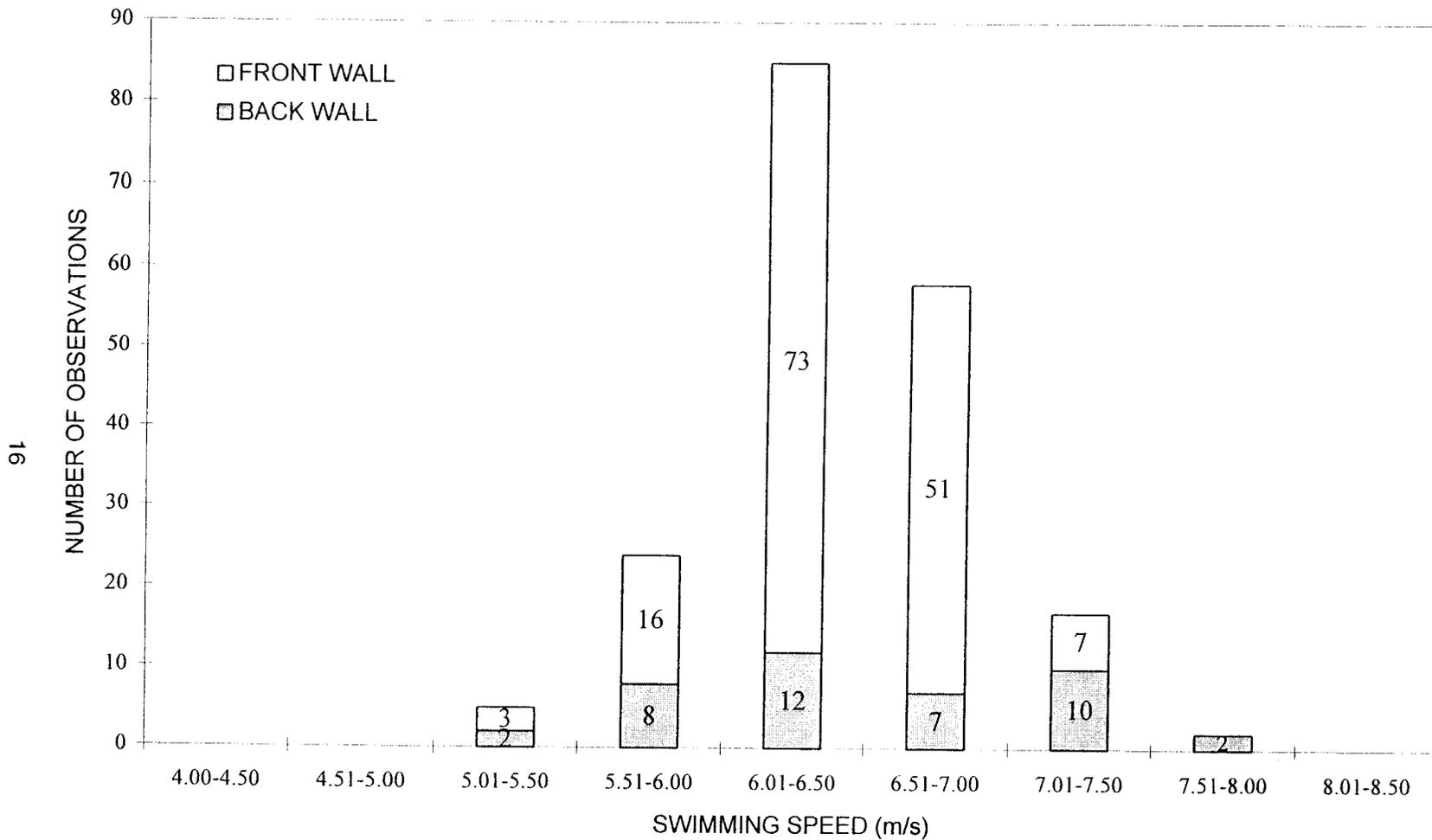


Figure 1c. Distribution of "fast" swimming speeds of a captive false killer whale (*Pseudorca crassidens*) indicating front and back wall measurement locations; total number of observations equals 191.

Table 4a. Summary of SeaWorld dolphin swimming speed data.

Dolphin ID #	Species	All Velocity Data					Back Platform Speed					Front Wall Speed				
		n	Max. Vel.		Avg. Vel.		n	Max. Vel.		Avg. Vel.		n	Max. Vel.		Avg. Vel.	
			m/s	L/s	m/s	L/s		m/s	L/s	m/s	bl/s		m/s	bl/s		
9026	<i>Tursiops truncatus</i>	97	7.74	3.76	6.52	3.17	25	7.74	3.76	6.42	3.12	72	7.67	3.73	6.56	3.19
8926	<i>Tursiops truncatus</i>	68	6.67	2.68	5.45	2.19	15	6.67	2.68	5.28	2.12	53	6.27	2.52	5.49	2.21
8003	<i>Tursiops truncatus</i>	111	6.79	2.65	5.72	2.23	30	6.49	2.53	5.51	2.15	81	6.79	2.65	5.79	2.26
8527	<i>Tursiops truncatus</i>	26	7.49	2.90	6.71	2.59	6	7.49	2.90	6.51	2.52	20	7.4	2.86	6.77	2.62
8738	<i>Tursiops truncatus</i>	142	8.15	3.03	6.55	2.43	35	8.15	3.03	6.50	2.42	107	7.76	2.88	6.57	2.44
8128	<i>Tursiops truncatus</i>	189	7.76	2.63	6.39	2.17	53	7.74	2.63	6.51	2.21	136	7.76	2.63	6.35	2.15
Total	<i>Tursiops truncatus</i>	633	8.15	3.76	6.24	2.41	164	8.15	3.76	6.20	2.38	469	7.76	3.73	6.25	2.42
8736B	<i>Delphinus delphis</i>	103	8.0	4.38	6.67	3.65	39	8.0	4.38	6.91	3.78	64	7.4	4.05	6.52	3.57
8826	<i>Pseudorca crassidens</i>	191	8.0	2.19	6.38	1.74	41	8.0	2.19	6.57	1.8	150	7.08	1.94	6.32	1.73

Note: n denotes the number of observations; L denotes the length of the dolphin.

3.1.2 Swimming Speed Inferred From Jump Height

The maximum flag height that could be reached by each of the three *Tursiops truncatus* trained to jump vertically was 6.7 m (ID# = 8128), 6.4 m (ID# = 8738), and 5.9 m (ID# = 8003) or in terms of body lengths 2.3 L, 2.4L, and 2.3L, respectively. These heights, when substituted into equations (2), (4), and (5), yield estimated underwater swimming speeds of 9.4 m/s (or 3.2 L/s, ID# = 8128), 9.2 m/s (or 3.4 L/s, ID# = 8738), and 8.8 m/s (or 3.4 L/s, ID# = 8003). Swimming speeds derived from maximum jump heights averaged about 20% greater than the maximum horizontal swimming speeds directly measured.

3.1.3 Strouhal Number

Strouhal numbers derived from recordings of swimming *Tursiops truncatus* (n = 51) ranged from 0.15 to 0.36 and averaged 0.25 ± 0.04^1 . Corresponding Strouhal numbers for *Pseudorca crassidens* (n = 23) ranged from 0.21 to 0.37 and averaged 0.29 ± 0.04 . Figures 2a and 2b show, respectively, the distribution of Strouhal numbers for all *Tursiops* and *Pseudorca*. Table 4b lists individual animal Strouhal numbers.

3.2 FREE-RANGING DOLPHINS—CAPTURE AND RELEASE

When assessed from the observation boat, swimming speeds of free-ranging dolphins (*Tursiops truncatus*) often appeared exceptionally fast immediately after release. However, the analysis of 16 recordings of dolphins being released resulted in a range of swimming speeds of only 1.6 to 5.6 m/s (figure 3). The maximum swimming speed of 5.7 m/s was maintained for at least 2.7 s. Some of the slower swimming speeds can be attributed to the initial release procedure during which animals were not released simultaneously. Under these circumstances, the first animal, upon release, often hesitated, sometimes turning towards the release point, before swimming away. When released in pairs, higher swimming speeds were generally observed, yet recorded movements often continued to show a seemingly apathetic exit. The 16 recordings analyzed did not show any indication of porpoising behavior immediately after their release.

3.3 FREE-RANGING DOLPHINS—RESPONDING TO AIRPLANE

Five airplane passes over a school of long-beaked common dolphins (*Delphinus capensis*) resulted in 1044 swimming-speed measurements. The highest swimming speed recorded of an individual *Delphinus* was 6.7 m/s, and was obtained during the third pass. Maximum swimming speeds for each pass in chronological order were 6.6, 5.9, 6.7, 5.6, and 5.8 m/s (see table 5). Average swimming speeds for the school, obtained during consecutive passes, were 4.6 ± 1.0^1 m/s (n = 80), 4.1 ± 0.6 m/s (n = 106), 4.7 ± 0.7 m/s (n = 310), 3.8 ± 0.5 m/s (n = 377), and 4.0 ± 0.5 m/s (n = 171) m/s. Swimming-speed measurements were obtained over 1- to 2-s periods. The five passes were completed in about 8.5 minutes. Although observations of splashes resulting from porpoising were common throughout the frames, all the swimming speeds analyzed were obtained from dolphins swimming just beneath the sea surface. Figure 4 shows the cumulative distribution of swimming speeds for all five passes.

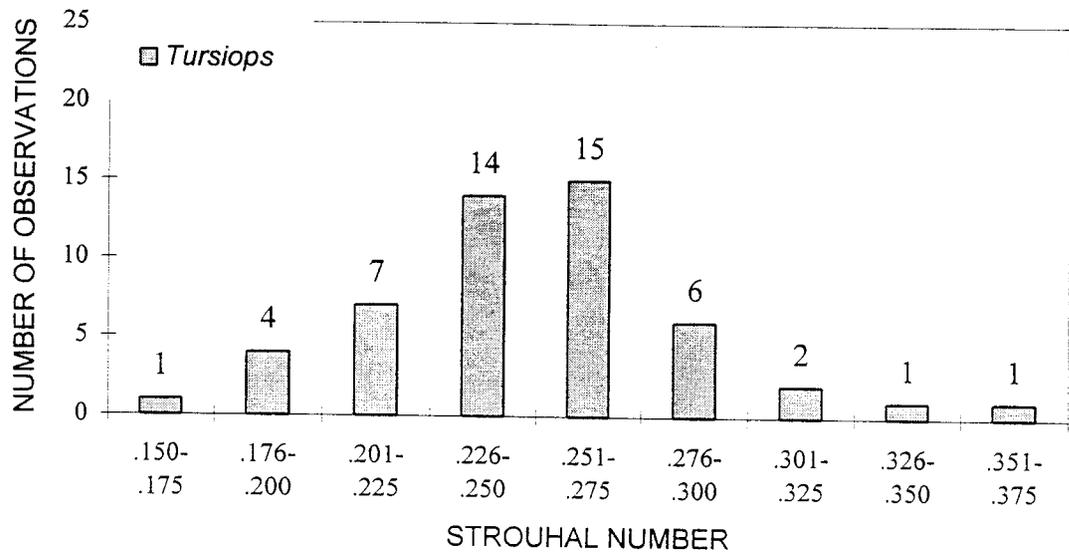


Figure 2a. Distribution of Strouhal numbers of captive bottlenose dolphins (*Tursiops truncatus*); total number of observations equals 51.

