MAXIMUM SWIM SPEEDS OF CAPTIVE AND FREE-RANGING DELPHINIDS: CRITICAL ANALYSIS OF EXTRAORDINARY PERFORMANCE

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ABSTRACT

Research into dolphin swimming historically was guided by false assumptions pertaining to maximum speed. Accurate measurements on swimming speed and duration of effort of free-ranging dolphins are rare. To examine the variance of maximum swimming speeds, nearly 2,000 speed measurements were obtained for both captive and free-ranging dolphins, including *Tursiops truncatus, Pseudorca crassidens, Delphinus capensis,* and *Delphinus delphis.* Measurements were made from videotapes of dolphins trained to swim fast around a large pool or jumping to a maximum height, videotapes of captured wild dolphins immediately after release, and sequential aerial photographs of a school of free-ranging dolphins startled by a passing airplane. Maximum horizontal speeds for trained animals were 8.2 m/sec for *T. truncatus,* 8.0 misec for *D. delphis,* and 8.0 m/sec for *P. crassidens.* Maximum speeds for *T. truncatus* swimming upwards, prior to vertical leaps ranged from 8.2 to 11.2 m/sec. Wild *7: truncatus* demonstrated a maximum speed of 5.7 m/sec. Maximum swimming speed of free-ranging *D. capensis* responding to multiple passes by a low flying airplane was 6.7 m/sec. There was no evidence that the free-ranging dolphins have superior swimming capabilities to captive animals. The

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results of this study imply that realistic maximum swimming speeds for dolphins are lower than previous reports which were based on sparse data and imprecise measurement techniques.

The simplest behavioral parameter that can be controlled by aquatic animals is swimming speed (Weihs and Webb 1983). High speeds allow increased foraging and active pursuit, but require large energy expenditures, because the resistive drag is proportional to the square of the velocity (Webb 1975, Vogel 1994). Despite these high energetic costs, dolphins have been reported since Aristotle to be among the fastest of marine organisms and to display extraordinary locomotor feats. For the fluid dynamicist, reports of exceptionally high swim speeds have served as an invitation to look for some underlying, perhaps yet to be discovered, drag-reducing mechanism (see reviews by Kramer 1965, Lang 1966, Hertel 1966, Fish and Hui 1991, Fish and Rohr 1999). Since there is no evidence that the muscles of dolphin are exceptionally powerful (reviewed by Fish and Hui 1991), the motivation to seek extraordinary drag-reducing mechanisms is derived solely from accounts of extraordinary swimming speeds during maximal efforts and burst swimming.

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 {Lang 1963, 1975]. Vogel (1994) has suggested that, in general, reports of speeds of swimming organisms often include so many egregious overestimates that extreme skepticism is recommended when dealing with the literature. The reason for questioning these reports is that estimates of swimming speeds based on observations from ships, airplanes, and the shoreline often were determined without fixed reference frames, information on currents or proximity to the ship, and the use of accurate timing instruments (Fish and Hui 1991, Fish and Rohr 1999). The most reliable dolphin burst swim speed data has been obtained from trained animals swimming in a free-ranging environment (Lang and Norris 1966, Lang and Pryor 1966). However, it has been acknowledged that trained animals may not be suitably motivated to swim at their maximum potential (Lang 1963, Lang and Daybell 1963, Lang 1975) and they may not be in as good athletic condition as free-ranging animals (Gray 1957). Measurements in captivity are further criticized because of the limited tank size (Lang 1975), and the shallowness of the water depth (Purves *et al.* 1975). Swimming near the water surface can limit maximum speed due to higher drag from energy loss in the production of waves (Hertel 1966).

The present maximum swim speed measurements were obtained from video recordings of captive delphinids (*Tursiops truncatus, Delphinus delphis,* and *Pseudorca crassidens)* trained to swim fast and jump high (courtesy of Sea World at San Diego), video recordings of the release of free-ranging dolphins in Sarasota Bay (*Tursiops truncatus,* courtesy of the Mote Marine Laboratory), and open-

Table 1. Vital statistics of Sea World dolphins. Length measured as linear distance from rostral tip to fluke notch.

Dolphin ID#	Species	Sex	Age (y)	Length (m)	Mass (kg)
9026	*T. truncatus*	M	3.5	2.06	149.2
7903	*T. truncatus*	F	Unknown	2.59	207.7
8003	*T. truncatus*	F	17.0	2.57	187.8
8128	*T. truncatus*	F	13.0	2.95	256.3
8527	*T. truncatus*	F	8.5	2.59	212.3
8738	*T. truncatus*	F	16.0	2.69	219.1
8926	*T. truncatus*	F	4.0	2.49	146.9
8736B	*D. delphis*	M	15.0	1.83	104.8
8826	*P. crassidens*	F	10.0	3.66	461.8

ocean aerial photographs of a school of dolphins responding to the sound of an approaching plane *(Delphinus cupensis,* courtesy of the NOAA, National Marine Fisheries Service). Although one or more of the previous criticisms may equally apply to the present study, it is nevertheless believed that through: (1) recording a large number of speed measurements of both free-ranging and trained delphinids, (2) utilizing different motivational strategies, and (3) recording the observations on film or tape for repeated analysis, the present effort will contribute towards a richer data base from which delphinid swimming capabilities may be more reliably assessed.

