MOVEMENT AND SPEED OF DOLPHIN SCHOOLS RESPONDING TO AN APPROACHING SHIP

D. AU AND W. PERRYMAN[1]

ABSTRACT

Eight dolphin schools of the species *Stenella attenuata*, *S. longirostris*, and *S. coeruleoalba* were approached by ship and observed from a helicopter in the eastern Pacific to study their response to the vessel. All schools swam away from the projected track of the aproaching ship. Their movement, relative to the ship, followed paths that curved around the ship. Average swimming speeds while avoiding the ship varied from 5.1 to 8.8 knots. In some cases avoidance apparently began at 6 or more miles away from the ship. The effect of this behavior on shipboard censusing of dolphins is discussed.

In the eastern tropical Pacific, tuna fishermen encircle with purse seine nets schools of certain small cetaceans, mainly spotted and spinner dolphins, *Stenella attenuata* and *S. longirostris*, to capture the yellowfin tuna, *Thunnus albacares*, with which they are associated (Perrin 1969, 1970). The resulting incidental kill of dolphins has led the National Marine Fisheries Service to study the status of these cetacean populations, as required by the Marine Mammal Protection Act of 1972. Data collected from commercial fishing boats and research vessels are important in determining the distribution and abundance of the dolphins.

In the areas of intensive "porpoise fishing," dolphins are apparently learning from their experience with nets and fishing vessels. The animals are recaptured with purse seines frequently enough to have possibly learned to position themselves within the net to better facilitate their own release (Pryor and Kang[2]). More importantly, they may also have developed various behaviors to avoid detection by a fishing vessel and to reduce their chances of capture (Pryor and Kang footnote 2; Stuntz and Perrin[3]). Dolphin schools, especially of the spotted and spinner dolphin species, commonly swim rapidly away from approaching ships. This behavior is our usual observation when studying dolphins from research ships.

In November 1976 we conducted a study to describe ship-avoidance behavior of dolphins. The purpose was to quantitatively describe school trajectories around an approaching ship and to evaluate the effect on shipboard censusing of dolphins. This study also allowed us to measure the swimming speeds of the schools and to make observations on school structure and behavior.

METHODS AND MATERIALS

We conducted this study from the NOAA Ship *Surveyor*, a 300-ft (91.4 m) steam-powered research vessel, and its Bell[4] 204 helicopter. We worked in the study area, the vicinity of Clipperton Island (lat. 10°15'N, long. 109°10'W) in the eastern Pacific, for 9 d (26 November to 4 December 1976). During six of these days, we made observations from the helicopter, flying twice daily in a crossing pattern ahead of the ship's track (Fig. 1). This enabled us to detect dolphin schools ahead of the ship and to follow the sequence of events leading to avoidance or the detection of the school by the shipboard observers. The 2.5-h flights began in mid-morning (ca. 0900 h) and early afternoon (ca. 1330 h) to take advantage of the best lighting conditions for aerial observations and photography. Air speed was about 80 kn (1 kn = 1.85 km/h) at altitudes between 1200 and 1800 ft (366-

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

[2]Pryor, K., and I. Kang. 1980. Social behavior and school structure in pelagic porpoises (*Stenella attenuata* and *S. longirostris*) during purse seining for tuna. Southwest Fish. Cent. Admin. Rep. LJ-80-11C.

[3]Stuntz, W. E., and W. F. Perrin. Learned evasive behavior by dolphins involved in the eastern tropical Pacific purse seine fishery. (Abstr.) Third Conference on the Biology of Marine Mammals, Seattle, Wash., October 7-11, 1979.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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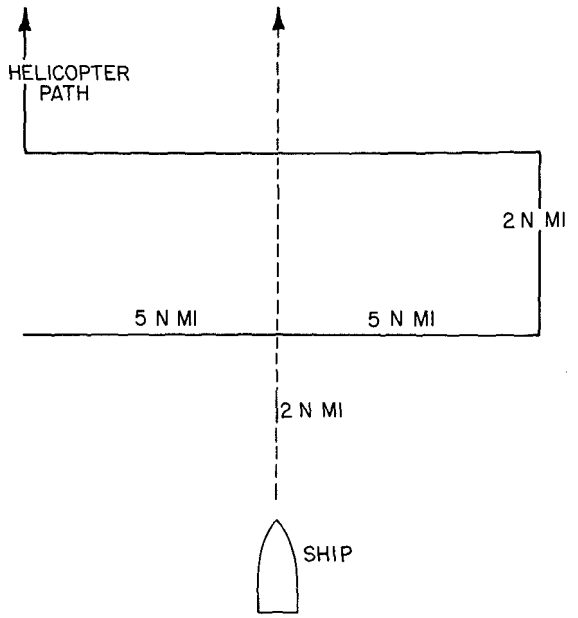

FIGURE 1.—Path of helicopter in front of ship during search phase of study.