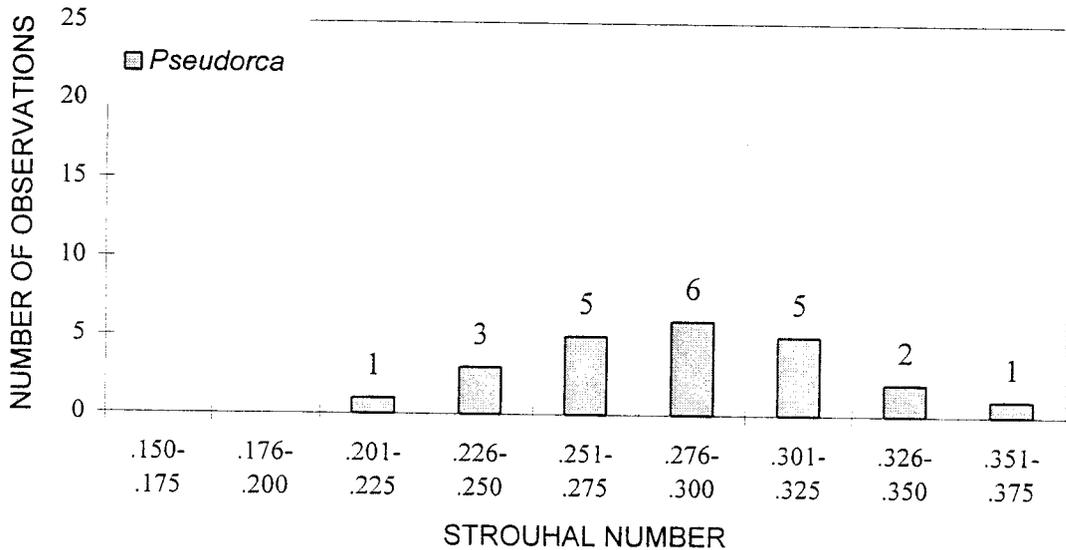


Figure 2b. Distribution of Strouhal numbers of a captive false killer whale (*Pseudorca crassidens*); total number of observations equals 23.

Table 4b. Summary of SeaWorld Strouhal data.

Dolphin ID #	Species	Strouhal Numbers		
		n	Average	Range
9026	<i>Tursiops truncatus</i>	8	0.22 ±.02	0.18 to 0.26
8926	<i>Tursiops truncatus</i>	4	0.22 ±.07	0.15 to 0.31
8003	<i>Tursiops truncatus</i>	11	0.26 ±.02	0.23 to 0.29
8738	<i>Tursiops truncatus</i>	13	0.26 ±.04	0.21 to 0.35
8128	<i>Tursiops truncatus</i>	15	0.26 ±.04	0.18 to 0.36
(Total)	<i>Tursiops truncatus</i>	51	0.25 ±.04	0.15 to 0.35
8826	<i>Pseudorca crassidens</i>	23	0.29 ±.04	0.21 to 0.37

Note: n denotes the number of observations.

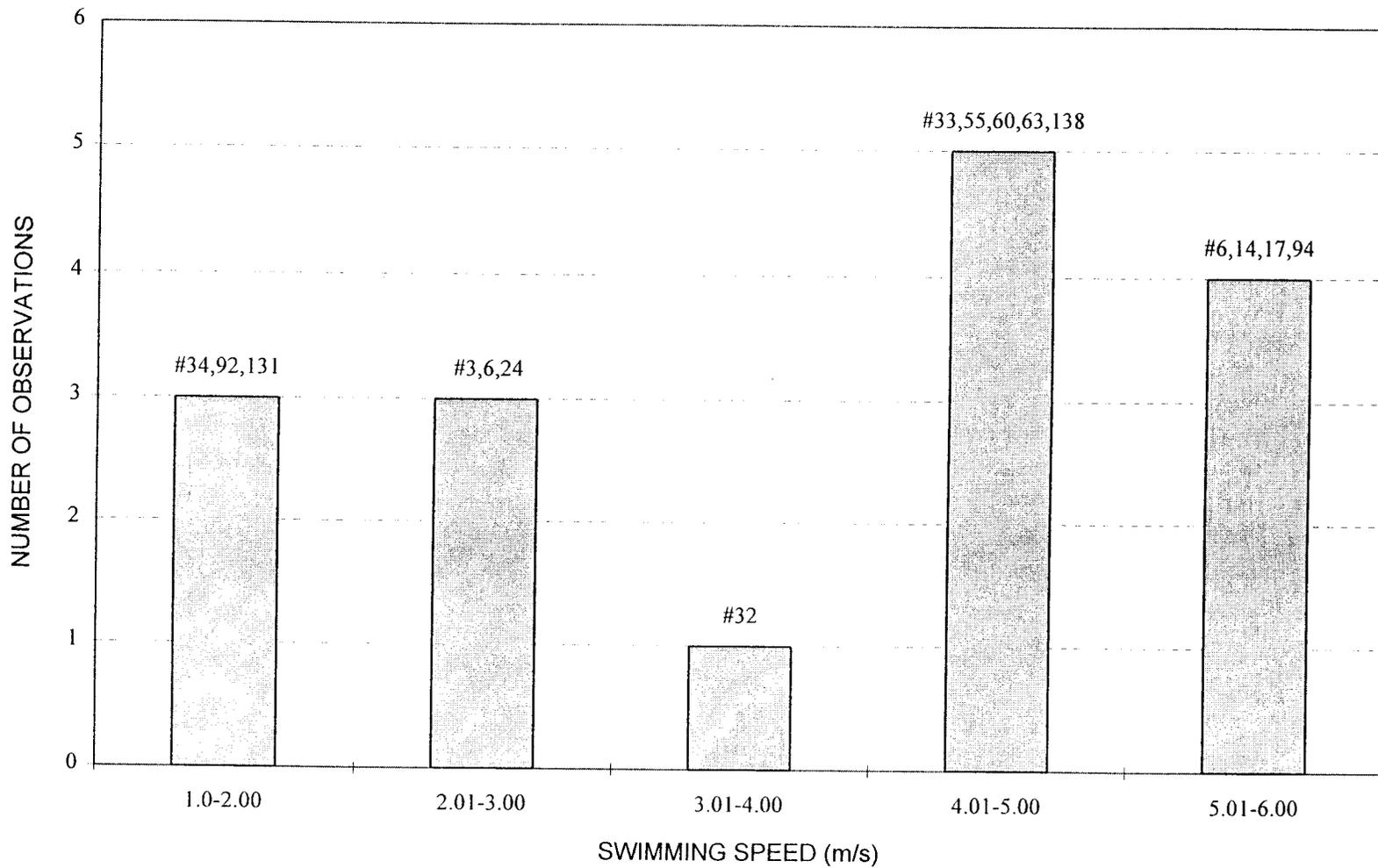


Figure 3. Distribution of swimming speeds of free-ranging bottlenose dolphins (*Tursiops truncatus*) immediately after release, individual dolphins are indicated by ID number (see table 3).

Table 5. Summary of long-beaked, common dolphin (*Delphinus capensis*) photogrammetric speed measurement data.

Pass	n	Average Velocity (m/s)	Maximum Velocity (m/s)	Velocity Range (m/s)	Duration of Pass (s)	Frames Captured	Average Speed Duration (s)	Range of Speed Duration (s)
1	80	4.50 ±0.89	6.60	2.69 to 6.60	18.6	35	1.44	1.0 to 2.1
2	106	4.13 ±0.60	5.89	2.49 to 5.89	15.2	21	1.24	1.0 to 1.7
3	310	4.67 ±0.66	6.70	3.07 to 6.70	18.4	31	1.42	1.0 to 1.7
4	377	3.80 ±0.52	5.56	2.27 to 5.56	14.2	26	1.23	1.0 to 1.7
5	171	4.00 ±0.51	5.78	2.40 to 5.78	18.4	29	1.48	1.0 to 1.7
1 to 5	1044	4.18	6.60	2.27 to 6.60	513.2	142	1.34	1.0 to 2.1

NOTE: n denotes the number of observations.

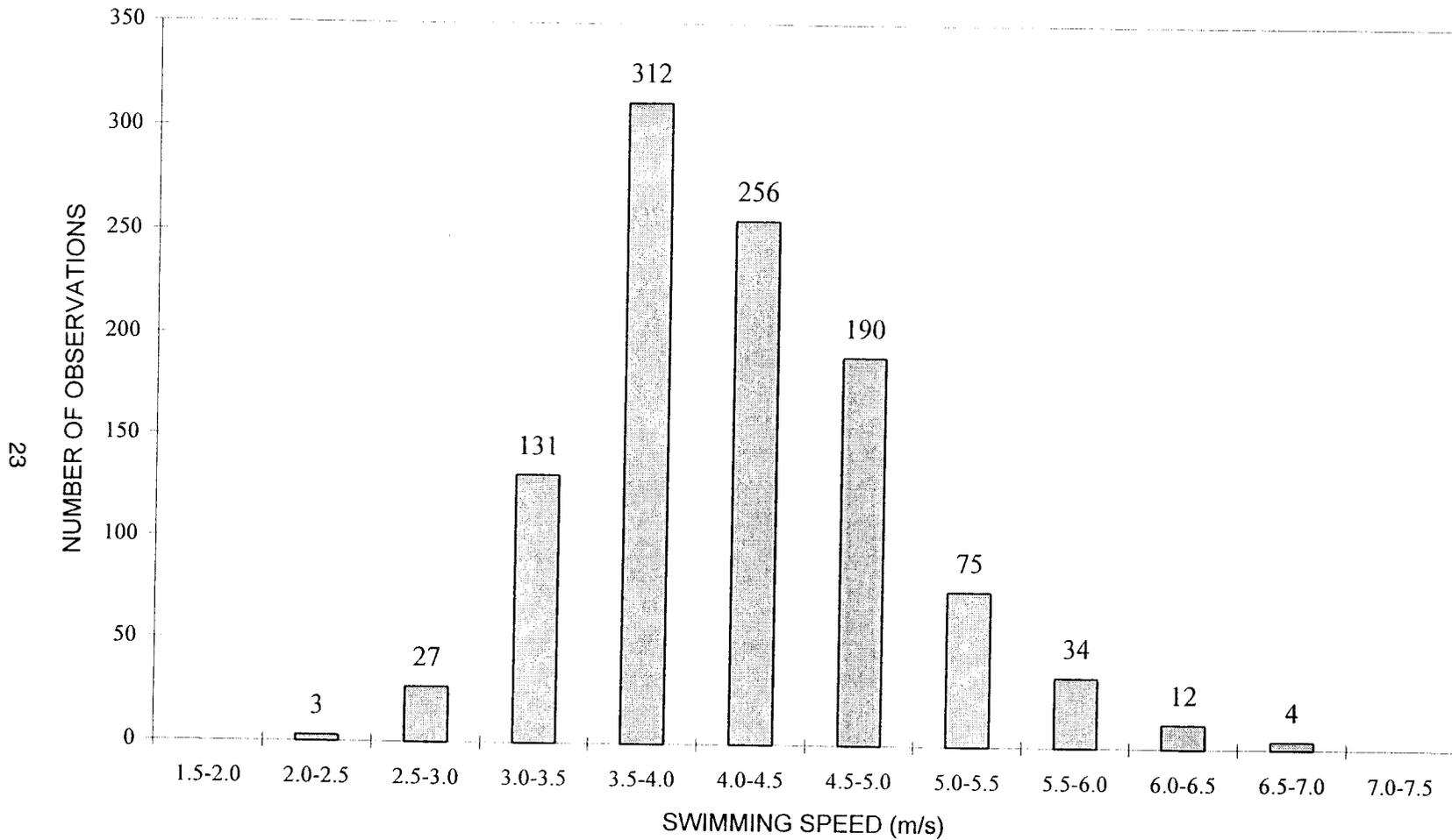


Figure 4. Total distribution of swimming speeds obtained from five airplane passes over a school of long-beaked, common dolphins (*Delphinus capensis*); total number of observations equals 1044.