METHODS

Trained Delphinids — Swimming Performance Tests

Nine trained delphinids consisting of seven Atlantic bottlenose dolphins *(Tursiops truncatus)*, one common dolphin *(Delphinus delphis),* and one false killer whale *(Pseudorcu crassidens)* were videotaped at the San Diego Sea World facility to investigate burst swimming capabilities. In addition to performing in shows, the dolphins in this study participated in training, play, husbandry, and exercise sessions on a regular basis. Approximately 18–20 h of their day consisted of non-structured play, free, and rest time. The dolphins subsisted on a diet of herring *(Clupea harengus)*, smelt *(Osmerus mordax)*, mackerel *(Scomber* sp.), and squid *(Loligo* sp.) supplemented with vitamins dispersed at irregular intervals throughout the day. Morphological measurements for each animal, designated by number, are summarized in Table 1.

To maintain physical fitness the delphinids performed "fast swims" around the circumference of the main performance pool as part of their daily exercise routine. Initial training involved instructing the animals to accelerate quickly and touch their rostrum to a boat pole held several meters out in front of them. Through successive approximations of positioning the boat pole farther and farther away, the delphinids learned to burst swim 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 peak performance, the boat pole was slapped on the surface of the water to induce the delphinids to swim more rapidly. Trainers frequently raced the Tursiops in pairs to provide additional incentive. A wide variety of rewards including tactile stimulation, environmental enrichment devices, and food were given for appropriate behaviors on an intermittent reinforcement schedule.

For performance in the daily shows, some of the Tursiops 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 three months of training, the flag height was one which the dolphins were incapable of reliably attaining. For the shows, the flag was normally positioned at about 5.2 m above the water surface. At this height the dolphins would be challenged, yet still achieve their goal consistently.

The delphinids were housed in a 1.2 million gallon, four pool complex at water temperatures ranging between 12" and 21°C. Video sequences were recorded in the semi-circular 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 7.8 m. The curved portion of the pool was constructed of clear acrylic panels, 1.7 m wide, separated by 0.2-m-wide posts allowing for a relatively unobstructed view of the animals as they swam.

Delphinid horizontal swim speed calculations — Delphinid swimming speeds were recorded with a Panasonic AG-180 camcorder at a rate of 60 Hz and analyzed using a Panasonic AG-7300 video cassette recorder. The camcorder was positioned 23 m above the performance pool allowing for a clear view of the entire area. Delphinid speeds were calculated along two different sections of the pool, either a straight 8.0-m portion along the back wall or a curved 5.5-m section behind the front clear acrylic wall. The distance between the animal and the walls was estimated to be typically 0.5 m or greater. Animals swam at depths of approximately 0.5 m. The section of video analyzed did not include the initial seconds during which time animals accelerated. Only video sequences in which the delphinids appeared to swim at a constant speed and with maximum effort were used for speed determinations.

Swim speed was determined by dividing the length of the section through which the delphinid swam, by the time it took to cross that distance. Delphinid swim speed measurements taken from the video could be accurately repeated within a few per cent. In order to assess parallax effects on the velocity calculations, video recordings of a model cast of a Tursiops dorsal fin were made as it was moved along the normal swimming trajectory of the animals during filming. The difference in distance between the actual position where the cast fin crossed the reference points, and that determined from the video recordings, was found to be insignificant.

Vertical Swim Speed Calculations from Leaping Dolphins — The velocity of dolphins swimming vertically before emerging through the water surface for a

Table *2.* Vital statistics of Sarasota Bay bottlenose dolphins (*Tursiops truncatus*). Length measured as linear distance from rostral tip to fluke notch.

Dolphin ID#	Sex	Age (yr)	Length (m)	Mass (kg)
14	M	ND	2.64	207.0
74	M	ND	2.58	172.0
55	F	8	2.37	177.0
66	M	10	2.43	175.0
72	M	6	2.15	127.0
66	M	10	2.43	171.0
33	F	12	2.50	186.0
32	M	4	2.40	190.0
131	F	6	2.26	141.0
24	M	5	2.29	136.0
38	M	20	2.83	264.0
17	F	33	2.62	208.0
3	F	5	2.07	112.5
60	M	34	ND	ND
63	F	40	ND	191.0
138	M	2	2.01	86.0

leap was determined from 60-Hz video recordings with a Sony DCR VX1000 camera in an underwater housing. The camera was mounted on the wall inside the pool at a depth between 1 and 1.5 m. The position of the camera was approximately 3–4 m from the position of the dolphin prior to emergence. The field of view of the camera permitted observation of the rostral tip over a distance of 1.5 body lengths beneath the surface of the water. Prior to speed trials, a marked pole was held by a trainer in the water at the emergence site and video recorded for scale.

Sequential positions of the rostral tip were digitized from individual fields of videotape with a Panasonic AG-7300 video recorder, Sony PVM 1341 monitor and AT-compatible computer with Peak 2D video analysis software (Version 4.2.4. Peak Performance Technologies, Inc.). Average velocity over the recorded field of view and over a time interval between 0.1 and 0.5 sec was calculated.