549 m). Maximum altitude was determined by the cloud ceiling. During each flight, two scientific observers aboard the ship searched independently with 20 × 120 mm binoculars for dolphins. The observers were not in communication with the helicopter and were generally unaware of its position because of its range and because of their visual concentration on the sea surface. The ship's speed was between 11 and 13 kn.

Once a school was located, the helicopter remained near the school to serve as a radar target to fix the position of the dolphins relative to the vessel. Each time the helicopter passed over the school, we signaled the deck officer aboard ship via radio to record our radar range and bearing. These measurements from the ship were taken at successive time intervals to enable tracking the movement of the school. There was no indication to us that the helicopter affected school behavior. Indeed, the schools usually appeared to be swimming calmly throughout the tracking, until the ship approached to within a mile of the dolphins. During this tracking phase, ship course changes were minimized in order to determine how closely the school would pass the approaching vessel if not pursued. In some cases the ship was turned so its projected track would pass near the school, but course changes were minimal thereafter.

The shipboard radar used was a Decca-RM 1630. Its rated accuracy is to within 300 yd (274 m) of range at a distance of 10 nmi (18.5 km) and to within 1° of angular bearing. The radar measurements were made by a trained deck officer.

At the end of the tracking phase the ship approached closely or followed each school until the observers aboard had completed their estimates of school size and species composition. Meanwhile, we continued to take aerial photographs (35 and 70 mm still and 16 mm movie) and notes on school size and behavior that had begun when the school was first sighted. The movements and speeds of the schools as described below do not refer to this last phase of the operation.

School movement and speed were calculated whenever possible from relative motion plots since such plots portray the situation as seen from a ship. Required information for each plot includes the time interval between radar fixes, the course and speed vector of the ship, and the relative motion vector of the school, as determined by the radar ranges and bearings (the method is described by Bowditch 1966). These data were then used to construct vector triangles which were solved to get school speed vectors. Distance (range) was measured in nautical miles (nmi) and speed in knots (kn). The results were checked by plotting the sequential, absolute positions of the vessel and school from the data on vessel speed and data on range and bearing of ship to helicopter (school). School movement was measured from this absolute plot, and speed determined from the time interval between fixes to give results that should be the same as those obtained from the relative motion plots. When the ship made a course change, disrupting the relative position analysis for that time interval, the absolute position plot was the only solution.

A hypothetical example of a relative motion plot is presented in Figure 2. The ship is at the center (0) of the polar plot, proceeding straight ahead (000° or top of plot). Sequential radar ranges and bearings, from the moving ship to a dolphin school, are obtained at 0800, 0815, ..., and 0900 h. These fixes are plotted, and the line connecting them shows the relative motion of the school that is passing around to the right of the ship. The actual swimming vectors of the school, which produce this relative motion, can be obtained by solving vector triangles such as that shown at the center of the plot. For example, the

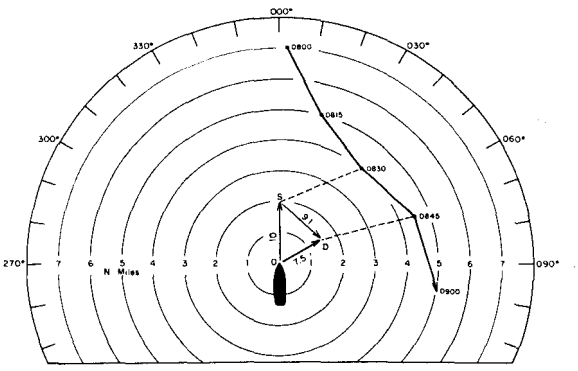

FIGURE 2.—Example of relative motion plot and calculation of school swimming vector.

relative motion between 0830 and 0845 h is equivalent to a relative velocity vector of 9.1 kn heading 134°. Projecting this vector (SD) onto the ship's vector (OS), which is 10 kn heading 000°, the school's swimming vector (OD) is obtained by vector subtraction as shown. In this case the swimming vector is 7.5 kn, heading 060°, and is the average swimming velocity between 0830 and 0845 h. Notice that the relative motion line is defined by ranges and bearings while the triangle at the center is composed of speed vectors, where, for convenience, 10 kn is defined as having magnitude 0 to 2 on the mile scale.

RESULTS

Vessel Avoidance

We were able to follow eight dolphin schools with the ship and helicopter (Table 1). The species were the spotted dolphin, the spinner dolphin, and the striped dolphin, *S. coeruleoalba*. All eight schools continuously adjusted their

TABLE 1.—Summary of dolphin schools observed from helicopter.