4. DISCUSSION

4.1 COMPARISON OF “FASTEST” DOLPHIN SWIMMING SPEEDS

The maximum swimming speeds directly recorded in this study for *Tursiops truncatus*, *Delphinus delphis*, and *Pseudorca crassidens* can be compared with values found throughout the scientific literature. In most cases, maximum swimming-speed comparisons for trained dolphins compare favorably. The 8.0-m/s maximum swimming speed reported here for *Pseudorca crassidens* agree reasonably well with the 7.5-m/s maximum observed by Fish (submitted) for captive *Pseudorca*, also swimming in a large pool. Ridgeway and Johnston (1966) have observed boat-following speeds of up to 7.8 m/s for trained *Tursiops*, which agree with the present maximum swimming-speed observation of 8.2 m/s. A similar top swimming speed of 8.3 m/s was observed by Lang and Norris (1966) for *Tursiops* (originally listed as *Tursiops gilli*), responding to acoustic commands in an enclosed lagoon. Lang and Norris (1966) note that this level of swimming speed compares closely with predicted turbulent values for this animal.

Wursig and Wursig (1979) have obtained theodolite measurements of free-ranging *Tursiops truncatus* while avoiding a pod of killer whales estimated to be about ½ km away, and report speeds of at least 8.3 m/s. Although this particular value of maximum swimming speed agrees with those reported in this study for trained *Tursiops*, in general, most “fast” swimming speeds reported for free-ranging dolphins are significantly higher. For example, swimming speeds reported for free-ranging *Tursiops* have been as high as 10.3 m/s (Lockyer, 1978), 12.5 m/s (Pershin, 1988), and 15 m/s (Lockyer and Morris, 1987). Maximum swimming speeds for free-ranging *Delphinus delphis* include 9.3 m/s (Kellogg, 1940; Johannesse and Harder, 1960); 10.3 m/s (Gray, 1936); 13.2 m/s (Pershin, 1969); and 13.9 m/s (Tomilin, 1957), all of which are considerably higher than the 8.0-m/s SeaWorld data maximum presented here. Unfortunately, many of the extraordinary swimming speeds reported for wild dolphins involve crude measurement techniques, few observations, and no estimation of uncertainty.

Using equation (3), underwater swimming speeds estimated from the maximum vertical jump heights of three trained *Tursiops truncatus* averaged 9.1 ± 0.3 m/s. For comparison's sake, the corresponding emergence speed at jump exit is calculated by neglecting the correction term. Equation (3) then reduces to the ballistic equation with an exit angle of 90° and yields an average exit speed of 10.0 ± 0.3 m/s. Using the same ballistic equation (with an exit angle typically of 45°), exit speeds have been calculated from the leap lengths of free-ranging dolphins porpoising at sea. Although the comparative jump heights of the free-ranging dolphins were for different species, nevertheless, computed exit speeds showed reasonable agreement with values for captive *Tursiops*. Au et al. (1988) have estimated an average leap exit ($n = 23$) of 8.2 m/s from an aerial photograph of a school of spotted dolphins (*Stenella attenuata*). The maximum exit speed they calculated was 9.4 m/s (courtesy M. D. Scott). It was estimated that the school had been swimming rapidly for less than 2 minutes before the photograph was taken². Similar use of the ballistic equation has been applied to

² The maximum swimming speed reported in the literature (Lang and Pryor, 1966) for *Stenella* is 11 m/s. In this case, the dolphin was trained to follow a lure towed by a boat. Maximum swimming speed was obtained 2.0 seconds after starting.

films of J. Y. Cousteau (Pershin, 1988). The highest exit velocity calculated ($n = 15$) for a group of *Delphinus delphis* was 9.1 m/s.

4.2 COMPARISON OF STROUHAL NUMBER AND SWIMMING KINEMATICS

4.2.1 Strouhal Number

Additional Strouhal number data for captive *Tursiops truncatus* were derived from the kinematic swim data ($n = 56$) of Fish (1993). Fish (1993) obtained measurements of swimming speed, tail-beat frequency, and tail-beat amplitude from films of five trained *Tursiops* swimming throughout a range of speeds at SeaWorld in Orlando, Florida, and at the National Aquarium in Baltimore. As for the present data, only video sequences in which the animals appeared to be swimming along a horizontal path at a steady rate were used.

Swimming speeds varied in response to cues from trainers, ranging from about 1 to 6 m/s (Fish, 1993). The swimming speeds in this study for *Tursiops truncatus* were usually higher, about 4 to 8 m/s, since the trainers sought to elicit maximum effort. Also included for comparison's sake are the data sets of Kayan and Pyatetskiy (1977; figures 2 and 3; steady swimming) for captive *Tursiops*; and of Lang and Daybell (1963; figure 21; no drag collar) as estimated by Trianthefyllou et al. (1993) for a captive *Lagenorhynchus obliquidens*.

The different dolphin Strouhal number data sets plotted as a function of Reynolds number (figure 5a), body length (figure 5b), and swimming speed—expressed either as meters per second (figure 5c) or body lengths per second (figure 5d), generally exhibit good agreement where the dependent variables overlap. Average Strouhal numbers for the comparison *Tursiops truncatus* data sets were 0.25 ± 0.02 ($n = 17$; Kayan and Pyatetskiy, 1977) and 0.27 ± 0.05 ($n = 56$; Fish, 1993), showing remarkable agreement with the 0.25 ± 0.4 ($n = 51$) value reported here. The average Strouhal number for *Lagenorhynchus obliquidens* (Trianthefyllou et al., 1993) and *Pseudorca crassidens* were higher, 0.30 ($n = 1$) and 0.29 ± 0.04 ($n = 23$), respectively.

Although the average Strouhal number for each of the dolphin data sets was within the 0.25 to 0.35 range predicted by Trianthefyllou et al. (1993), this range included only 56% of all the data compared to 76% of the data residing between Strouhal numbers 0.2 and 0.3, and 89% of the data residing between Strouhal numbers 0.2 and 0.35. A Strouhal number range of 0.2 to 0.3 better characterized *Tursiops truncatus*, as it contained 78% of the data compared to the 51% residing between 0.25 to 0.35. In contrast, for *Pseudorca crassidens*, a Strouhal number range of 0.25 to 0.35 contained 78% of the data whereas only 70% were between 0.20 to 0.30.

The present dolphin Strouhal number data set and that of Fish (1993) appear to be largely independent of Reynolds number (figure 5a) over the measured range of about 2.5×10^6 to 2.5×10^7 . Pershin (1973), however, has reported that the Strouhal number variance increases with increasing Reynolds number. Pershin's (1973) Reynolds number range extends from about 10^3 , where Strouhal numbers varied between 0.3 to 0.4, to 10^7 where Strouhal numbers varied between 0.15 to 0.4. Strouhal number data were obtained from insects, birds, fish, and dolphins (Pershin, 1973). Nonetheless, over the limited range where Reynolds numbers overlap, Pershin's (1973) and present Strouhal numbers (figure 5a) are in reasonable agreement.

The data set of Kayan and Pyatetskiy (1977) for *Tursiops truncatus* displays another feature, tending to peak around a Reynolds number of 5×10^6 at a Strouhal number of about 0.27 (figure 5a). Semonov (1974) reported a similar trend for *Delphinus delphis*, but with the peak occurring around a Reynolds number of 1.75×10^6 at a Strouhal number around 0.35. No such conspicuous peaks have been found for similar measurements of fish (Pershin, 1988). Unfortunately, the scatter in the Fish (1993) and present data sets (figures 4a, 4b) precludes resolving these Strouhal number peaks. It is yet to be determined whether this scatter results from measurement uncertainties, particularly of tail-beat amplitude, or from the natural variation of the animals swimming motion (Rosen, 1959). Kayan and Pyatetskiy (1977) have also reported for captive *Tursiops truncatus* a dependence of Strouhal number on acceleration (these data not included in figure 5a). A reanalysis of the present video data throughout the measurement range of Kayan and Pyatetskiy (1977) reaffirmed that acceleration was not an issue.

Taken together, the Strouhal number data of Fish (1993) and that presented here showed little dependence on body length (figure 5b) or swimming speed when expressed in m/s ($U \approx 1-7.5$ m/s; figure 5c). However, when swimming speed was expressed in body lengths per second (L/s) all the Strouhal numbers for speeds greater than about 2.50 L/s, were conspicuously lower than the average value of 0.27 (figure 5d). These particular Strouhal number data (>2.5 L/s) were all associated with observations of the smallest dolphin (ID# = 9026), and their relatively low values can be understood in terms of the underlying kinematic relationships to be subsequently discussed.

The only reference to Strouhal numbers that we have found for free-ranging dolphins is by Pershin (1988), who reports a value of 0.37 for what he refers to as a common dolphin. Unlike the captive dolphins, this dolphin was not swimming near the surface. Pershin makes no reference to swimming speed, length of the dolphin, or how the recordings were obtained. A Strouhal number of 0.37 is conspicuously higher than the average values reported here for captive dolphins. Yet even if this value is representative of this free-ranging species, it cannot be known whether this disparity reflects differences between species, captive and free-ranging animals, or swimming at or several body widths from the surface of the water.

4.2.2 Swimming Kinematics

Individual kinematic components comprising the Strouhal number exhibit different dependencies on swimming speed. Tail-beat peak-to-peak amplitude (A_{p-p}) expressed in body lengths (L) for all dolphin data, remained approximately constant throughout the range of tail-beat frequencies (0.75 to 3 Hz; figure 6a) and relative swimming speeds (0.5 to 3.25 L/s; figure 6b). Again, where the dependent variable overlapped, good agreement is generally found between different dolphin data sets. Average tail-beat peak-to-peak amplitude for *Tursiops truncatus* is $19\% \pm 1\%$ of its body length for the data of Kayan and Pyatetskiy (1977; $n = 30$); $20\% \pm 3\%$ for the data of Fish (1993; $n = 56$); and $22\% \pm 2\%$ for the present data ($n = 51$). For *Lagenorhynchus obliquidens* (Lang and Daybill; figure 21; $n = 1$) and *Pseudorca crassidens* (present data, $n = 23$), similar calculations of A_{p-p}/L resulted in 25% and $23\% \pm 2\%$, respectively. These values of A_{p-p}/L are at or near the 20% reported for many species of fish swimming in carangiform modes (Bainbridge, 1958; Webb, 1975). When tail-beat amplitude and swimming speed are presented respectively in meters and meters per second (figure 6c), as opposed to body lengths and body lengths per second (figure 6b), the *Tursiops* (average $L = 2.55$ m) and *Pseudorca* (average $L = 3.66$ m) data sets exhibit conspicuously poorer agreement.

Tail-beat frequency plotted as a function of swimming speed, whether expressed in meters per second (figure 7a) or body lengths per second (figure 7b), show good agreement between the available data sets for captive dolphins. When swimming speed is expressed in meters per second (figure 7a), tail-beat frequency increases approximately linearly with swimming speed, with a squared correlation coefficient (R^2) of 0.79 according to the equation:

$$f = 0.54 + 0.34U[\text{m/s}] \quad (R^2 = 0.79; \text{Fish, 1993 + present}). \quad (7)$$

Linear fits to the individual data sets are

$$f = 0.47 + 0.37U[\text{m/s}] \quad (R^2 = 0.72; \text{Fish, 1993}), \text{ and} \quad (8)$$

$$f = 0.45 + 0.35U[\text{m/s}] \quad (R^2 = 0.67, \text{ present}). \quad (9)$$

When swimming speed is expressed in body lengths per second (figure 7b), the present tail-beat frequency data for *Tursiops truncatus* increase almost linearly with relative swimming speed until about 2.5 L/s, and thereafter remains approximately constant between 2.5 and 3.0 Hz. Where comparisons can be made, which is between tail-beat frequencies of about 1 to 2.5 Hz, good agreement is found between the various dolphin data sets. The captive *Tursiops* data of Kayan and Pyatetskiy (1977) are represented as a line (figure 7b) based on their equation:

$$f = 0.15 + 1.1 U[\text{L/s}]. \quad (10)$$

When tail-beat frequency is plotted as a function of swimming speed expressed as meters per second, the collapse of the *Tursiops* and *Pseudorca crassidens* data sets are noticeably poorer (figure 7c).