Free-Ranging Dolphins—Capture and Release

Since 1970, subsets of the resident population of Atlantic bottlenose dolphins inhabiting the nearshore waters of Sarasota Bay, Florida, have been temporarily captured for life history and health status studies (Wells *et al.* 1987, Scott *et al.* 1990). Motivation to video-record the animals upon their release derived from past accounts of what appeared to be extraordinarily fast swim speeds. Morphological characteristics of the animals, which were typically released one to two hours after capture, are listed in Table 2.

The dolphin's release was recorded with a Sony CCD-TR81 camcorder, suspended from a balloon between 45 and 60 m above the release point. The

camcorder recorded at 60 Hz, with swimming sequences recorded between 5 and 10 sec. The balloon 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 $1,000 \text{ m}^3$ of helium gas, the balloon was capable of supporting the video camera, tilt and pan maneuvering mechanisms, cable and tether (approximately 10 kg). A television monitor attached by a coaxial cable to the camcorder enabled the orientation of the camera to be adjusted 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. A similar observation platform was used to record behaviors of dolphins (Nowacek and Tyack 2001).

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 the pixel distance that the dolphin traveled between frames to be calculated. The corresponding physical distances swam by the dolphin were achieved by 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 the fastest dolphin video sequences were reanalyzed by an independent researcher, using a different digitizing scheme, swimming speeds were within 5%.

Free-Ranging Dolphins — Swimming School Responding to Plane

Aerial photographs of a school of longbeaked common dolphins (*Delphinus capensis*) were taken offshore of Morro Bay, California on 23 April 1995. Photographs were taken with a high resolution, 126-mm 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 and 145 m and at a ground speed of 213 km/h. The camera had a fixed 152-mm lens. During flights, photographers adjusted camera f-stop (to 4.0 or 5.6) and shutter-speed (range: 1/1500–1/2000 sec) based on ambient light conditions. The camera also featured forward-motion-compensation which eliminates photograph image "blur" resulting from the forward movement of the aircraft. The forward motion of the plane was compensated for by advancing the film in the camera along a stationary plate, while the shutter was open, at the same rate and direction as the image recorded by the camera (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 phoro-pass typically contained 10−12 exposed frames of the school. For this analysis, five phoro-passes were completed. To facilitate the simultaneous re-cording of time and altitude data with each camera exposure (or photo-frame) of the dolphin school, an electronic "Tattletale" analog to digital signal con-verter was interfaced with a Honeywell radar altimeter, the aerial camera and a lap-top computer. Photographed targets of known length were used to make small corrections to the radar altimeter readings (Ghosh 1988, Gilpatrick 1996), and establish uncertainty limits in the length estimations made from the plane (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 (using 95% CL) translated to an error of ± 0.9 cm (or $\pm 0.45\%$) of the estimated length.

Dolphin swim speed was determined by calculating the time it took a dolphin to swim a measured straight-line distance along the sea surface. To accomplish this calculation the film reader would srart at the beginning of a phoro-pass, identify a dolphin, make a pen mark on an acetate overlay at the tip of the dolphin's rostrum, and note the time (recorded to 1/100 sec on the lap-top computer). Also marked on the acetate were splash marks occurring throughout the field of view which could be identified in consecutive frames of interest. The persistence of splash marks on the ocean surface allowed the acetate to be properly superimposed on subsequent frames, which permitted the identification of 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 recorded. 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, described below.

The video-image analysis system consisted of a Cohu Inc. CCD video camera linked by an adapter to a Bausch and Lomb dissection microscope with a 1−7X 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, and mea-surements were made using the image processing software NIH Image. A computer mouse was used to set the measurement point locations. The soft-ware then computed the distance in between measurement points. The esti-mated "true" distance (TD) traveled by the dolphin along the sea surface was then calculated using the following photogrammetric scale factor:

$$TD = (A/F)\, D \tag{1}$$

where A is the altitude in meters from which the photograph was taken, F is the focal length of the camera lens ($F = 0.1524$ m), and D is the distance traveled by the dolphin as measured on the transparency in microns.

In order to evaluate the variance associated with the measurement tech-

niques applied in this study, swim speeds were calculated from four replicate independent distance measurements taken for 30 individual dolphins in the photographs. The precision of the replicate swim speed calculations were then compared using the coefficient of variation (CV) which averaged 2.9% (range: 0.72%–5.3%). The standard deviation is given with means.

RESULTS

Trained Delphinids—Swimming Performance Tests

A total of 927 recordings of delphinids (*Tursiops truncatus, Delphinus delphis* and *Pseudorca crassidens)* at Sea World of San Diego were acceptable for horizontal swim speed determinations. The time interval during which the swim speeds were determined varied between 0.7 and 2.8 sec. 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). None of these swim data included leap-swim or "porpoising" behavior which, in general, was seldom observed during the Sea World recordings.