School	Species	Date and position	Local time (h)	Initial Range (nmi)	Initial Speed (kn)	School[1] size	Behavior relative to distance from ship[2]
1	*Stenella attenuata* + *Stenella longirostris*	11-26-76 (11°54'N 107°13'W)	0950	5.6	5.8	100	At 3.5 mi ship changes course and school increases speed to 8.3 kn. Between 1.9 and 2.6 mi school veers 40° to right across ship's path; as ship's path is crossed, school alters course again to head directly ahead of ship. At 2 mi school is in 2 groups running very purposefully with little intraschool deviations. Cruising smoothly at 5-6 kn with little splashing during most of vessel approach; strong evasive maneuvers at 100 m by group closest to ship. Two species incompletely mixed; many adults and juveniles in school.
2	*Stenella coeruleoalba*	11-27-76 (8°27'N 107°07'W)	0938	6.2	4.3	50	School initially "porpoising" gently as a loose aggregation, moving away to ship's right. At ca. 6.0 mi ship changes course; school veers 108° to left, accelerating to 5.8 kn. At ca. 5.0 mi school turns left again, still moving away at ca. 5.5 kn. At ca. 3.3 mi ship changes course and school accelerates to 6.3 kn temporarily. Between 2.0 and 3.0 mi school turns more to left; still running smoothly at 5.5 kn with little splashing. As ship passes 2.0 mi to right of school, it veers sharply left, continuing on almost opposite course as ship. Individuals bunching up at 1.8 mi. At times school composed of 4 groups. At 1.5 mi school speed is 8.3 kn. At 0.9 mi school running smoothly ahead of ship; a portion breaks off to right at ca. 100 m distance.
3	*Stenella attenuata*	12-1-76 (10°00'N 108°01'W)	0935	5.2	6.4	15	School initially seen under ca. 100 feeding boobies (*Sula* sp.), moving away from ship. At ca. 4.3 mi school accelerates to 7.8 kn then slows to 6.2 kn. At 3.5 mi school turning to right. Between 2.0 and 3.0 mi school swimming smoothly at ca. 5.0 kn; birds flying, rafting, or diving; most working ahead of school; later they form 2 large rafts behind school. By 1.5 mi school speed has increased to 7.2 kn. As school passes to left of ship at ca. 1.5 mi, it accelerates to 13 kn and veers to left. Birds have ceased feeding inside of 2 mi distance. School begins strong evasive maneuver at ca. 1/4 mi distance.
4	*Stenella attenuata*	12-2-76 (9°30'N 109°39'W)	0823	6.2	3.8	350	Initially detected as bird target by radar. Between 4.2 and 4.9 mi school changes course sharply away from ship, increasing speed to 4.6 kn, then slowing to 2.9 kn. At 3.0 mi much splashing in running school; some long, flat leaps seen. School becoming more scattered. Birds toward rear of school; later are scattered over school. At ca. 3.2 mi ship makes 90° turn to left; school veers 94° to left and increases speed; much running leaps seen; by 3.0 mi school speed is 6.5 kn. Between 2.5 and 3.0 mi main group in school turns toward ship; moments later they reverse their course again.

directions of swimming, by small increments, so that the distance between the school and the ship's projected track tended to increase continuously with time. The schools were either already proceeding on courses directed away from the ship when first sighted or made sharp course changes away from the vessel soon after. Several schools were moving off at relatively high speed when first seen. All the schools were evidently avoiding the ship. The behavior that indicated avoidance is summarized in Table 2 for each school. It appeared that avoidance behavior sometimes had begun when the school was still 6 or more nautical miles away from the ship.

Sufficient positioning data were collected from six of these schools to prepare diagrams of their movement relative to the approaching ship (Figs. 3, 4). The first school, school 1, is not plotted because frequent course changes by the ship during its tracking made relative movement difficult to portray. The path of relative movement of any of these schools, drawn by connecting the sequential series of radar fixes of the school as the ship moved forward, does not

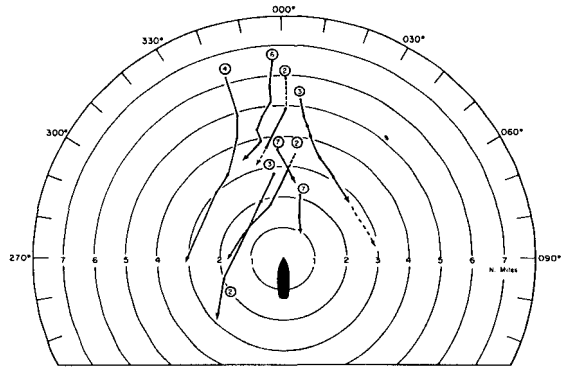

FIGURE 3.—Relative movement plots of five schools (nos. 2, 3, 4, 6, 7), showing the apparent motion as seen by a shipboard observer. Dotted lines are by dead reckoning.