Curiously, the present tail-beat frequency data remain nearly constant for swimming speeds greater than about 2.5 L s^{-1} . The data in this range are comprised almost entirely of swimming-speed measurements obtained from the smallest dolphin (ID# = 9026). Further measurements at high, relative swimming speeds are necessary to corroborate this feature. Nevertheless, it is this independence of tail-beat frequency on relative swimming speeds greater than around 2.5 L/s (figure 7b) that is responsible for conspicuous reduction of the corresponding Strouhal numbers displayed in figure 5d.

4.3 MOTIVATION: FREE-RANGING AND CAPTIVE DOLPHINS

Surprisingly, where one might expect motivation to have been strongest, swimming speeds recorded of the release of free-ranging *Tursiops truncatus* were significantly lower than speeds measured for trained *Tursiops* swimming in pools. This may have occurred because many of the released dolphins had been captured several times previously and were accustomed to the procedure. A lack of strong desire to flee from the release point may also reflect the extraordinary measures taken by the researchers to minimize stress to the animal. In light of the many subjective impressions of dolphin swimming speeds, it is noteworthy that swimming-speed estimates made visually by observers from the boat were often significantly higher than those calculated from the recordings. Lang (1975) has also reported large discrepancies between swimming speeds based on qualitative observations and quantitative measurements. The shallowness of the water at the release point (about 1.3 m) may have also affected swim speed.

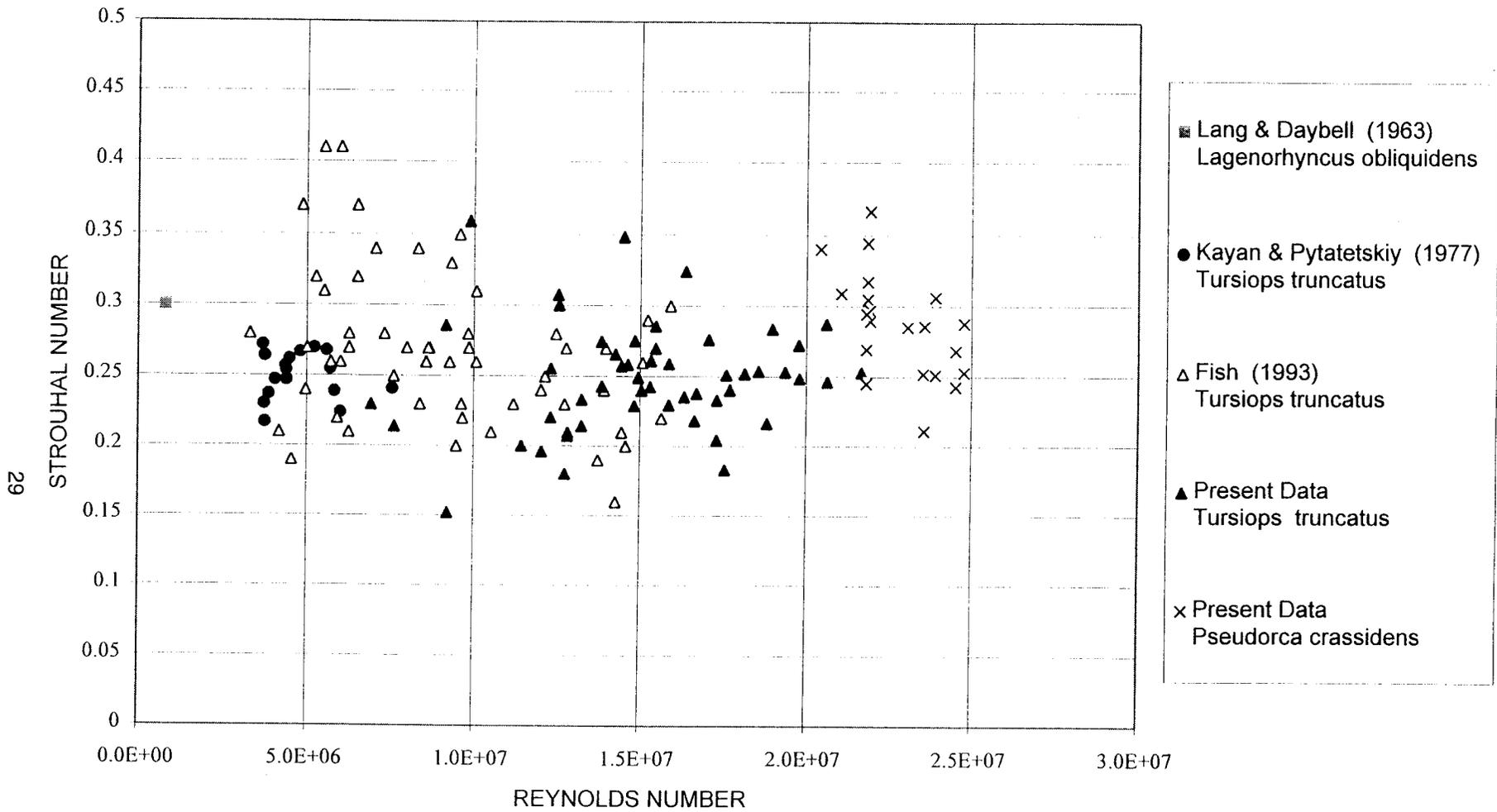


Figure 5a. Dolphin Strouhal number plotted as a function of Reynolds number.

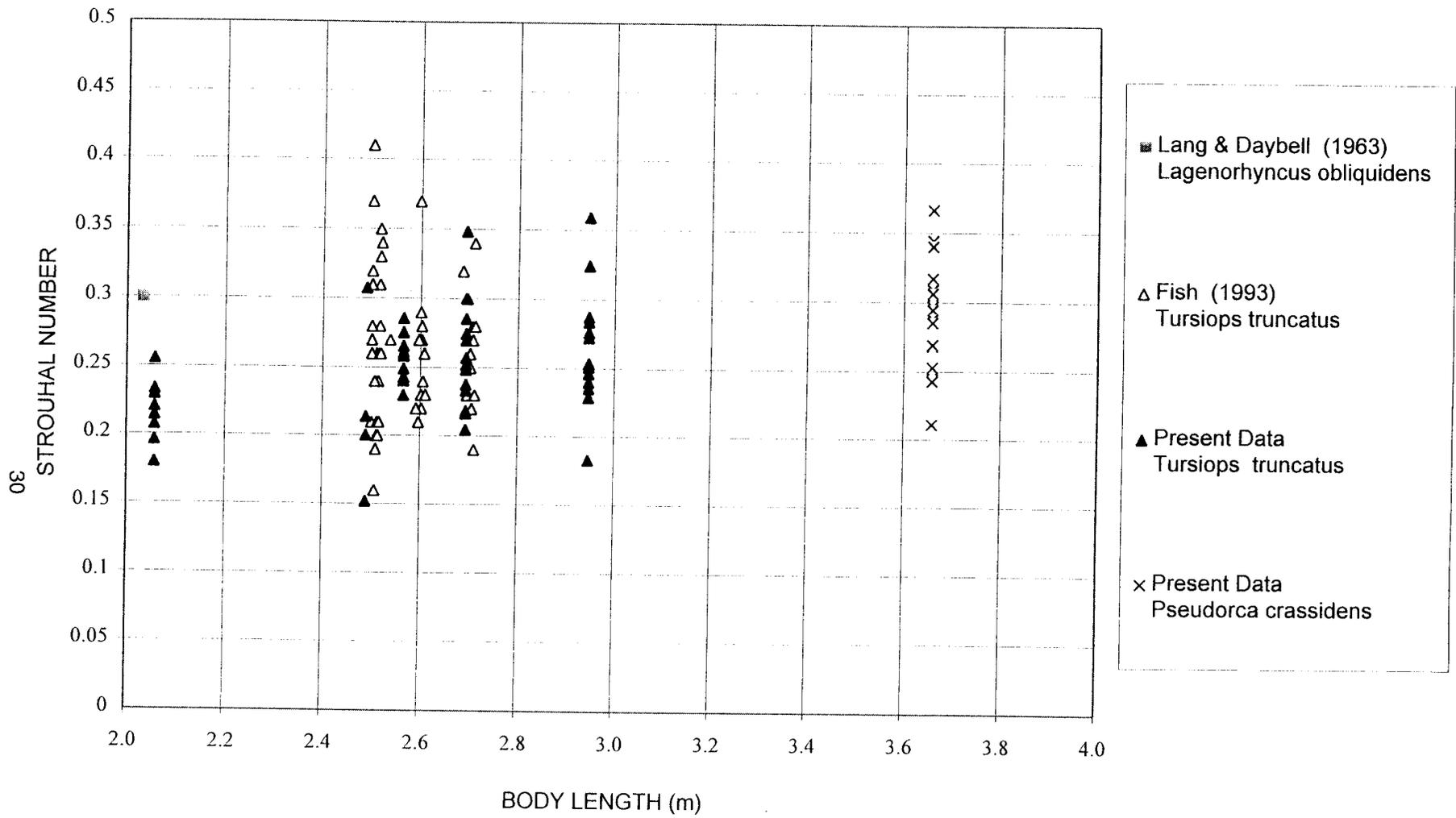


Figure 5b. Dolphin Strouhal number plotted as a function of body length, expressed in meters.

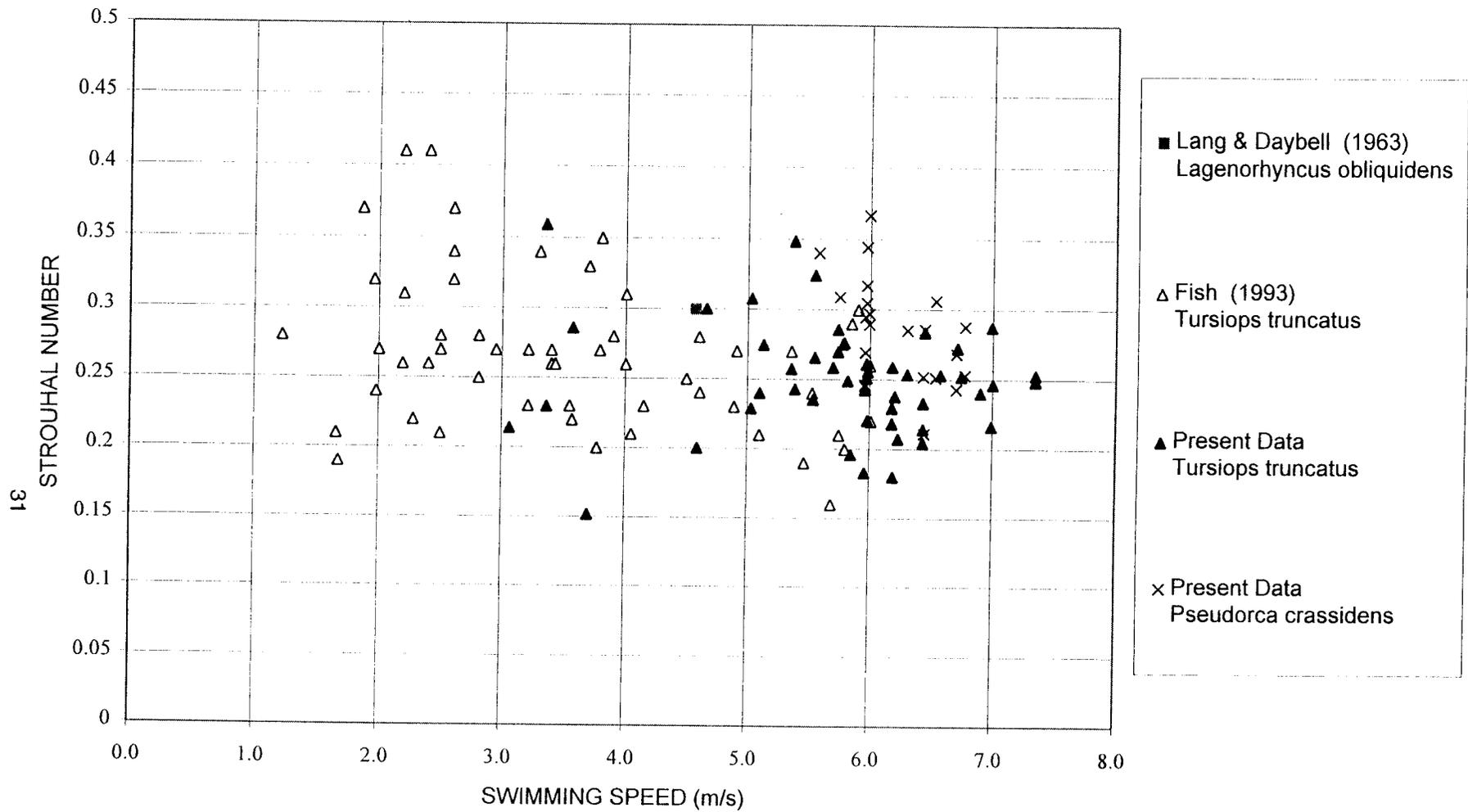


Figure 5c. Dolphin Strouhal number plotted as a function of swimming speed, expressed in meters per second.