The maximum horizontal swimming speed ($n = 633$) for six *Tursiops* was 8.2 misec (Table 3). Four of the six *Tursiops* observed exhibited maximums within 5% of 8 misec. The maximum swim speeds of the *Delphinus (n =* 103) and *Pseudorca (n =* 191) were both 8.0 m/sec. The corresponding mean of high swim speeds were 6.2 ± 0.7 misec for all the *Tursiops,* 6.7 ± 0.5 misec for *Delphinus* and 6.4 ± 0.5 misec for *Pseudorca.* In terms of body length, BL, the maximum swim speeds for *Tursiops, Delphinus,* and *Pseudorca* were 3.8 BL/sec, 4.4 BL/sec, and 2.2 BLisec, respectively. The mean high swim speeds, expressed as BL/sec, were 2.4 BL/sec for *Tursiops,* 3.7 BL/sec for *Delphinus,* and 1.7 BL/sec for *Pseudorca.*

The distribution of swimming speeds for each of the three delphinid species are shown in Figure 1. The distributions are comprised of measurements obtained along the back wall and behind the front acrylic wall of the pool. For data on means of swimming speeds from individual *Tursiops,* no significant difference *(t =* 1.93; df = *5; P >* 0.11; Statistica Version *4.1,* Statsoft) in high swimming speed was found for swimming along either the front or back walls. However, *Delphinus* and *Pseudorca* had significantly higher speeds along the back wall than the front wall *(P <* 0.05; unpaired t-test; Data Desk 3.0, Odesta Corp.). Maximum speeds along the back wall were 8.0% and 13.0% higher than those recorded behind the front wall for *Delphinus* and *Pseudorca,* respectively; whereas, mean high swim speeds were 6.0% and *4.0%* higher, respectively (Table 3).

A total of 47 leaps by three *Tursiops* were analyzed which were recorded over intervals of 0.1–0.5 sec. Maximum velocity varied from 8.2 to 11.2 mi sec with a mean of 9.7 ± 0.8 misec. Mean leaping velocity over the recording interval was 8.8 ± 0.7 misec, which was 42% greater than the mean high speed for *Tursiops* swimming at high speeds horizontally near the surface.

Table 3. Summary of Sea World dolphin swimming speed data for high speed runs.

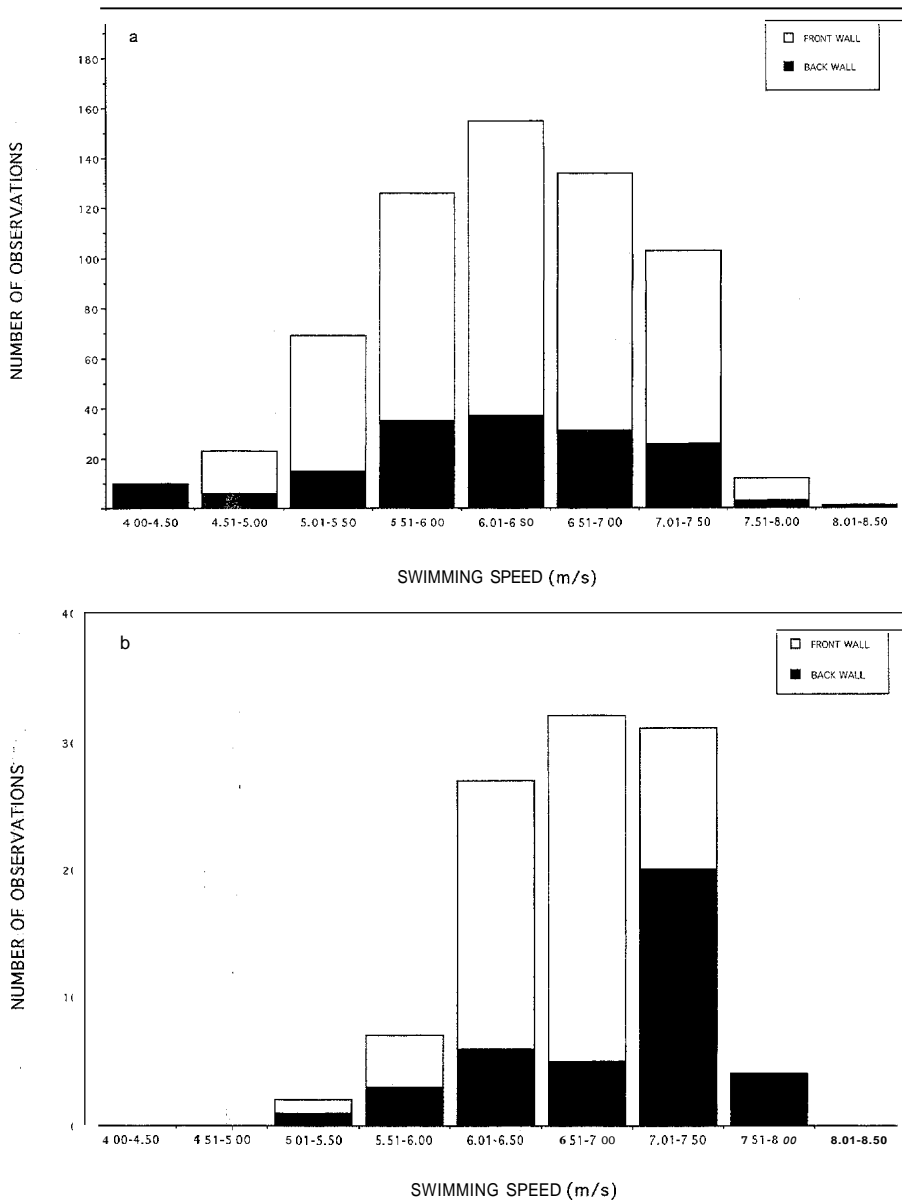| Dolphin ID#	Species	n	Back wall speed					n	Front wall speed			
			Maximum		Mean				Maximum		Mean	
			m/sec	BL/sec	m/sec	BL/sec			m/sec	BL/sec	m/sec	BL/sec
9026	T. truncatus	25	7.74	3.76	6.42	3.12		72	7.67	3.73	6.56	3.1
8926	T. truncatus	15	6.67	2.68	5.28	2.12		53	6.27	2.52	5.49	2.2s
8003	T. truncatus	30	6.49	2.53	5.51	2.15		81	6.79	2.65	5.79	2.26
8527	T. truncatus	6	7.49	2.90	6.51	2.52		20	7.4	2.86	6.77	2.62
8738	T. truncatus	35	8.15	3.03	6.50	2.42		107	7.76	2.88	6.57	2.44
8128	T. truncatus	53	7.74	2.63	6.51	2.21		136	7.76	2.63	6.35	2.15
8736B	D. delphis	39	8.0	4.38	6.91	3.78		64	7.4	4.05	6.52	3.57
8826	P. crassidens	41	8.0	2.19	6.57	1.8		150	7.08	1.94	6.32	1.73