TABLE 1.—*continued.*

School	Species	Date and position	Local time (h)	Initial Range (nmi)	Initial Speed (kn)	School[1] size	Behavior relative to distance from ship[2]
							At 2.5 mi individuals begin to bunch up; school in form of large arc with some scattered animals on the sides; birds no longer feeding.
							At 1.6 mi school is again scattered. Within 0.5 mi parts of school breaking away from ship's path; birds rafting nearby.
5	*Stenella attenuata* + *Stenella longirostris*	12-2-76 (9°39'N 109°48'W)	0953	5.8	ca. 2.6	300	Initially seen with many birds ahead and to right of school. School speed is ca. 2.6 kn.
							At 3.3 mi school changes course sharply away from ship and speed accelerates. Animals running with compact ranks at rear of school; few birds over school now.
							At 3.0 mi school running smoothly at ca. 8.4 kn.
							At 2.2 mi individuals appear confused, going in various directions within oval shaped school.
							At 2.0 mi a group temporarily heads toward ship before reversing course; school speed is 9.3 kn.
							At 0.6 mi many circuitous movements seen among small subgroups. School passes to ship's left; all individuals uniformly running from ship at 8-9 kn; birds rafting ahead.
							Ship turns toward school at ca. 0.5 mi; school splits ahead of ship at ca. 200 m; each dolphin species goes to different side of ship.
6	*Stenella attenuata*	12-3-76 ca. (9°31'N 110°30'W)	1032	6.9	ca. 10.0	40	School initially seen as running, oval mass moving off at ca. 10.0 kn with much splashing.
							At 6.5 mi school is in 2 groups moving smoothly in arc with little splashing.
							At 5.7 mi school is in 2 groups moving smoothly at 8.5 kn.
							At 5.1 mi school is composed of a dense and a scattered section; many direction changes among subgroups. School speed is down to 7.0 kn.
							At 4.5 mi school is scattered; composed of 3 large groups; many direction changes seen; speed is ca. 9.0 kn again.
							Between 3.5 and 4.0 mi school speed decreases to 7.6 kn then increases to 9.3 kn as school begins passing to ship's left.
7	*Stenella attenuata* + *Stenella longirostris*	12-3-76 (10°00'N 110°30'W)	1440	3.6	8.8	150	Initially swimming smoothly at ca. 8.8 kn with little splashing; scattered individuals at rear of school.
							At ca. 3.0 mi school still holding similar course with speed of ca. 7.0 kn; 50-70 birds over school.
							At 2.4 mi ship changes course and school also changes course and increases speed; birds scattered over the scattered school.
							At 1.4 mi school running smoothly in loose groups, going ca. 6.0 kn.
							At <1.0 mi smoothly running school is scattered by ship.
8	*Stenella coeruleoalba*	12-2-76 (10°27'N 110°01'W)	1420	0.9	—	65	A leaping, loosely aggregated school at 0.9 mi.
							At 0.7 mi school running with increasing speed as ship turns toward school.
							At 1/4 mi school forming an arc ahead of ship.

[1]Estimated from aircraft.
[2]Distances and behavior from radar ranging and bearing, interpolation of movement trajectories, and field notes. Distances in nautical miles.

TABLE 2.—Range and behavior when vessel avoidance was first seen.

School number	Species	Range (nmi)	Behavioral indication of vessel avoidance
1	*S. attenuata* *S. longirostris*	5.6	School rapidly swimming away from ship at 5.8 kn when first sighted from helicopter.
2	*S. coeruleoalba*	ca. 6.0	As ship turned toward this school, the animals accelerated from 4.3 to 5.8 kn and turned away from the ship.
3	*S. attenuata*	5.2	School rapidly swimming away from ship at 6.4 kn when first sighted from helicopter.
4	*S. attenuata*	ca. 4.6	School made sharp course change away from ship and accelerated to 4.6 kn.
5	*S. attenuata* *S. longirostris*	3.3	School turned away from ship and accelerated from 2.6 to 8.4 kn.
6	*S. attenuata*	6.9	School moving away from ship at high speed (ca. 10 kn) when first sighted from helicopter.
7	*S. attenuata* *S. longirostris*	3.6	School moving away from ship at high speed (8.8 kn) when first sighted from helicopter.
8	*S. coeruleoalba*	0.9	School leaping away from ship when first sighted from helicopter.