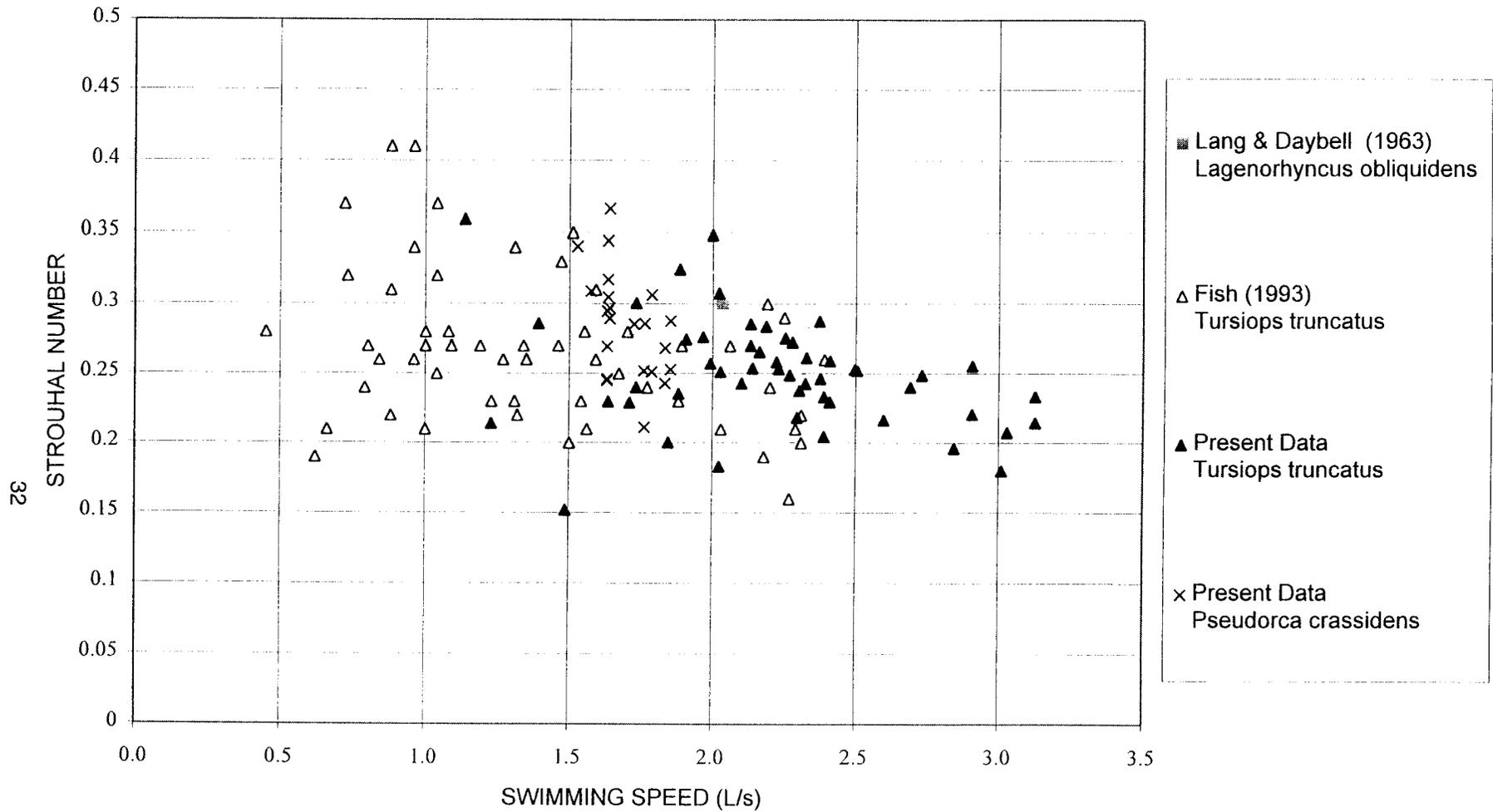


Figure 5d. Dolphin Strouhal number plotted as a function of swimming speed, expressed in body lengths per second (L/s).

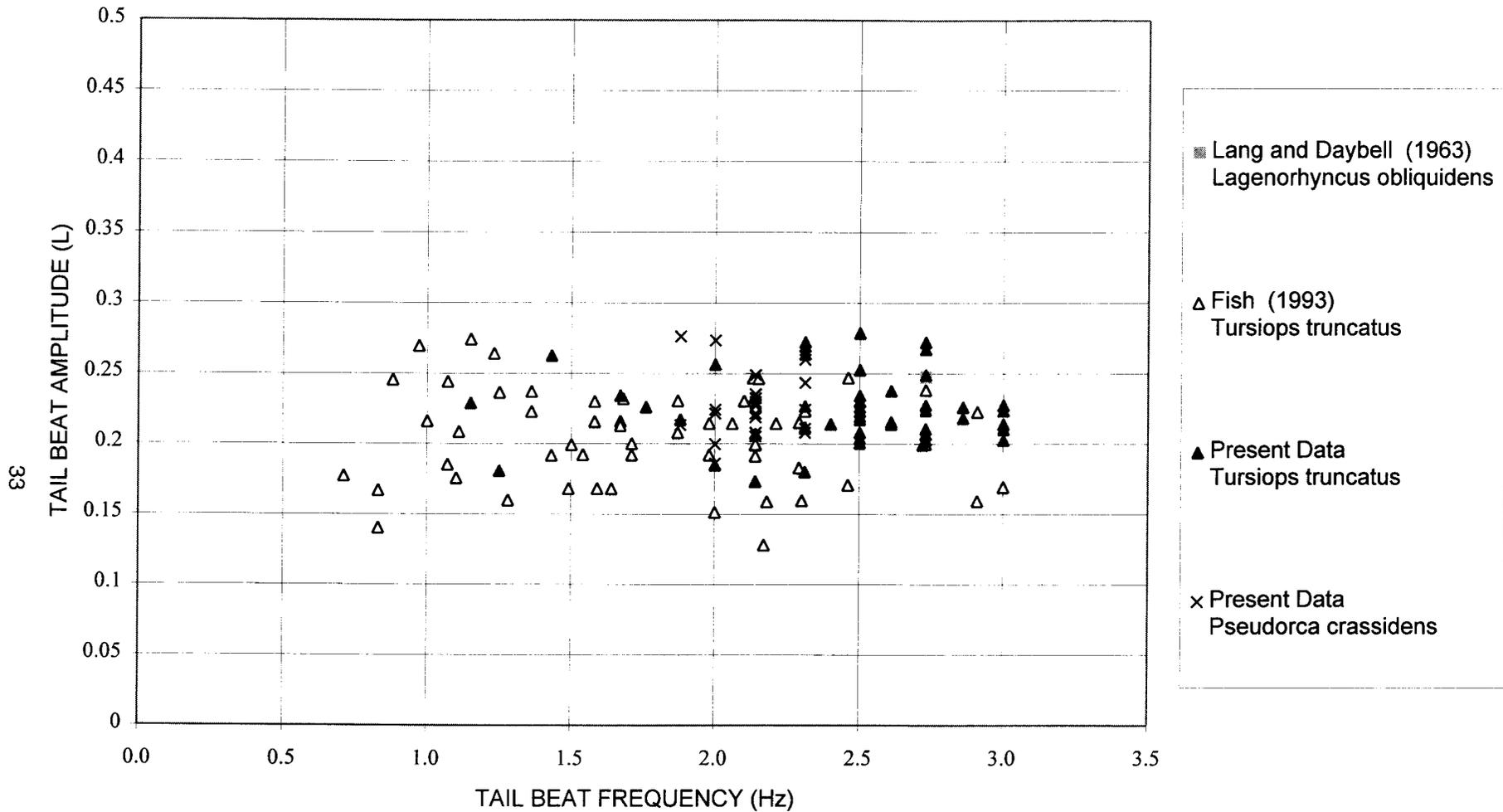


Figure 6a. Dolphin tail-beat peak-to-peak amplitude, expressed in body lengths (L), plotted as a function of tail-beat frequency.

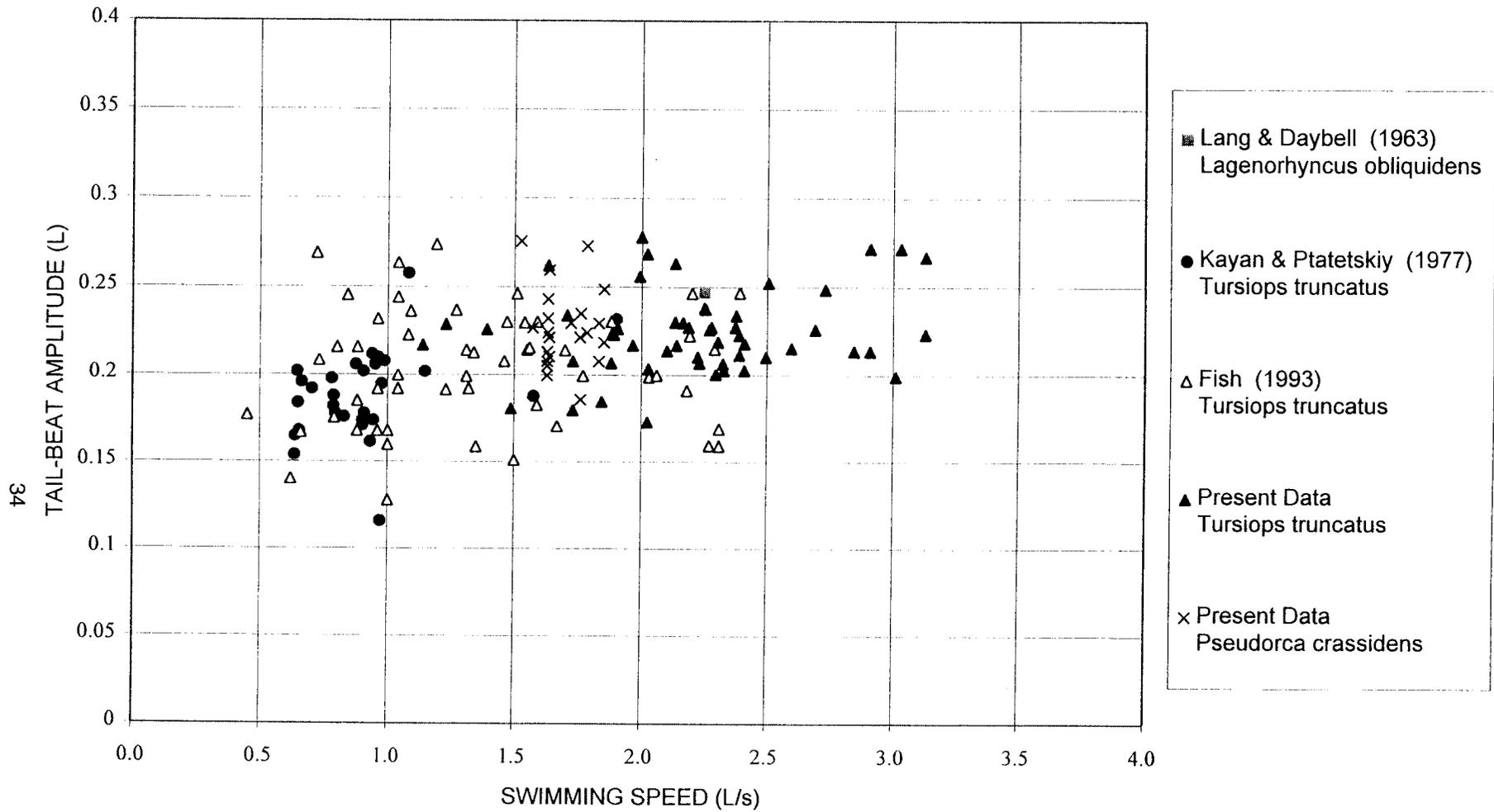


Figure 6b. Dolphin tail-beat peak-to-peak amplitude, expressed in body lengths (L), plotted as a function of swimming speed, expressed in body lengths per second (L/s).