Figure 1. Distribution of "fast" swimming speeds of (a) six captive bottlenose dolphins (*Tursiops truncatus*), (b) a captive, short-beaked, common dolphin (*Delphinus delphis),* and (c) a captive false killer whale (*Pseudorca crassidens*). Speeds recorded along the front (open bar) and back (shaded bar) walls of the test pool are provided.
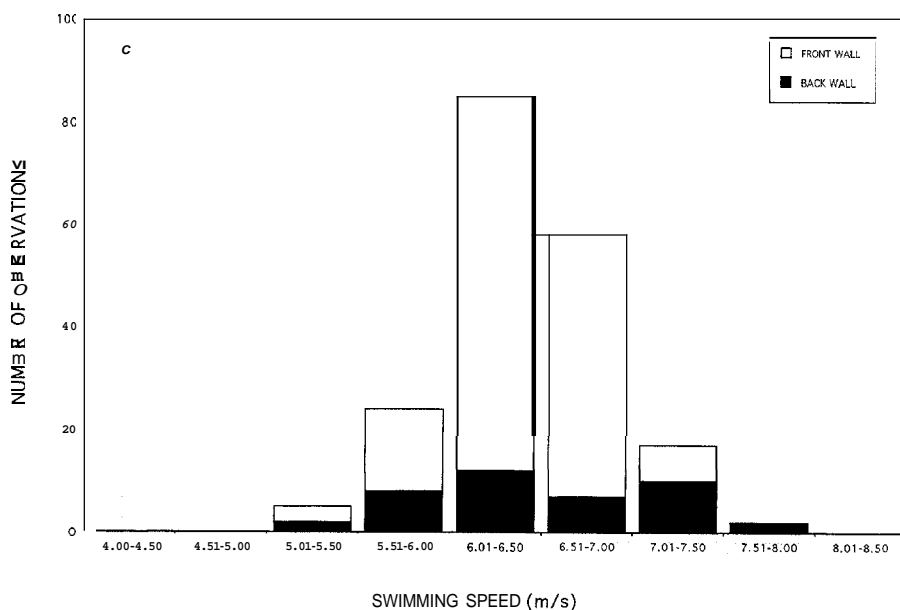
Figure 1. Continued.

Free-Ranging Dolphins — Capture and Release

When assessed from the observational boat immediately after release, dolphin *(Tursiops truncutus)* swim speeds often appeared exceptionally fast. The analysis of *14* release recordings resulted in a range of swimming speeds from *1.6* to *5.6* misec (Fig. *2*). Some of the slower swimming speeds can be attributed to the simultaneous capture of two animals, when animals were not released at the same time. Under these circumstances the first animal released often appeared to hesitate, sometimes turning towards the release point, before swimming away. When released in pairs higher swimming speeds were generally recorded. However, even when a single dolphin was captured and released, its recorded movements often were rather slow. The *14* recordings analyzed did not show any indication of porpoising behavior immediately after release. The swim speeds of captive *Tursiops* (Fig. 1a) were higher than those for the released *Tursiops* (Fig. 2).