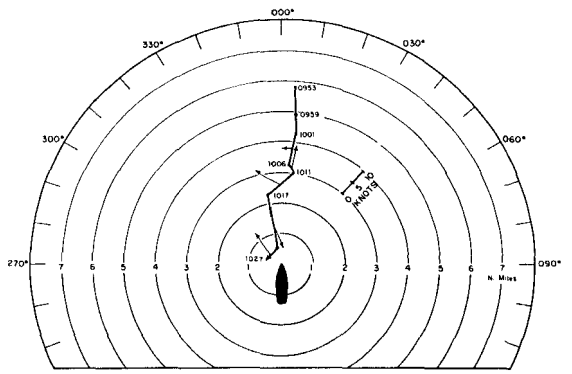

FIGURE 4.—Relative motion plot of school 5, showing its apparent motion as seen by a shipboard observer. Small arrows show actual school velocities at various distances. Note heading reversal shown at 1.5 mi.

represent the actual swimming directions of the school, but rather the resultant of the swimming velocity of the school and the movement of the vessel. The ship's position remains at the center of each diagram, and swimming direction is depicted relative to the ship's heading, which is toward the top of the page. The plots therefore show the apparent motion of the schools as seen by an observer aboard the ship. A break in the relative motion line for a school represents a course change by the ship.

The relative movement of five schools (schools 2, 3, 4, 6, and 7) are depicted in Figure 3 where, for clarity, swimming speed vectors and the times of radar fixes are not included. It is important to realize however, that along each relative motion line the school is generally swimming away from the oncoming ship. We have extrapolated parts of the movements of schools 2 and 3, based upon our observations of their activity. The movement of each of the five schools is depicted as though moving relative to the same ship heading (000°). These schools are described in two groups.

The first group (schools 2, 3, 4, and 6 in Figure 3) was initially located between 5 and 7 nmi from the ship. After some initial adjustments in heading, the schools' swimming directions remained relatively constant. The resultant paths of the dolphin schools thus veered from the track line at a nearly constant angle after this initial period. Assuming that the schools would remain approximately on the same course and extending their lines of relative movement, it appeared that these schools would have passed no closer than 2.4 nmi from the ship, had it remained on the same course. School 4 exhibited additional notable behavior that is not shown in Figure 3. When the school had passed abeam, the ship was turned towards the school. Five minutes later, at a range of about 2.5 nmi, a large section of the school turned and headed toward the ship in a tightly aggregated group. Within a minute this section reversed course again and rejoined the original school.

The second group (schools 2, 3, and 7 in Figure 3) consists of schools that were between 2.6 and 3.7 nmi away, either when first sighted (school 7) or after the ship had turned toward the school at the end of an initial tracking period (schools 2 and 3). The lower and separated segments of the latter schools' tracks represent the relative movements after the ship had turned. These schools were then within 0.4 nmi of the ship's projected track. Even so schools 2 and 3 subsequently came no closer than 1.4 nmi to the ship. School 7, by its initial projected trajectory, would have come no closer than 1.5 nmi, but after the ship turned toward it, its new resultant path would have taken it about 0.7 nmi from the ship.

School 5 behaved quite differently from the others. Both relative movement, time of radar fixes, and swimming speed vectors are shown for this school (Fig. 4). The swimming speed vectors, shown as arrows attached to the relative motion line between various time and distance intervals, are drawn proportional to the calculated swimming speeds (Table 3).

School 5 was probably feeding when the bird flock associated with it was first detected on the ship's radar at a distance of 5.8 nmi. The distance and bearing plots of the birds indicated erratic movement. Later, in the tracking-by-helicopter phase, the first two ranges and bearings showed the school moving at only 2.6 kn. The inferred feeding behavior from this is consistent with the feeding behavior described by Norris et al. (1978), as well as other observations by us in the eastern Pacific. At a closer range of about 3.3 nmi from the ship, the school's behavior changed radically as it altered course by 97° to the right and increased its speed to 8.4 kn, turning on a course that would have taken it 2.0-2.5 nmi abeam of the passing ship. Between 2.3 and 3.0 nmi the school again shifted course, this time by 70° to the left, and increased its speed to 9.4 kn. When this school reached a point about 0.5 nmi from the track line and 2.3 nmi from the ship, its behavior changed again. Individuals and subgroups within the school began swimming in many different directions, making large changes in course heading. Suddenly the main body of the school turned nearly 180° and swam toward the ship at high speed (~9 kn). After closing to within 1 nmi of the ship, the school reversed itself again, and thereafter swam rapidly away from the vessel. This type of "error" in choice of avoidance heading was only seen in schools 4 and 5, which were both relatively large schools (300-350 individuals estimated).