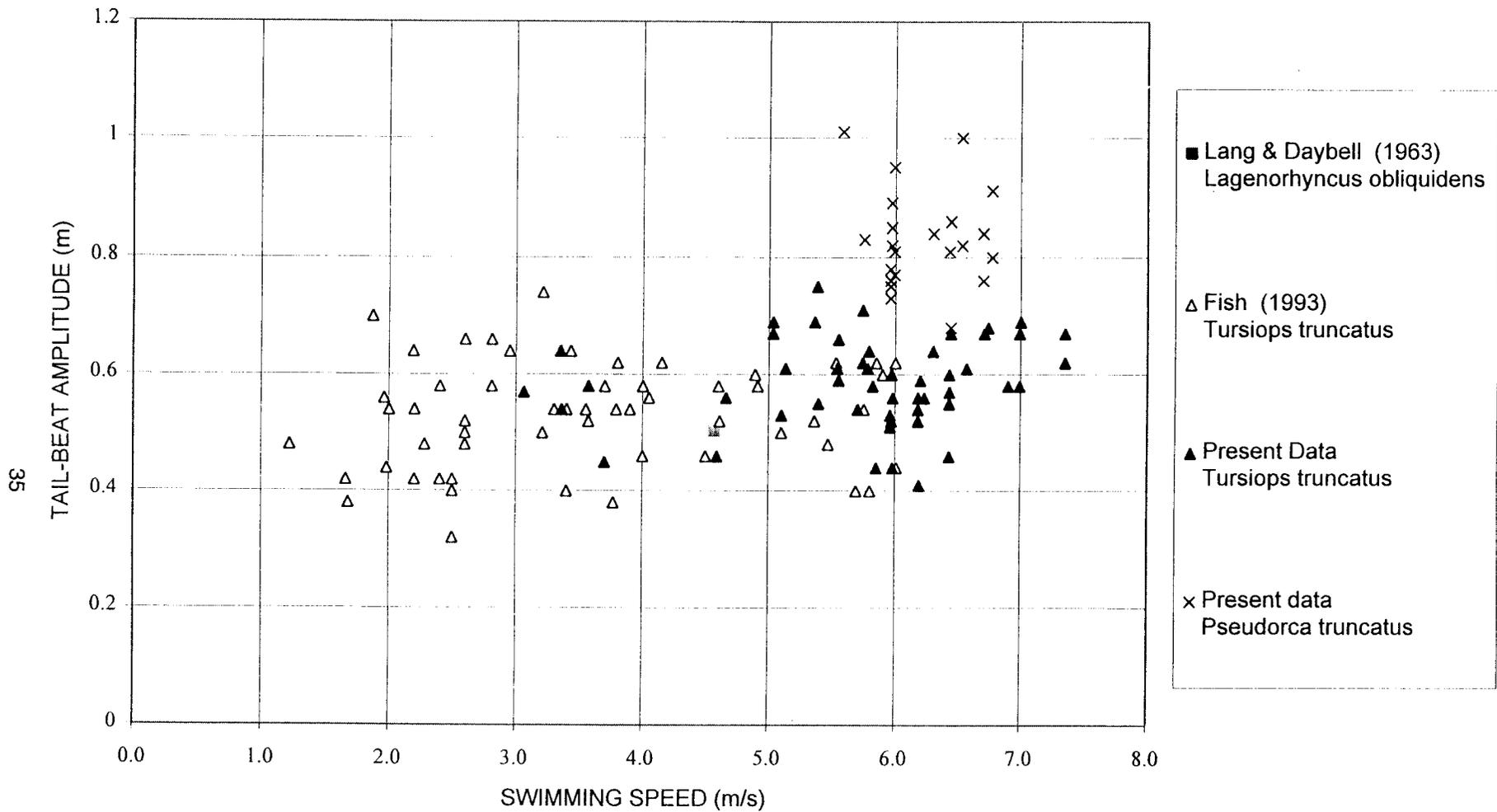


Figure 6c. Dolphin tail-beat peak-to-peak amplitude, expressed in meters, plotted as a function of swimming speed, expressed in meters per second.

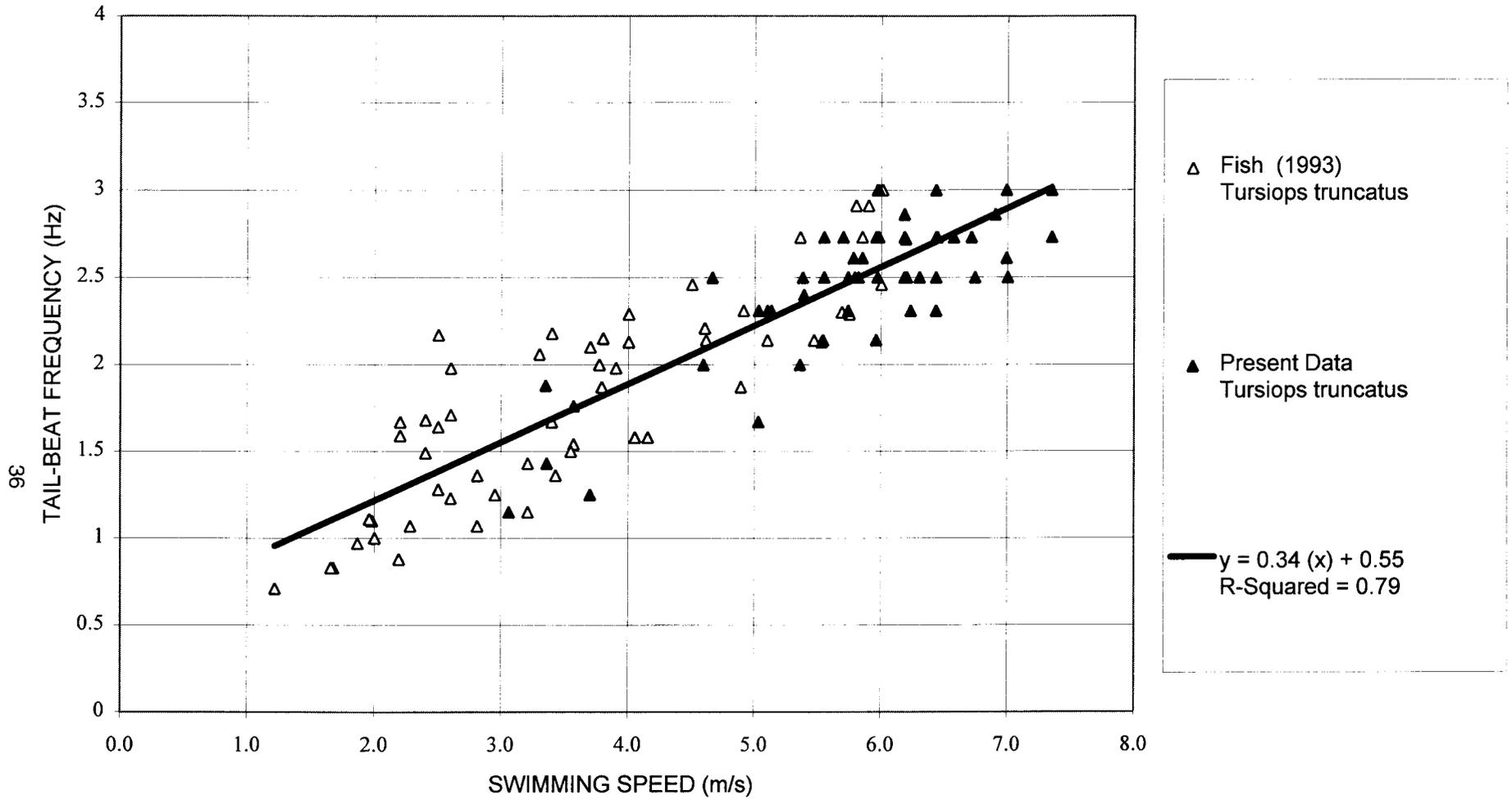


Figure 7a. Tail-beat frequency of *Tursiops truncatus* plotted as a function of swimming speed, expressed in meters per second.

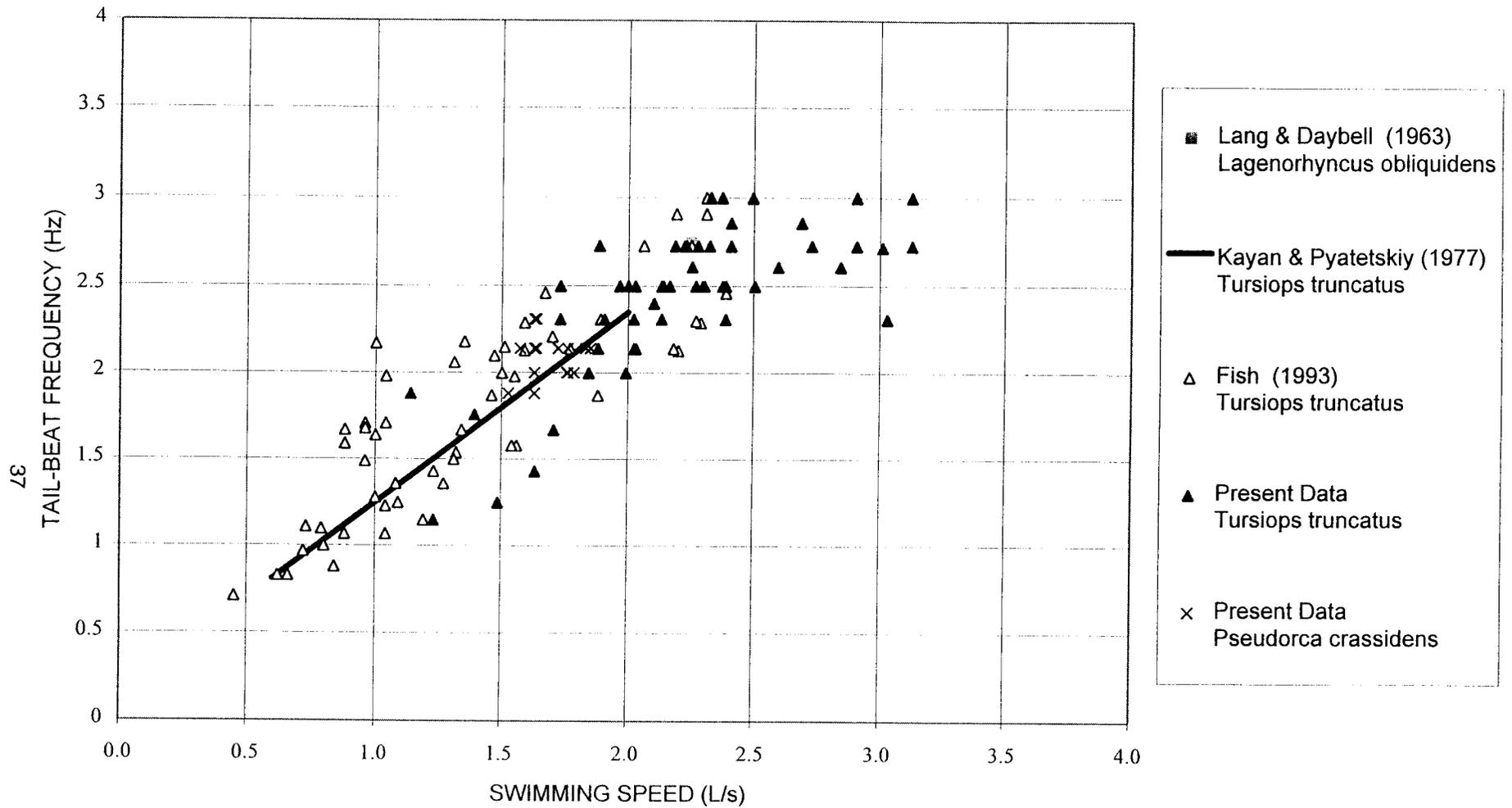


Figure 7b. Dolphin tail-beat frequency plotted as a function of swimming speed, expressed in body lengths per second (L/s).