Free-Ranging Dolphins — Open Ocean

Five plane passes over a school of longbeaked common dolphins *(Delphinus cupensis)* resulted in *1,045* swim speed measurements. A significant difference was found in swim speeds between passes *(P* < 0.001; ANOVA; Statistica Version *4.1,* Statsoft). The highest swim speed recorded was 8.8 misec, observed during the first pass. Maximum swim speeds for subsequent passes were *5.9, 6.7, 5.6,* and *5.8* misec (Table *4*). Mean high swim speeds for each consecutive pass were *4.6* + 1.0 misec *(n* = 81), *4.1* ± *0.6* misec *(n* = 106), *4.7*
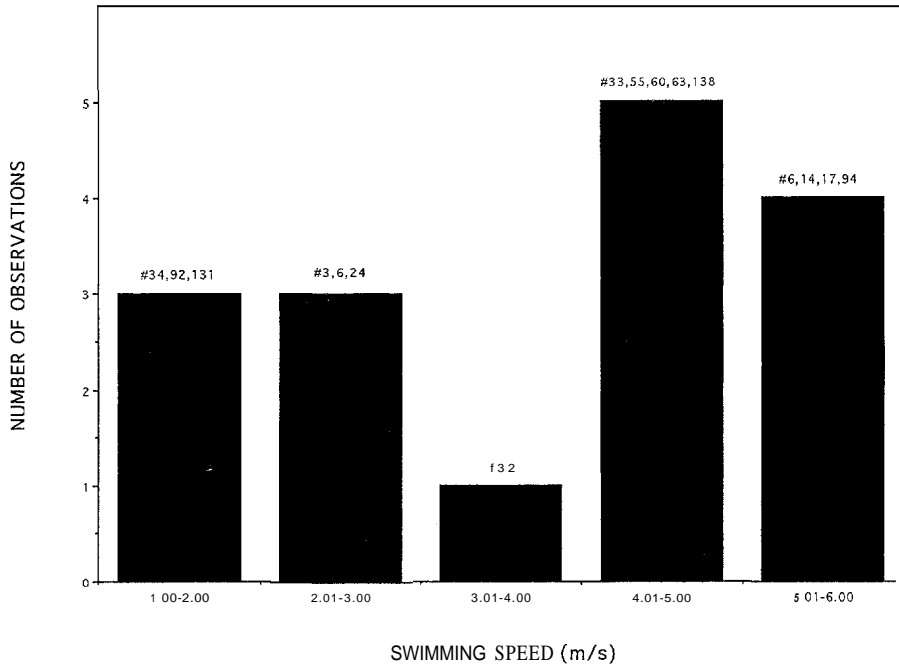
Figure 2. Distribution of swimming speeds of free-ranging bottlenose dolphins *(Tursiops truncatus)* immediately after release. Individual dolphins are indicated by ID number (Table *2).*

± 0.7 m/sec (*n* = 310), 3.8 ± *0.5* m/sec *(n* = 377), and *4.0* ± 0.5 m/sec (*n* = 171). Swim speed measurements were obtained over 1–2-sec periods. The five passes were completed in about *8.5* min. Although observations of splashes resulting from porpoising were common throughout the frames, none of the swimming speeds analyzed were obtained from dolphins which were porpoising. The distribution of swimming speeds for all of the five passes is shown in Figure 3.

Table 4. Summary of longbeaked common dolphin (*Delphinus capensis*) photogrammetric speed measurement data determined from multiple passes of reconnaissance aircraft.

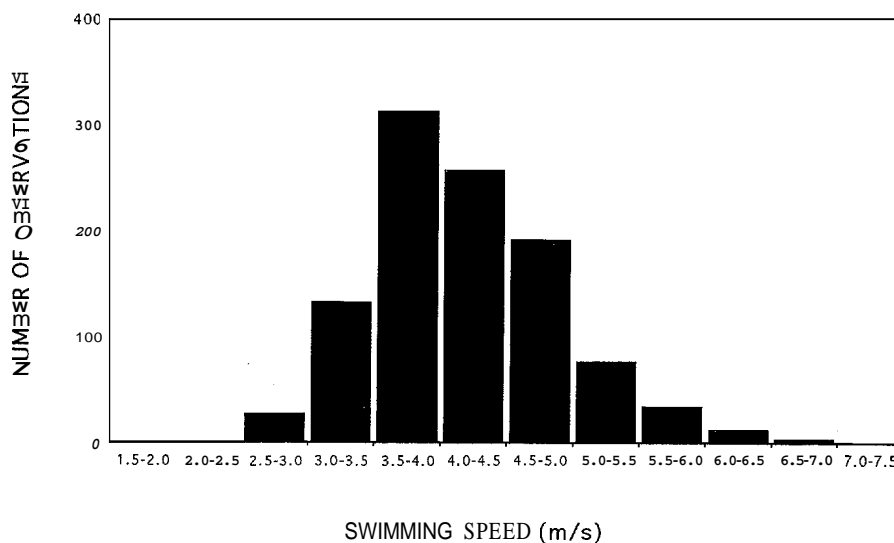| Pass	*n*	Average speed (misec ± SD)	Maximum speed (misec)	Minimum speed (misec)	Duration of pass (sec)
1	*80*	*4.50 ± 0.89*	*6.60*	*2.69*	*18.6*
2	*106*	*4.13 ± 0.60*	*5.89*	*2.49*	*15.2*
3	*310*	*4.67 ± 0.66*	*6.70*	*3.07*	*18.4*
4	*377*	*3.80 ± 0.52*	*5.56*	*2.27*	*14.2*
5	*171*	*4.00 ± 0.51*	*5.78*	*2.40*	*18.4*