School Speed

While avoiding the ship, the speeds of the first seven schools varied between 2.5 and 13.1 kn, with average speeds between 5.1 and 8.8 kn (Table 3). The eighth school was too close to the ship for ranging measurements by radar. There was no apparent difference in swimming speeds among the three species observed. Substantial variation in speed occurred in all seven schools. Schools 1, 2, 3, and 4 swam at speeds that averaged between 5 and 7 kn. Schools 6 and 7 had the

TABLE 3.—School swimming speed vectors.

School	Time (h)	Range[1] (nmi)	Bearing[1]	Course[2]	Speed[2] (kn)	
1	0950	5.6	088°			
	1015	3.6	105	128.2°	5.8	
	1022	3.3	107	128.6	8.3	
	1030	2.6	104	126.3	5.7	
	1035	1.9	112	166.7	5.3	
	1042	1.4	115	114.5	6.2	
	1049	0.8	110	100.0	6.8	
	1101	0.7	310	092.0	4.0	
					[3]$\bar{x}$=6.0	
2	0938	6.2	016			
	0942	5.9	026	118.3	4.3	
	0952	4.9	026	010.6	5.8	
	1000	3.7	017	330.7	5.5	
	1006	2.9	008	324.6	6.3	
	1013	1.8	352	304.6	5.5	
	1019	1.5	320	315.2	8.3	
	1028	2.0	255	285.2	5.7	
	1033	3.0	230	216.5	5.6	
	1045	2.5	212	223.6	6.0	
	1051	2.0	200	229.0	5.9	
	1104	0.9	179	182.8	6.3	
					$\bar{x}$=5.9	
3	0935	5.2	295			
	0940	4.7	297	300.9	6.4	
	0943	4.4	299	308.9	6.5	
	0947	4.1	301	298.8	7.8	
	0953	3.5	308	316.6	6.2	
	0959	3.1	320	326.2	7.8	
	1006	2.8	340	335.1	6.2	
	1016	2.9	019	354.2	5.0	
	1023	2.0	010	337.0	[4]4.9 (1017-1023)	
	1029	1.6	353	005.0	6.6	
	1032	1.5	335	334.5	7.2	
	1035	1.8	296	264.0	13.1	
					$\bar{x}$=7.1	
4	0823	6.2	333			
	0829	4.9	333	086.5	3.8	
	0835	4.2	330	349.5	4.6	
	0841	3.2	318	261.9	2.9	
	0845	3.0	305	282.5	6.5	
	0857	3.2	256	263.2	5.2	
	0915	1.6	255	265.8	6.2	
					[4]$\bar{x}$=5.1 (0835-0915)	
5	[5]1001	4.3	356			
	1006	3.3	354	264.2	2.6	
	1011	3.0	357	001.2	8.4	
	1017	2.3	339	290.8	9.4	
	1022	0.6	334	148.4	9.3	
	1027	0.5	268	314.7	7.9	
					[4]$\bar{x}$=8.8 (1011-1027)	
6	1032	6.9	281			
	1038	6.5	278	273.6	10.0	
	1050	5.7	277	279.2	8.5	
	1056	5.1	277	284.4	7.0	
	1102	4.7	273	262.0	9.2	
	1108	4.3	270	270.1	8.8	
	1112	3.9	271	297.4	7.6	
	1121	3.4	258	253.3	9.3	
					$\bar{x}$=8.6	
7	1440	3.6	167			
	1446	3.2	170	182.4	8.8	
	1452	2.6	177	199.1	6.6	
	1458	2.1	191	215.3	7.5	
	1505	1.4	197	175.6	6.0	
	1508	1.0	205	164.6	2.5	
	1519	1.1	240	242.0	11.5	
					$\bar{x}$=7.2	

[1]Range and bearing of school from ship at times appropriate to the speed calculation. If notable, behavior at these and other times are reported in Table 1.
[2]Speed vectors pertain to time intervals ending at times listed unless otherwise indicated. Calculations are from relative or absolute plots involving ship motion.
[3]Mean school speed refers to times when school is responding to ship.
[4]Time interval for this calculation.
[5]This school was actually sighted at 0953, but measurements did not begin until 1001.

highest initial speeds, 10.0 and 8.8 kn, respectively, and had average speeds of 8.6 and 7.2 kn, respectively. Both were moving with the waves in a Beaufort 4 sea state (11-16 kn wind) and were probably utilizing the forward momentum of the swell as described by Lang (1975). The speed of school 5 was also high (>8 kn) after the first 5 min that it was observed. Its average speed while actively avoiding the ship was 8.8 kn. This higher sustained speed may have been related to its level of excitement that was evident in its apparently confused state, when it turned toward and then away from the ship (Table 1, Fig. 4). Schools 3 through 7 showed some tendency for increased speeds as the ship drew nearer.