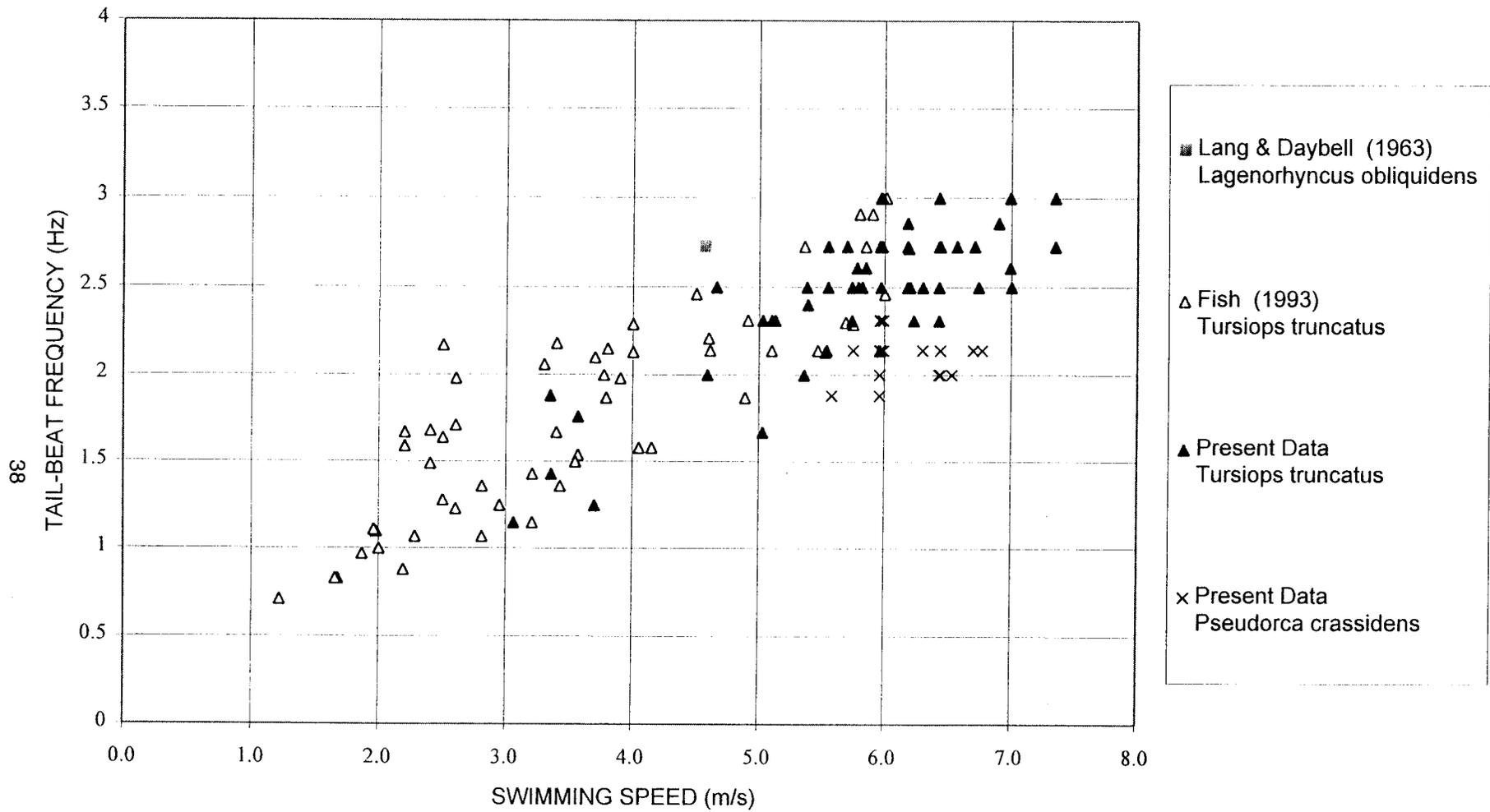


Figure 7c. Dolphin tail-beat frequency plotted as a function of swimming speed, expressed in meters per second.

Although it was obvious that the approach of the airplane increased the swimming speed of the school of *Delphinus capensis*, it was also evident that this motivation was not sufficient to produce burst speeds. It was not until the third photo-pass, about 5 minutes after the initial approach of the airplane, that the maximum swimming speed of the school (4.7 m/s) and of an individual dolphin (6.7 m/s) was recorded. The average swimming speed of the school for the five photo-passes, which took about 8 minutes to complete, was 4.2 ± 0.36 m/s. This swimming speed is representative of those reported for dolphin schools of *Stenella attenuata*, *S. longirostris*, and *S. coeruleoalba* when displaying ship-avoidance behavior (Au and Perryman, 1983). The shape of the swimming speed distribution of the school for photo-pass 3 (not shown) is generally similar to the composite distribution (figure 4), being slightly skewed to the right (more animals swimming at lower speeds). Such a right-skewed distribution further suggests that the swimming speeds recorded were not approaching some biological limit, in which case, the distribution would tend to be left-skewed, bunching-up at the limiting swimming speed (Gould, 1996).

The swimming speed of individuals comprising the school may have been lower than expected because of the presence of newborn dolphins. Although speed was not calculated for any of these calves, it is documented that their maximum swim speed is likely to be markedly less than that attained by adult-sized animals (Edwards, 1992). For schools containing breeding groups, there may be social pressure to limit overall swim speeds so that calves and nursing cows remain sheltered within the confines of the school and are not left behind where they would be vulnerable to predators.

It can only be speculated how the pool dimensions and motivation provided limited burst swimming speeds for the trained dolphins at SeaWorld. The fact that the largest (ID# = 8826—3.66 m, *Pseudorca crassidens*) and smallest (ID# = 8736B—1.83 m, *Delphinus delphis*) dolphins shared the same maximum (8.0 m/s) and similar average (6.4 and 6.7 m/s, respectively) swimming speeds, suggests that the size of the pool for most of the dolphins, with the possible exception of the *Pseudorca*, was not particularly restricting. Moreover, the similarity of maximum swimming speeds of trained *Tursiops truncatus* obtained in a free-ranging environment (7.7 m/s, Ridgeway and Johnston, 1966; 8.3 m/s, Lang and Norris, 1966) and in large pools (8.2 m/s, reported here), further suggests that the dimensions of the pool are not necessarily performance-limiting.

Swimming-speed distributions of individual dolphins recorded at SeaWorld are shown in figure 8. Several of the swimming-speed distributions were to some degree skewed to the left (figures 8a through 8d), which could be indicative of the animal approaching optimal performance for the given situation. This inference is plausible only if the dolphin was equally motivated and equally healthy for each run. The choice of histogram bin width can also effect the degree of skewness exhibited by the swimming-speed distribution. As an illustration of the effect of bin size, the skewness of the swimming-speed distributions for *Delphinus delphis* (ID# = 8736B; figures 1b, 8g) and *Pseudorca crassidens* (ID# = 8826; figures 1c, 8h) can be compared when plotted in increments of 0.25 L/s (figures 8g, 8h) and 0.5 m/s (figures 1b, 1c).

Underwater swimming speeds inferred from jump height may be higher ($\approx 20\%$) than speeds recorded of dolphins swimming near the surface of the pool for several reasons. Generally, the swimming duration prior to jumping is shorter and, therefore, more burst-like. In addition, as the dolphin is swimming towards the surface, there is no drag associated with wave resistance. Wave drag experienced by the dolphin when swimming near the surface can be the largest component of the total

drag on the animal (Hertel, 1966). The dolphin may also derive a thrust advantage when jumping from the reactive forces due to the presence of the pool bottom. This is similar to the “ground effect” that can enhance lift for wings (Hoerner, 1985). The coefficient in the correction factor, $1/3DL$ in equation (2), may also be too small. The arguments of Lang and Daybell (1963) for incorporating a correction factor suggest that this coefficient must be less than one. However, the average correction factor required to best reconcile swimming speeds (2 to 3 meters below the surface) derived from jump heights with those measured when the animal was swimming about 0.5 m from the surface is 1.25. Consequently, adjusting the coefficient in the correction factor, although possibly warranted, cannot by itself resolve these discrepancies. Another possibility is that the motivation of the dolphin may be significantly greater for jumping than swimming fast along the surface, as the goal is more clearly defined and can be made incrementally harder to achieve.