Figure 3.   Total distribution of swimming speeds obtained from five airplane passes over a school of longbeaked common dolphins *(Delphinus capensis).* Total number of observations equals *1044.*

DISCUSSION

Comparison of Maximum Delphinid Swim Speeds

Maximum swim speeds recorded in this study for four species can be compared with other values found throughout the literature. Generally there is good agreement. For example, Ridgway and Johnston (1966) observed boat-following speeds of up to 7.8 mlsec for *Tursiops truncatus,* which compares well with our observation of 8.2 misec. A top speed of 8.3 mlsec was found by Lang and Norris (1966) for a Pacific bottlenose dolphin, *Tursiops gilli,* also trained to pursue a boat. Wiirsig and Wursig (1979) obtained theodelite measurements of *Tursiops truncatus* at speeds of at least 8.3 misec while avoiding a pod of killer whales that was within *0.5* km of the dolphins. For *Delphinus* as well, several reports of maximum swim speeds for free-ranging animals (9.3 mlsec) are near to the maximum (8.8 misec) presented here (Kellogg 1940, Johannessen and Harder 1960). Finally, the 8 m/sec maximum swim speed reported here for *Pseudorca crassidens* is also close to the 7.5 misec maximum observed by Fish (1998), under similar experimental conditions.

However, burst speed values of free-ranging dolphins have been reported as high as 10.3 misec (Lockyer 1978) and 15 misec (Lockyer and Morris 1987) for *Tursiops truncatus;* and 10.1 misec (Gray 1936), 12.5–13.9 misec (Tomilin 1957), and 13.2 mlsec (Pershin 1969) for *Delphinus delphis.* These reports of extraordinary speeds were disputed on the basis of the non-repeatability of these data and the methodology in data collection (Kooyman 1989, Fein 1998, Fish 1998). The highest value of 15 misec (Lockyer and Morris 1987) was determined from a cliff-top observation using the distance traveled by the

dolphin estimated from charts. In cases where speed data were collected from ships (Gray 1936, Steven 1950, Johannessen and Harder 1960), the dolphins were swimming close to the ship, thereby probably utilizing a free-riding behavior (Lang 1966, Fish and Hui 1991, Fish and Rohr 1999). Free-riding behaviors, such as drafting and bow-riding, allow dolphins to swim at higher speed with less effort than when swimming in undisturbed water (Williams *et al.* 1992, Fish 1999).

Swimming speed is related to duration of the activity (Lang and Norris 1966). Open-water speed trials conducted with a *Tarsiops truncatus* (*gilli*) showed that the animal could swim at 3.08 m/sec indefinitely, at 6.09 misec for 50 sec, at 7.01 misec for 10 sec, and at a maximum speed of 8.3 misec for 7.5 sec (Lang and Norris 1966). A maximum swimming speed of 11.1 m/sec was measured for *Stenella attenuata* during a 2-sec acceleration (Lang and Pryor 1966). The inability to maintain high levels of performance for prolonged periods is dependent on the magnitude of the resistive forces (*i.e.,* drag which increases with the square of velocity) and contraction characteristics (*i.e.,* contraction frequency, power output) of the types of muscle fibers recruited (*i.e.,* slow oxidative, fast glycolytic) (Webb 1975, Fish and Rohr 1999).

Although the absolute values of maximum swimming speeds overlap between different species, there is a marked dependence of length-specific speed on size (Webb 1975). The larger *Pseudorca* had a length-specific speed that was 29% lower than *Tarsiops* and 54.1% lower than *Delphinus,* the smallest animal examined in this study. Large cetaceans have low length-specific swimming speeds compared to smaller dolphins and porpoises (Webb 1975, Fish and Rohr 1999). In ascending order of body mass, maximum length-specific speeds for various dolphins reported were 6.0 BL/sec *(Stenella attenuata*; 52.7 kg; Lang and Pryor 1966), *4.4* BL/sec (*Delphinus delphis;* 104.8 kg; this study), 4.3 BLisec *(Tarsiops truncatus gilli;* 89 kg; Lang and Norris 1966), 3.8 BL/sec (*Tursiops truncatus*; 149.2 kg; this study), 2.2 BLisec *(Pseudorca crassidens;* 461.8 kg; this study), 1.5 BLisec (*Orcinus orca*; 1995.8 kg; Fish, 1998). A 27.4-m blue whale (*Balaenoptera musculus*) sprinting at 10.2 m/sec (Tomilin 1957) would have a length-specific speed of only 0.37 BL/sec. This trend is explained as a matter of scaling. The proportion of muscle mass and the force generation by the muscles are independent of size (Hill 1950). The speed of shortening by the muscle is, however, size dependent (Schmidt-Nielsen, 1984). Thus, power output (force X velocity) is also size dependent. Because the contraction frequency of muscles is indirectly related to size, smaller animals have relatively greater muscular power outputs per volume than larger animals (Hill 1950, Pedley 1977).