Swimming Behavior and School Structure

Field descriptions of each school, and later study of the aerial movie and still photographs, revealed no obvious indication of dominant, or leading, individuals or subgroups. The schools were seen to progress in an almost amoeboid fashion with subgroups of two to five individuals striking off in different directions or accelerating to higher speeds, then drifting back to the main body of the school if not followed by others in the school. Although individuals and subgroups within a school were constantly changing course, sometimes abruptly, the heading of the main body of the school remained nearly constant or changed slowly. The schools appeared as loose aggregations of individuals and small subgroups, most proceeding along similar headings. Individualistic rather than coordinated movements were the general feature of these schools. The schools appeared to be one-layered, i.e., groups of animals were not swimming beneath others.

As the vessel closed to within 2 nmi of the schools, the subgroups within the schools were seen to be increasingly oriented in lines abreast. Animals in the rear third of a school could be seen swimming faster than those ahead. The result was that the width of a school in the direction of its swimming axis narrowed as the distance between ship and school decreased.

DISCUSSION

Our first impression from the observed school behavior and structure was that the dolphins were not noticeably disturbed by the vessel's presence. Only at a distance of less than a mile did bunching or compaction of the relatively dispersed individuals and small subgroups become common and did the schools obviously appear to be running, i.e., in flight (Table 1). Radical, evasive maneuvers were not regularly seen until the last 200 m of distance between ship and school. Examination of the relative motion plots and the consecutive vectors of swimming speed and course made it clear, however, that the dolphins were actually avoiding the ship much earlier, sometimes beginning at distances approaching the horizon for a shipboard observer. Though ship-avoidance behavior should not be surprising, considering the extent of "porpoise fishing," in the study area, it is a behavior not easily studied from a surface platform. These observations have important implications relative to population studies of dolphins, especially those conducted from ships.

Because a shipboard observer sees a dolphin school increasingly in profile view as distance increases, an understanding of its structure and behavior is helpful for proper interpretation of its characteristics. A travelling school appears to be a loose aggregation of relatively widely separated individuals or subgroups of 2-5 animals. Rather than being made up of relatively few, tight subgroups of various sizes, as observed for spotted dolphins in a purse seine (Norris et al. 1978), most of the animals in these schools appeared to be swimming independently, as individuals or in pairs. This school configuration appeared typical all during vessel avoidance, except at radial distances of less than a mile from the ship.

The schools we observed remained inconspicuous to the shipboard observers because they swam smoothly, without much splashing, at speeds that averaged 6.8 kn. Even at swimming speeds of 7-9 kn, the animals often broke the water surface with little commotion and swam most of the distance between breaths just under the surface. Bursts of higher speed, with attendant long leaps (2-3 body lengths) and large splashes, occurred only temporarily.

The swimming speeds presented in Table 3 pertain to these pelagic dolphins when swimming in the cruising mode, i.e., moving smoothly with little splashing for sustained periods. The higher observed speeds of 7-9 kn are still in the upper range for prolonged cruising speeds of smaller dolphins (Webb 1975). That this must be so is indicated by the fact that research ships

moving at 10 kn can always closely approach these dolphins, provided that the schools can be followed. Evidently school speeds greater than that of the ship can be maintained only temporarily. Dolphins that do break into the "running," or leaping swimming mode, must be exceeding a certain "crossover speed." This is the swimming speed above which a leaping locomotion becomes more efficient. It is calculated to be somewhat in excess of 10 kn (Au and Weihs 1980). Thus several lines of evidence indicate that cruising speeds are <10 kn, as we in fact measured. Dolphins of course are capable of temporary higher speeds than reported here. Top burst speeds as high as 14.5 kn have been measured for *Tursiops truncatus* (Lang and Norris 1966) and 21.4 kn for *S. attenuata* (Lang and Pryor 1966).

Because the faster, leaping locomotion produces much splashing, dolphins that avoid ships by moving away more slowly at cruising speed obviously are more difficult to detect from the ships. The initial avoidance probably proceeds at cruising speed because the dolphins are not yet highly alarmed at the distances at which detection of the ship and evasion begins.