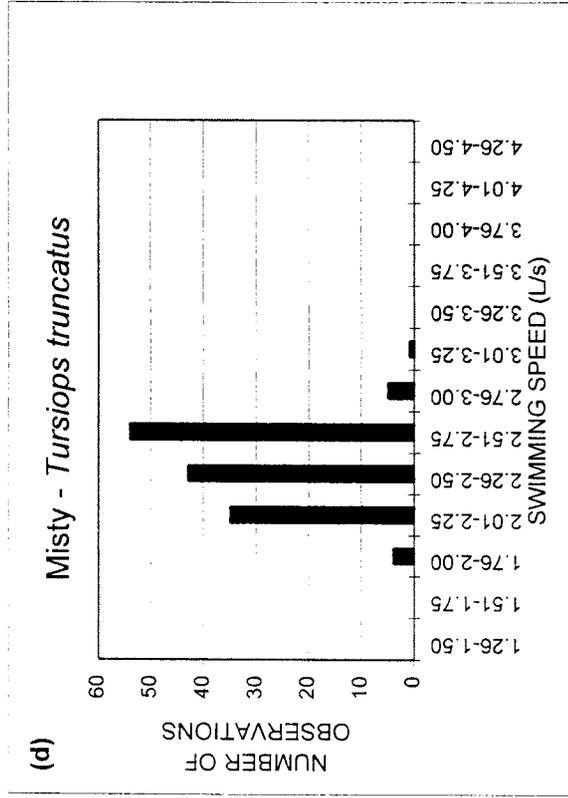
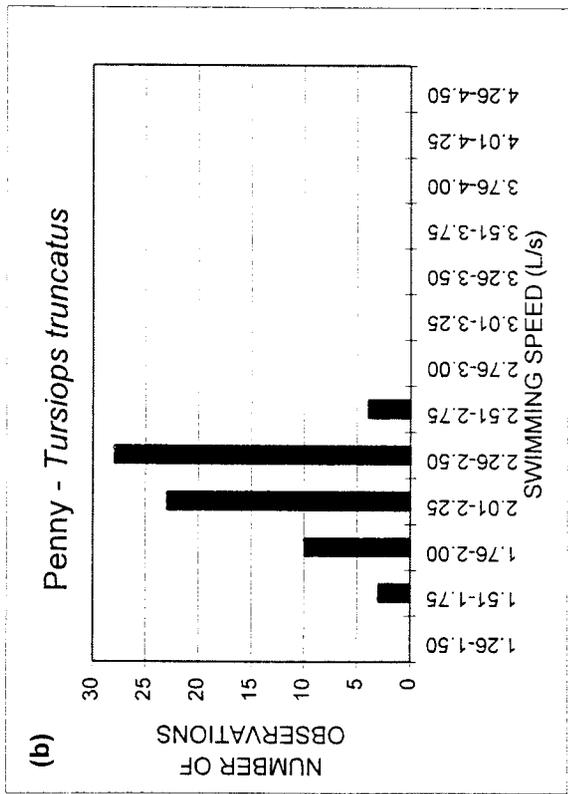
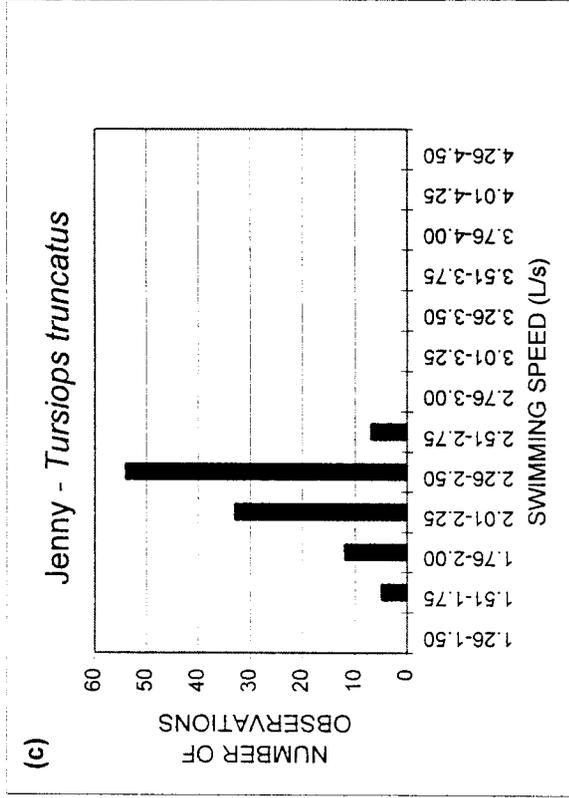
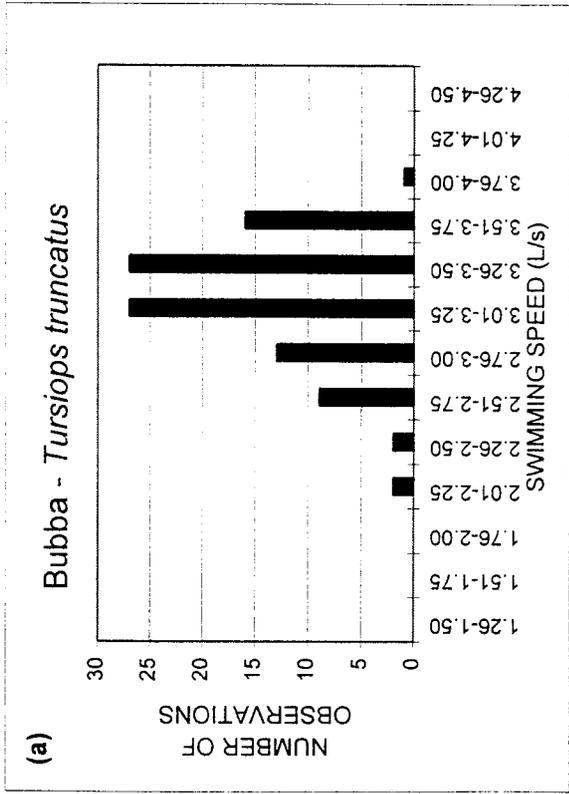


Figure 8a-d. Distributions of "fast" swimming speeds of individual captive dolphins, expressed in body lengths per second (L/s).

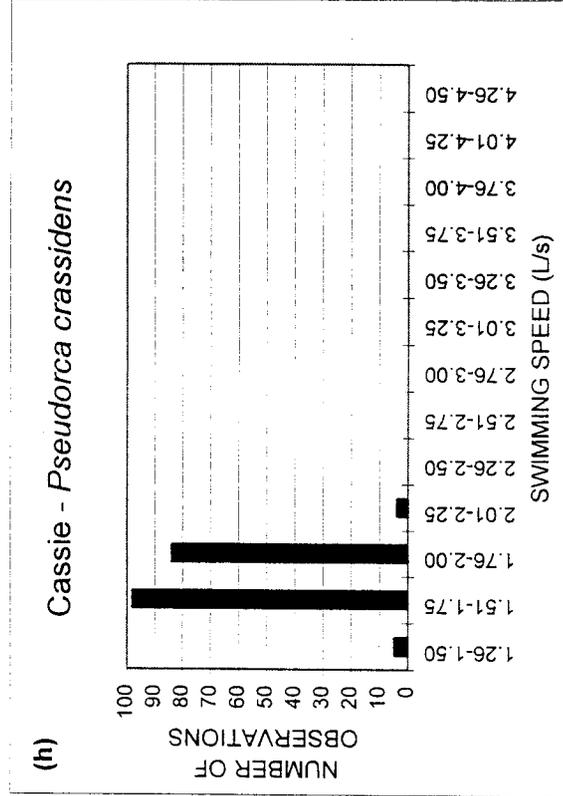
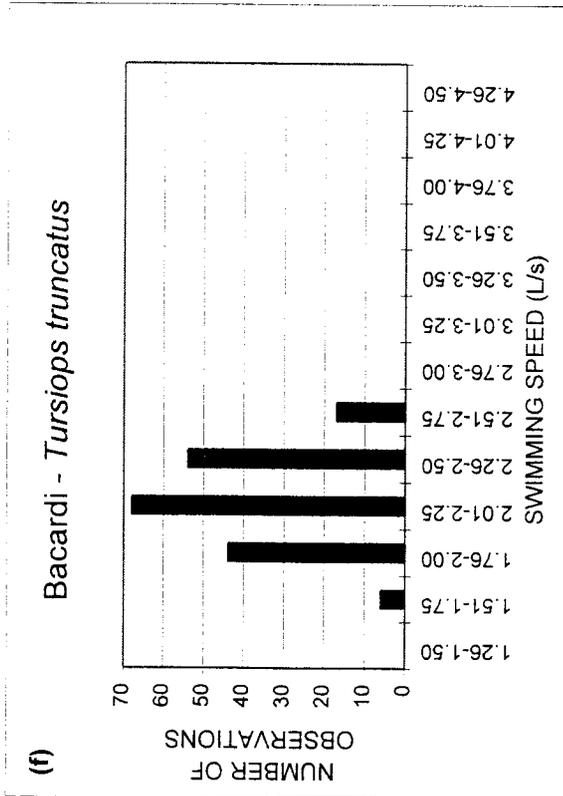
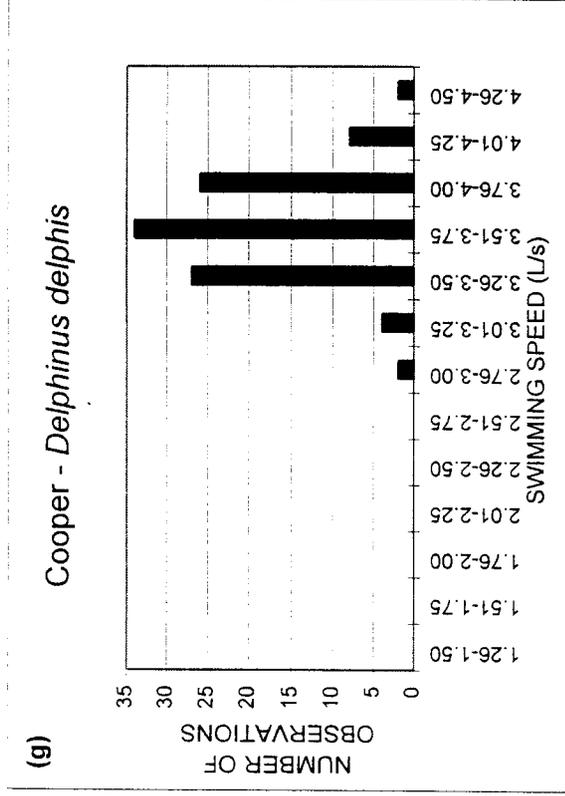
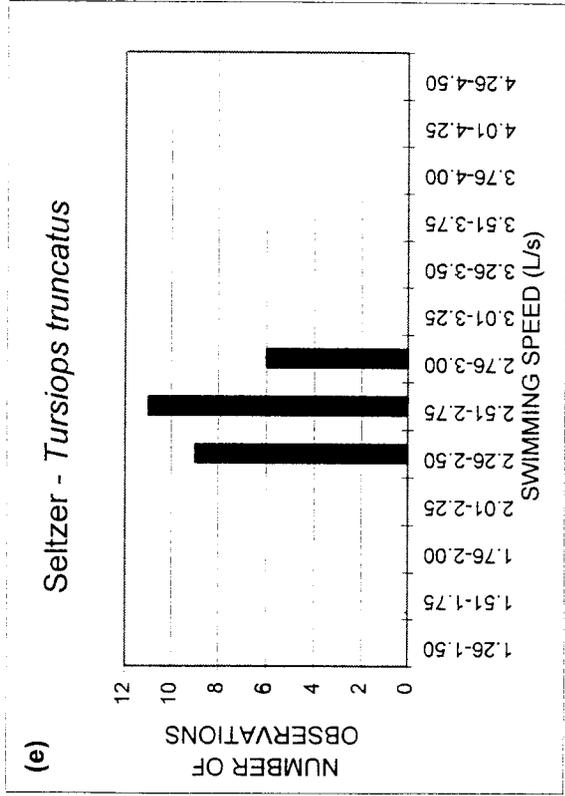


Figure 8e-h. Distributions of "fast" swimming speeds of individual captive dolphins, expressed in body lengths per second (L/s).

5. CONCLUSIONS

The data presented here show no indication that the high-speed swimming capability of captive, regularly exercised dolphins is less than free-ranging dolphins. A similar observation for slower cruising speeds (≈ 2 m/s) has been made for *Tursiops truncatus* (Williams et al., 1993). Comparison of maximum speeds sustained for a few seconds of captive *Tursiops* swimming in large pools (8.2 m/s, reported here), and in free-range environments (7.8 m/s, Ridgeway and Johnston, 1966; 8.3 m/s, Lang and Norris, 1966) suggests that the dimensions of the pool do not necessarily limit performance levels. Nonetheless, given the large disparity which exists between measurements of the fastest swimming speeds of trained dolphins and those previously reported for free-ranging dolphins, and the low probability of recording burst speeds, further data recording efforts of this nature are desirable.

Although comparison is limited, it is nevertheless noteworthy that swimming speeds inferred from jump heights of captive and free-ranging dolphins are in reasonable agreement. The discrepancy between swimming speeds inferred from jump heights ($\approx 20\%$ higher) and determined from recordings of surface swimming for the same dolphin, could be best addressed by recording the underwater swimming speed of the dolphin prior to its leap. This would provide an opportunity to better determine the effect of wave drag and the coefficient of the correction term in equation (3), as well as to assess the different motivational strategies seeking to elicit maximum jump heights and swimming speeds.

Kinematic and Strouhal data also indicate that the swimming motion of captive dolphins studied are similar to that of other dolphins and fish swimming in various carangiform modes. Strouhal numbers for the various dolphin data sets generally ranged between 0.25 to 0.35 (56% of the data), and are in reasonable agreement with what Triantafyllou et al. (1993) predicted for maximum propulsive efficiency. It is interesting that although for captive dolphins there is evidence for a Strouhal number dependence on acceleration and deceleration (Kayan and Pyatetskiy, 1977), a 1.91-cm drag collar had almost no effect (Lang and Daybell, 1964). Further investigation of these relationships as well as how Strouhal numbers compare with free-ranging and deep-swimming dolphins is desirable.

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13. ABSTRACT (Maximum 200 words) The objective of this study was to record maximum dolphin swimming speeds sustainable for several seconds with free-ranging and captive dolphins utilizing different motivational strategies. Recordings were used to determine relationships between the various kinematic parameters, particularly the Strouhal number, which characterizes dolphin swimming motion. Comparisons are made, where possible, with results from previous studies.			
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