Motivation: Captive vs. *Free Ranging*

Surprisingly, where motivation was thought to have been strongest, that associated with the temporary capture and subsequent release of wild dolphins, maximum swim speeds were lower than speeds for captive *Tursiops.* The shape of the swim speed distribution curve (Fig. 2), as well as the trajectories of

many of the released animals, further indicate that the capture experience did not provide suitable inducement for the animals to swim swiftly upon release.

In regards to the motivation of the dolphin school of *Delphinus capensis* filmed from a plane, it was obvious that the approach of the plane increased the speed of the school. Similar avoidance behavior to planes has been reported by Au *et al.* (1988) for a school of spotted dolphins *(Stenella attenuata)*. However, the average swim speed of the school did not monotonically decrease with subsequent passes (Table *4),* suggesting perhaps that motivation was not sufficient to produce maximal swim speeds during the first pass. In addition, 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 these calves, their maximum swim speed is likely to be markedly less than the adults (Edwards, 1992). Furthermore, drafting by newborn calves on mothers would increase the drag and decrease speed by the adult (Lang 1966, Fish 1999).

Dolphins swimming around the periphery of the pool at Sea World were trained with rewards for maximum effort. To what effect the pool dimensions limited maximum swimming speeds of the trained delphinids is not known. No significant difference in swimming speed was detected for *Tursiops* swimming along the curved front wall and straight back wall of the pool; whereas higher speeds along the straightaway were measured for *Delphinus* and *Pseudorca. Stenella attenuata* was capable of 11.05 misec in open-ocean trials when chasing a lure, but specimens of the same species were capable of top speeds of only 7.7−8.3 m/sec when swimming in a pool along a 70-m circular path (Lang and Pryor 1966).

The data presented here show no indication that the high speed swimming capability of regularly exercised captive and free-ranging dolphins are sufficiently different. The conflicting factors that could artificially produce higher speeds make the data reported in previous studies of free-ranging animals suspect (Kooyman 1989, Fein 1998, Fish and Hui 1991). Singular episodes of maximum swimming speed in this study, although higher for captive dolphins than free-ranging animals, are extreme cases of three standard deviations above the mean. It is impossible to say which burst speeds are most representative of the maximum exertions which healthy animals can sustain for several seconds. Nevertheless, a defensible supposition can be made that burst swim speeds of the delphinids *Tursiops, Delphinus* and *Pseudorcu* are approximately 6 m/sec, and can range up to 8–9 m/sec.

Surface Effects

Depth can limit maximum swimming speed. When swimming submerged at a depth greater than three times the maximum diameter of the body, the drag is dependent only on the viscous and pressure forces around the animal (Hertel 1966, Webb 1975, Fish 1993). However, as the dolphin swims at or near the water surface, the animal experiences increased resistance from energy lost in the production of surface waves (Fish 1993). This wave drag can the-

oretically increase the drag on the body by up to five times (Lang and Daybell 1963, Hertel 1966, Williams and Kooyman 1985).

It is impossible to determine the extent of wave drag on the speed of free-ranging dolphins, because the overhead views did not allow for depth determination. However, the limited depth available for dolphins in Sarasota Bay and observations of animals breaking the surface indicated that wave drag could be a factor in the reduced performance. Trained animals swam at a shallow depth, approximately equal to the maximum body diameter. This depth potentially would increase the drag by three times due to wave drag (Hertel 1966), although the high swimming speeds reduce the magnitude of the wave drag (Lang and Daybell 1963).

The elimination of wave drag for vertically swimming *Tursiops* would help to explain the significantly higher swimming speeds prior to leaping. Because the dolphin was sufficiently deep as it accelerated toward the water surface from the bottom of the pool, the effect of wave drag on speed would be negated. In addition, the streamlined body of the dolphin produces an insignificant drag augmentation as it perpendicularly approaches the water surface (Goldman 1999).

Maximum swimming speed can be further augmented for vertical swimming from the reactive force produced from the presence of the solid pool bottom. The dolphin would effectively push off the bottom using a "ground effect" that is similar to enhancing lift on wings of aircraft when flying near the ground (Hoerner and Borst 1985). An additional upward direct force on the dolphin is produced by increased positive buoyancy as the animal accelerates from the pool bottom. The buoyant force of the body is equal to the weight of fluid displaced. Because lung volume varies inversely with depth, due to the changes in pressure, the expansion of the lungs as the dolphin ascends from depth will increase its buoyancy and increase its net force upward (Skrovan *et al.,* 1999). A 197-kg **Tursiops** (mean size from this study) would have a total lung capacity of 15.9 liters, based on equation 5.2 in Kooyman (1989). The lungs of a *Tursiops* would be reduced by 46% (Skrovan *et al.* 1999) to a volume of 8.6 liters at a depth of 8.5 m. Re-expansion of the lungs as the dolphin approaches the surface would increase the buoyancy by an amount equal to the weight of an equivalent volume of water displaced. The change in buoyancy is calculated as the product of water density (1,025 kg/m^3), gravitational acceleration (9.8 m/sec^2), and change in lung volume (7.3 liters) and is equal to 7.3×10^4 N. This increased buoyancy when surfacing is an important mechanism for reduction of energy costs during diving (Williams *et d.* 1999).

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