The evasive behavior of dolphins perhaps has its most important implication relative to school density studies conducted from ships. In particular the line-transect method (Seber 1973; Burnham and Anderson 1976), which can be employed for absolute density estimation of schools, may be affected. An important requirement of the method is that the schools do not move, or move randomly or little, relative to the speed of the observer. However, schools are evidently capable of avoidance movements at speeds approaching that of the ship. Therefore positions of schools relative to the ship and prior to movement that are required to describe the probability of sighting a school cannot be obtained if there is movement. Only if the school trajectories were known could the observed positions be corrected. The probability of sighting is usually obtained from the distribution of perpendicular distances that are a transformation of the relative positions of sighted schools. Laake (1978) and Burnham et al. (1980) emphasized that when school movement occurs, both the probability functions describing detectability and the altered animal distribution are completely confounded in the distribution of observed perpendicular distances. School movement also violates the critical assumption that all schools initially on the track line will be seen. Therefore, line transect methods for absolute density estimation usually cannot be used when avoidance movements occur.

It is easy, however, to understand how avoidance behavior reduces the probability of sighting a school from a ship. Without movement this probability would be (Burnham and Anderson 1976)

$$\frac{1}{w}\int_0^w g(x)dx$$

where w is the half width of the swath being searched, which could be the horizon distance, and $g(x)$, the detection function, is the probability of sighting a school that is initially at perpendicular distance x from the track line. The function, $g(x)$, is monotonically decreasing from 1 on the trackline ($g(0) = 1$). Therefore, schools avoiding a ship by effectively moving farther abeam must obtain a value to $g(x)$, say $g(x)^1$, that is less that that at its initial distance x. These reduced values, $g(x)^1$, replace the original values of $g(x)$ at all initial perpendicular distances where avoidance movements began. The area under this altered detection curve (i.e., the plot of $g(x)^1$ against x), which determines the new probability of sighting a school from the track, is accordingly reduced. Reasonable models of the detection function and how it is altered by avoidance behavior can be constructed to show that this reduction can be considerable.

If dolphins do obtain lower $g(x)$ values from their avoidance trajectories, the behavior would be advantageous. This seems entirely possible considering that the schools can cruise at speeds approaching that of many research ships (Table 3) and apparently can detect and continue to sense a ship from considerable distance. Evidence of the latter are the distances at which avoidance behavior was apparent (Table 2) and the near simultaneous changes in school course or speed following course changes by the ship. Such changes occurred at 3.5 mi in school 1, at 6.0 and 3.3 mi in school 2, at 3.2 mi in school 4, and at 2.4 mi in school 7 (Table 1).

With significant reduction in sighting probability possible from avoidance, it would be useful to empirically determine the actual probabilities, $g(x)^1$, or to model this behavior. We expect, however, that the specifics of avoidance trajectories as well as the probabilities would

vary greatly with species, populations and their experience, and the specific behavioral activity of the school when encountered. The type of ship involved and environmental conditions may also affect avoidance behavior.

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LITERATURE CITED

AU, D., AND D. WEIHS.
1980. At high speeds dolphins save energy by leaping. Nature (Lond.) 284:548-550.

BOWDITCH, N.
1966. American practical navigator. U.S. Navy Oceanogr. Off. Publ. 9, 1524 p. U.S. Gov. Print. Off., Wash., D.C.

BURNHAM, K. P., AND D. R. ANDERSON.
1976. Mathematical models for nonparametric inferences from line transect data. Biometrics 32:325-336.

BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAAKE.
1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72, 202 p.

LAAKE, J. L.
1978. Line transect estimators robust to animal movement. M.S. Thesis, Utah State Univ., Logan, 55 p.

LANG, T. G.
1975. Speed, power, and drag measurements of dolphins and porpoises. *In* T. Y. T. Wu, C. J. Borkaw, and C. Brennen (editors), Swimming and flying in nature, Vol. 2, p. 553-572. Plenum, N.Y.

LANG, T. G., AND K. PRYOR.
1966. Hydrodynamic performance of porpoises (*Stenella attenuata*). Science (Wash., D.C.) 152:531-533.

LANG, T. G., AND K. S. NORRIS.
1966. Swimming speed of a Pacific bottlenose porpoise. Science (Wash., D.C.) 151:588-590.

NORRIS, K. S., W. E. STUNTZ, AND W. ROGERS.
1978. The behavior of porpoises and tuna in the eastern tropical Pacific yellowfin tuna fishery-preliminary studies. Available Natl. Tech. Inf. Serv., Springfield, Va., as PB 283970, 86 p.

PERRIN, W. F.
1969. Using porpoise to catch tuna. World Fish. 8:42-45.
1970. The problem of porpoise mortality in the U.S. tropical tuna fishery. Proc. 6th Annu. Conf. Biol. Sonar and Diving Mammals, p. 45-48. Stanford Res. Inst., Menlo Park, Calif.

SEBER, G. A. F.
1973. The estimation of animal abundance and related parameters. Hafner Press, N.Y., 506 p.

WEBB, P. W.
1975. Hydrodynamics and energetics of fish propulsion. Fish. Res. Board Can., Bull. 190, 158 p.